Fine sediment on leaves: shredder removal of sediment does not enhance fungal colonisation

Isis Sanpera-Calbet · Eric Chauvet · John S. Richardson

Abstract Inorganic fine sediments are easily carried into streams and rivers from disturbed land. These sediments can affect the stream biota, including detritivorous invertebrates (shredders) and impair ecosystem functions, such as leaf litter decomposition. We hypothesized that fine sediment (kaolin) deposited on leaves would reduce or suppress fungal development, reducing decomposition rates of leaves. Moreover, we predicted that shredders would act as ecosystem engineers by perturbing sediment deposition, reducing its impact on decomposition and fungi. We used a fully crossed experimental design of sediment addition (control, 400 mg L^{-1}) and shredders (none, *Gammarus*, *Potamophylax*) in laboratory aquaria. Leaf mass loss, suspended solids, microbial respiration, fungal biomass and spore production were measured. Sediment addition had no significant effects on the leaf mass remaining nor on shredders' consumption rates. However, sediment slightly reduced fungal assemblage richness and the sporulation rate of three fungal species. The presence of shredders substantially increased the resuspension of fine sediments (>300%), resulting in higher suspended loads. However, the action of shredders did not have a significant effect on fungal biomass nor on leaf mass loss. Even if shredders did not enhance fungal colonisation, they affected the settlement of fine sediment, serving as allogenic engineers. Our study suggests that concentrations of fine sediment of 400 mg L^{-1} with short exposure times (192 h) can have some effect on leaf decomposition.

Keywords Fine sediments · Litter breakdown · Aquatic hyphomycetes · Detritivorous invertebrates · Stream disturbance

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Introduction

The presence of fine sediment is a natural feature in streams. However, human use and modification of soils, for instance from agriculture, forestry and mining, can lead to increased flows of fine sediments (Wood and Armitage 1997). In most cases, sediment input to water is accompanied by other factors, such as nutrient imports caused by watershed logging (Benfield et al. 2001) or chemicals in agricultural streams (Liess et al. 1999).

The term fine inorganic sediment describes, in general, particles <2 mm, and includes sand, silt and clay (Wood and Armitage 1997), although according to some authors, it can be considered as particles <250 μm (e.g. Kreutzweiser et al. 2005). Fine sediment is arguably an important pollution issue for streams, which has been the subject of several reviews (Cordone and Kelley 1961; Newcombe and Macdonald 1991; Waters 1995; Wood and Armitage 1997). These

particles are transported by flow, producing elevated turbidity or are deposited on the river bed, leading to effects on biota, from primary producers (Davies-Colley et al. 1992; Izagirre et al. 2009) to benthic invertebrates (Suren and Jowett 2001; Larsen and Ormerod 2010) and fish (Galbraith et al. 2006; Shaw and Richardson 2001), and ultimately affecting ecosystem processes (Parkhill and Gulliver 2002).

In headwater forested streams of temperate regions, decomposition of terrestrial leaf litter is a key process supporting the productive capacity of the ecosystem (Fisher and Likens 1973; Cummins 1974). Sediments may influence the rates of decomposition of leaf litter (Bunn 1988; Benfield et al. 2001; Schofield et al. 2004), with sediment deposited on leaf packs generally decreasing decomposition rates (Benfield et al. 2001). This effect can be mediated through effects on detritivorous invertebrates (hereafter shredders) (Sponseller and Benfield 2001), the trophic structure of the invertebrate community (Lecerf and Richardson 2010a) or through changes in microbial colonisation (Schofield et al. 2004). Leaf decomposition, as an ecosystem integrative process, has been proposed as an indicator of stream integrity (Gessner and Chauvet 2002; Young et al. 2008). Relyea et al. (2000) proposed stream insects as bioindicators of disturbance by fine sediment.

The aquatic fauna may locally influence the accumulation of fine sediments in the stream bed or on leaf litter through their activities such as movement, cleaning of the surroundings by sessile species or through foraging (Gayraud et al. 2002; Pringle et al. 1993). According to Jones et al. (1994), ecosystem engineers are organisms that can directly or indirectly modulate the availability of resources to other species, by causing changes in the physical state of biotic or abiotic materials. As a result of their activities, they modify, create or maintain habitat features. Invertebrates have been proposed to act as ecosystem engineers in streams (Moore 2006). For example, net-spinning caddisflies have been demonstrated to increase the stability of benthic substrates, generating refugia for other species (Cardinale et al. 2004; Takao et al. 2006). Crayfish was found to decrease algal growth and increase eggs survival of fish due to direct erosion and to influence detritus decomposition, benthic diversity and particulate organic matter and fine sediment accumulation (Statzner et al. 2000; Zhang et al. 2004).

The purpose of this study was to test the effects of fine sediment on leaf decomposition, by measuring the effects on the microbial community, and the interaction of sediments and shredders. The effects of sediment on aquatic fungi could explain the mechanisms by which sediment impairs leaf decomposition, since fungi, namely aquatic hyphomycetes, are major leaf decomposers (Gessner and Chauvet 1994). To our knowledge, no study has assessed the direct effects of sediment on fungal community structure and composition in controlled conditions; i.e. in situations where sediments are not associated with other potential stressors. We hypothesised that fine inorganic sediments deposited on leaf litter would reduce or inhibit the growth and diversity of fungal decomposers resulting in diminished leaf decomposition. We predicted these impacts to be reduced by shredders through bioturbation of sediments, the extent of which would depend on the species of shredder. In this case, shredders could act as *allogenic* ecosystem engineers (sensu Jones et al. (1994)). To test these hypotheses, we conducted a laboratory experiment crossing the effects of fine sediment and shredders on leaf decomposition.

Materials and methods

Experimental design

The study consisted of a randomized complete block design with two factors; 'sediment' and 'shredders'. Sediment at two levels (without and with) and shredders at three levels [none, *Gammarus* sp. (Amphipoda: Gammaridae; *G*), and *Potamophylax* sp. (Trichoptera: Limnephilidae; *P*)]. All factors were crossed, therefore, we had six treatments: without sediment and without shredders (*C*), without sediment and with shredders (*G* or *P*), with sediment without shredders (*CS*) and with sediment and shredders (*GS* or *PS*).

The replicates were distributed in three trials of 8 days each (blocks), sequentially through time, with one sampling occasion at the end of each. Eight days were a suitable period to observe the effects of sediment on the fungal community because it covers the early stages of leaf decomposition; i.e. leaching and microbial colonisation phases (Allan and Castillo 2008).

The total number of replicates was 56, although due to an error during the aquaria installation, the specific number of replicates was unbalanced (but always with replication), with eight replicates for each of the *G* and *PS* treatments, six replicates for each of the *GS* and *P* treatments, and 14 replicates for each of the treatments without shredders, *C* and *CS*.

We chose a non-perturbed stream as a source for water and shredders, and as a site to incubate the leaves. This site was a stretch of the Lampy (2°11′E, 43°25′N), a second-order stream situated in the Montagne Noire (south-western France), at 705 m elevation with a high diversity of riparian vegetation (Laitung and Chauvet 2005). The stream is oligotrophic, with low conductivity (32–60 μS cm^{-1}). Water temperature was recorded with data loggers (Signatrol Ltd., Gloucesterhire, UK) and it ranged from 3.0 to 11.5°C during the leaf incubation period (9.4°C on average).

As sediment, we used kaolin (kaolin K13, SIFRACO–SIKA, Hostun, France), an abundant, fine, inorganic siliceous clay that is used as a standard in fish studies (Goldes et al. 1988; Boubée et al. 1997) and commercially available. Its maximal particle size is 45 μm, it has a pH of 7.5, a volume-specific mass of 2.6 g cm^{-3} and is insoluble. In natural streams, inorganic particles down through the size of silt are derived largely from silicate rocks (Waters 1995). In moving water, some portion of the clay is deposited (such as on leaf litter accumulated on the stream bed), but can be easily re-entrained into the water column.

In the treatments with sediment, we added 2 g of kaolin, obtaining a concentration of 400 mg L^{-1}. This concentration of suspended sediment was susceptible to be deleterious to aquatic organisms (European inland fisheries advisory commission 1964; Galbraith et al. 2006) with concentrations as low as 200 mg L^{-1} being reported to cause mortality of stream invertebrates (Dodds and Whiles 2004). In our trials, a portion of the added sediment was deposited, so that the final concentration of suspended sediment fell within the range of concentrations susceptible to cause impacts to stream biota.

Shredders used in the experiment were *Gammarus* and *Potamophylax*, which are dominant in terms of biomass and abundance in the Montagne Noire (Lecerf et al. 2005; Sanpera-Calbet et al. 2009). Both genera have different traits (Tachet et al. 2000). *Gammarus* is a laterally flattened crustacean; it has the capacity of crawling and swimming and can be interstitial. Moreover, its life cycle is holobiotic with mainly passive aquatic dispersion. *Potamophylax* is a case-bearing caddisfly larva with a crawling locomotion. It is amphibiotic (adults are terrestrial) with an active aerial dispersion. Because *Potamophylax* makes its case primarily of gravel, we added 4 g of gravel (1–2 mm) to each aquarium.

We put 20 individuals of *Gammarus* or 10 *Potamophylax* in the corresponding treatments to partly compensate for biomass differences between the two taxa, these densities being similar to the densities per initial leaf weight found by Lecerf et al. (2005) on alder leaves in the Montagne Noire. The average dry mass (DM) of the shredders introduced to the aquaria was 110.6 mg (±2.5 SE) for *Gammarus* and 307.5 mg (±17.6 SE) for *Potamophylax*.

Experimental set-up

The experiment was performed in microcosms, each consisting of 12 L aquaria with 5 L of stream water, filtered through 21 μm to eliminate most of the suspended matter. A bubbler connected to an air pump was placed at the bottom, near one end of the aquarium and a deflector made by expanded polystyrene was placed at a 45° angle above the bubbler to create a flow of water and sediments, and allow water oxygenation (Fig. 1).

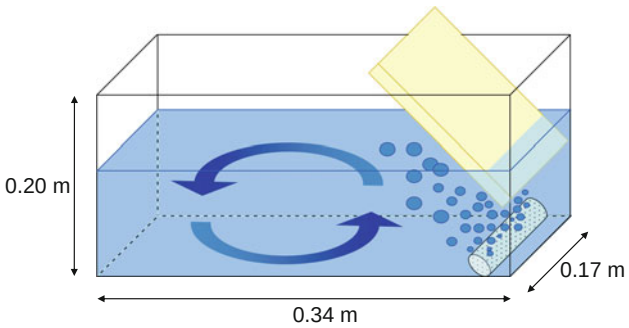

Fig. 1 Design for the aquaria using a bubbler at the *bottom* along with a deflector of polystyrene angled at 45° to create a current that could circulate water and sediments. *Numbers beside the arrows* indicate the aquaria dimensions in metres

We used alder [*Alnus glutinosa* (L.) Gaertn.] leaves because it is a common riparian tree species, widely used in leaf decomposition studies (e.g. Chauvet 1987; Hieber and Gessner 2002; Costantini and Rossi 2010), although it was not present as a riparian species at the stream site but further upstream. Alder leaves are of high nutritional quality, and therefore classified as fast decomposing (Petersen and Cummins 1974), permitting the observation of short-term effects. During autumn 2006, alder leaves were collected after abscission in a mountainous location in south-western France and air-dried in the laboratory.

To allow colonisation by aquatic hyphomycetes, leaves were exposed for 11 days in the stream before each trial (block). This fungal conditioning time optimized leaf consumption by shredders (Bärlocher and Kendrick 1975; Graça 2001). We introduced 4.00 g (±0.004 SE) of air-dried alder leaves (3.67 g DM) in fine mesh bags (0.5 mm mesh) to limit access to most macroinvertebrates, in particular shredders (Petersen and Cummins 1974; Lecerf et al. 2005). Leaves were wetted with vaporized distilled water before placing them in the bags to avoid breakage during handling. Three extra leaf packs were used to determine leaf mass loss during the colonisation period.

Shredders were collected 3 days before each laboratory trial from the Lampy, then put in the dark at 10°C to acclimatize them to laboratory conditions and fed with leaves from the source stream.

One day before starting the experiment, leaf packs were retrieved from the stream and washed carefully with tap water to eliminate sediment, and then gravel was carefully placed in the aquaria to avoid putting it on the leaves. Depending on the treatment, shredders and sediment were added to the aquaria to begin the experiment. Microcosms were installed in the dark at 10°C; i.e. at a temperature close to average stream temperature.

The whole experiment (field and laboratory) was run from 1 March to 13 April 2007.

At the start and end of each trial, pH, oxygen, temperature (WTW GmbH, Weilheim, Germany), conductivity (HANNA Instruments Inc., Woonsocket, RI, USA) and turbidity (YSI 6600, YSI Inc., Yellow Springs, OH, USA) were measured in each aquarium. To assess the changes produced in these parameters during the experiment, we calculated the difference between the initial and final values relative to the initial values. All aquaria were visually inspected regularly.

Sampling was performed at the end of each trial period. A water sample was taken from each aquarium to determine the concentration of suspended matter, shredders were removed and their DM measured. We selected five representative leaves from each aquarium and cut three 12-mm discs from each using a cork borer. Each of the three sets of five discs was used to determine one parameter; i.e. microbial respiration, fungal biomass, and aquatic hyphomycete sporulation rate and species identification. Discs were then oven-dried at 70°C to a constant mass and weighed (to the nearest 0.1 mg). Details on each analysis are given below.

Suspended solids

Water samples (170 mL) from each aquarium were filtered through a 0.7 µm glass fibre filter (Whatman GF/F, Whatman International Ltd., Maidstone, UK). Prior to use, filters were cleaned (60 mL of deionised water), dried, burned at 550°C for 15 min and weighed. Filters with the samples were then oven-dried at 70°C to a constant mass, weighed (to the nearest 0.1 mg), burned at 550°C for 15 min and weighed again, to determine ash-free dry mass (AFDM). In this way, we determined the mass of total suspended solids (TSS) and suspended inorganic and organic matter (SIM and SOM, respectively) and referred them to the water volume. The stress index (Newcombe and Macdonald 1991), indicating the severity of sediment pollution for invertebrates, was calculated through the natural logarithm of the product of the sediment concentration and exposure duration.

The quantity of sediment resuspended by shredders, hereafter sediment mobilization rate (SMR), was calculated for each replicate of treatments with sediment and shredders (*GS*, *PS*) accounting for the control treatments; i.e. with sediment and without shredders (SIM without shredders) following this formula:

$$\mathrm{SMR} = \frac{(\mathrm{SIM\ with\ shredders} - \mathrm{SIM\ without\ shredders})(\mathrm{mg\,L^{-1}})}{\mathrm{shredders\ DM\ (g)}}$$

Microbial parameters

Microbial respiration, mostly due to bacteria, fungi and protozoans colonising the leaf surface, was determined by measuring the oxygen uptake rate using oxygen microprobes in hermetically sealed chambers, thermoregulated at 10°C (Strath-Kelvin 928 System, North Lanarkshire, UK). Leaf discs were put in the chambers with 3 mL filtered stream water (0.2 µm sterile cellulose membrane; Whatman International Ltd., Maidstone, UK). Oxygen uptake rate is the slope of the regression of oxygen consumption versus time over 30 min. For each series of measures, we subtracted the slope from that of a control chamber; i.e. without leaf discs. The rate was expressed as mg O_2 g^{-1} leaf AFDM h^{-1}.

Mycelial biomass was estimated through the ergosterol concentration in leaves (Gessner et al. 2003). Leaf discs (kept at −18°C) were freeze-dried and weighed (to the nearest 0.1 mg), extraction was then performed using a solid phase extraction and high performance liquid chromatography (see Gessner et al. 2003; Lecerf et al. 2005). Extraction efficiency was measured for each sample series and ranged from 93 to 98%. Results were expressed as micrograms of ergosterol per leaf AFDM and transformed to fungal biomass by multiplying the ergosterol content by a factor of 182 as determined for aquatic hyphomycetes; i.e. the dominant fungi on leaf litter decomposing in streams (Gessner and Chauvet 1993; Nikolcheva et al. 2005).

To determine aquatic hyphomycete sporulation rate, we followed the protocol explained in Lecerf et al. (2005) with slight modifications, which are summarized below. The day after the end of trials, five leaf discs for each replicate (kept at 4°C) were incubated for 48 h at 10°C in stream water and stirred on an orbital shaker to induce sporulation. The spore suspension was transferred to conical tubes and formalin was added (final concentration 2%). Leaf discs were kept to determine their DM and spore suspensions were stored until analysis. To count and identify the spores, 200 µL of Triton X-100 (1% solution) were added to samples. Then, 2–10 mL of suspension were filtered and the spores on the filter were stained with 0.02% Trypan blue in 60% lactic acid. Depending on the number of spores, the whole filter or filter portions were scanned under the microscope (×200). Spores of aquatic hyphomycetes were identified to species, when possible, and sporulation rate was expressed as the number of spores mg^{-1} leaf AFDM day^{-1}.

Remaining leaf mass

The remaining leaves from aquaria were dried at 70°C to a constant mass, weighed (to the nearest 0.1 mg), burned at 550°C for 3 h and weighed again, to determine AFDM. The DM of leaf discs used to determine microbial respiration, fungal biomass and sporulation were added to the mass of leaves to calculate the total remaining leaf DM and

AFDM. From the three extra leaf packs, we calculated the mean leaf mass loss (AFDM) during the initial period of microbial colonisation in the stream. The remaining AFDM at the end of the experiment was expressed as a ratio between AFDM loss and initial AFDM; i.e. at the beginning of the laboratory experiment.

The consumption rate (CR) of the two shredder taxa over the trial period (8 days) was calculated by using the formula below for the treatments with shredders (*G*, *GS*, *P*, *PS*):

$$\mathrm{CR} = \frac{\%\ \text{leaf AFDM loss with shredder} - \%\ \text{leaf AFDM loss without shredder}}{\text{shredders DM (g)}}$$

Statistical analyses

We tested for correlations between variables using the Pearson coefficient. Normality of residuals (Kolmogorov–Smirnov's test) and homoscedasticity (Levene's test) were achieved in all variables using different transformations (x^3, $\log_{10}(x + 1)$, square root and arcsine square root), except for the oxygen and pH relative changes (no homoscedasticity) and relative abundance of aquatic hyphomycete species.

We analysed physico-chemical parameters and univariate measures using a general linear model (GLM) ANOVA with a type III sum of squares, testing the fixed effects of sediment (2 levels), shredder treatment (3 levels) and its interaction, with trials as a block factor (3 levels). The design was unbalanced due to the different number of replicates of *Gammarus* and *Potamophylax* treatments. We tested the hypothesis about the presence of the shredders (2 levels) and its interaction with the sediment factor using pre-planned contrasts. We used Tukey as the post hoc test. When only the treatments with sediment or with shredders were analysed, as for the suspended inorganic matter per shredder DM, ANOVA was performed. Two turbidity values were not taken into account [one outlier (extreme atypical value in SPSS box-plot) and one negative value due to a measurement error]. Moreover, three values of leaf mass loss percentage and nine of suspended matter (organic and inorganic) were considered as missing because, due to the error associated to the scales masking little mass changes, negative values appeared. In SMR and CR calculations, we used the mean values of the control treatments as constant (i.e. not taking into account the error of these values) because the control treatments were not coupled with the treatments with shredders (see mention in the "Results"). Degrees of freedom from 'within group variation' changed depending if the analysis took into account all replicates (df = 48), replicates where only invertebrates were present (df = 20) or replicates with both sediment and invertebrates (df = 10). The significance level for all analyses was $P = 0.05$. These analyses were performed with the PASW Statistics 18 (SPSS Inc., Chicago, IL, 2009).

From the sporulation data, we constructed a matrix for the multivariate analyses with the relative contribution of each species to the total pool of spores of each treatment. Because different numbers of spores were counted in each sample, which may have affected the evaluation of fungal species richness (Gotelli and Colwell 2001), two additional biodiversity measures, less sensitive to abundance variations, were performed on species abundance; the Shannon diversity index (H′; calculated with the natural logarithm) and the Pielou's evenness (J′). Differences for these indices were analysed with the GLM used for the other variables in PASW. The similarity between the assemblage composition from the two matrices was calculated using the Jaccard index, which compares the presence/absence of the species, and the Bray–Curtis index, which takes into account the species abundance. Results were graphically represented using the nonmetric multidimensional scaling (NMDS) overlaid with a cluster analysis to visualise the similarity between samples. The effect of the treatments on the relative abundance of aquatic hyphomycete species was tested using the analysis of similarity (ANOSIM). Multivariate analyses and calculations of biodiversity indices were performed using PRIMER 6 (PRIMER-E Ltd., Plymouth, UK).

Results

Physico-chemical parameters

Throughout the three trials, the final mean temperature in the aquaria was 10.2°C (±0.1 SE), oxygen concentration was 10.1 mg L^{-1} (±0.1 SE), pH was 6.58 (±0.05 SE) and conductivity was 41 µS cm^{-1} (±1 SE). None of these parameters was affected by the sediment addition ($P > 0.079$). However, conductivity was affected by the shredder treatment ($F_{2,48} = 54.67$, $P < 0.001$), increasing the most in treatments with *Potamophylax*, from 38 to 48 µS cm^{-1} (initial to final) compared to the rest of the treatments, where it changed from 37 to 39 µS cm^{-1}.

Suspended solids

Turbidity (log-transformed) changed with all the factors (sediment presence, shredder treatment, shredders presence and block factor) and their interactions (Fig. 2a), but the ones which contributed more to its increase were sediment addition ($F_{1,46} = 2{,}289.33$, $P < 0.001$) and the presence of shredders ($F_{1,46} = 461.09$, $P < 0.001$). Maximum values of turbidity were observed in *PS* treatments (81.0 NTUs), while in *CS* treatments it was much lower (11.1 NTUs).

TSS and turbidity (both log-transformed) were positively correlated (Pearson, r = 0.942, $P < 0.001$, n = 54). Furthermore, TSS values exhibited significant effects for all factors and their interactions, with sediment addition ($F_{1,48} = 361.27$, $P < 0.001$) and shredders presence ($F_{1,48} = 185.42$, $P < 0.001$) contributing the most to the TSS increase. When shredders were present with sediment, the concentration of TSS increased by five-fold on average (from 8.0 in the *CS* treatments to 40.5 mg L^{-1} with sediment and shredders). In relation to the quantity of sediment added to the aquaria, 1.34% was suspended in the *CS* treatment due to the recirculation of water, whereas in the aquaria with *Gammarus* (*GS*) the suspended portion was 6.59% and with *Potamophylax* (*PS*) it was 8.95%; the increase from the *CS* being attributable to the shredder activity. SOM represented on average 28% of the TSS, meaning that turbidity was mainly created by the SIM (72%). The stress index value for invertebrates was 8.72, taking into account the mean value of the SIM in treatments with invertebrates (31.76 mg L^{-1}) and the duration of exposure (192 h). The quantity of SOM in each aquarium was positively correlated with SIM (Pearson, r = 0.860, $P < 0.001$, n = 47).

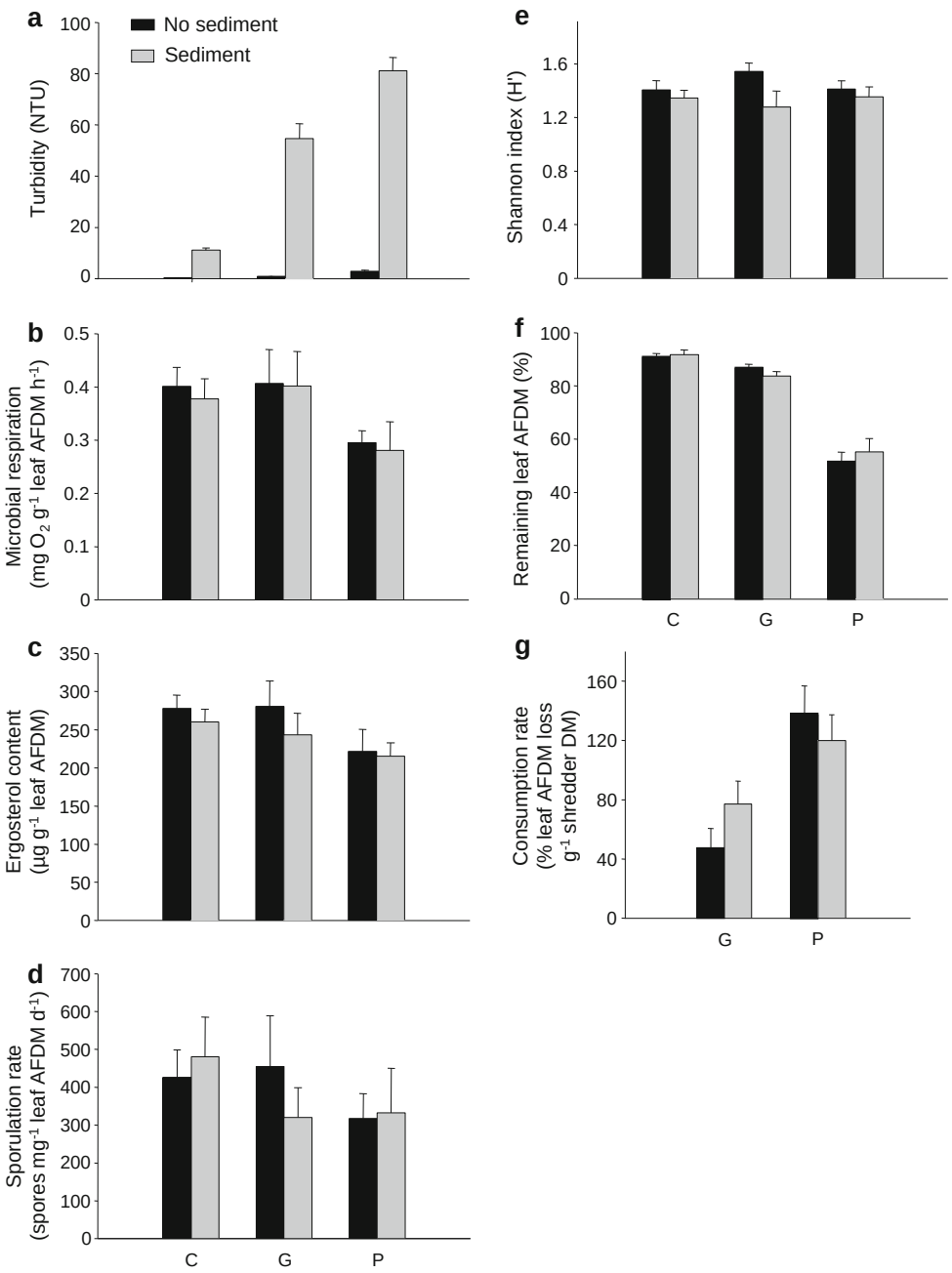

Fig. 2 **a** Turbidity values in nephelometric turbidity units (NTU), **b** microbial respiration, **c** ergosterol content, **d** sporulation rate of leaf-associated fungi, **e** Shannon index (H′) for the fungal assemblages calculated with the natural logarithm, **f** remaining leaf AFDM in percentage after the experiment and **g** shredders consumption rate (CR) in percentage of leaf AFDM loss per shredder DM in the different treatments. *Letters* on the *X* axis mean controls without shredders (*C*), *Gammarus* (*G*) and *Potamophylax* (*P*); without (*black bars*) and with (*grey bars*) sediment. *Bars* represent the mean (+1 SE)

The average value of the *CS* treatments (used as the "SIM without shredders" term in the SMR calculations) was 5.38 mg L^{-1} (±0.58 SE). *Gammarus* resuspended sediment at a higher rate (SMR = 191.59 mg L^{-1} g^{-1}) than did *Potamophylax* (SMR = 99.69 mg L^{-1} g^{-1}) ($F_{1,10} = 17.937$, $P = 0.002$).

Microbial respiration and fungal biomass

There were no significant effects of sediment on microbial respiration rate (log-transformed) ($F_{1,48} = 0.883$, $P = 0.352$; Fig. 2b). For fungal biomass (Fig. 2c), even though differences were not significant ($F_{1,48} = 1.67$, $P = 0.202$), a trend towards a decrease of fungal biomass (ergosterol content) by 8.5% on average (from 266.33 to 243.73 µg g^{-1} leaf AFDM) in presence of sediment was observed. Both variables were lower in treatments with *Potamophylax* (*P* & *PS*) than in the other treatments (microbial respiration: $F_{2,48} = 5.91$, $P = 0.005$; fungal biomass: $F_{2,48} = 3.81$, $P = 0.029$) decreasing from 0.40 to 0.29 mg O_2 g^{-1} AFDM h^{-1} and from 277.66 to 217.93 µg g^{-1} leaf AFDM, respectively, in the *C* treatments versus all treatments with *Potamophylax*. Both variables were higher in the first than in the following two blocks ($F_{2,48} = 18.92$, $P < 0.001$; $F_{2,48} = 15.37$, $P < 0.001$). A positive correlation was observed between microbial respiration (log-transformed) and fungal biomass (Pearson, r = 0.585, $P < 0.001$, n = 56).

Aquatic hyphomycete sporulation

The sporulation rate was not affected by any factor, including sediment ($F_{1,48} = 0.90$, $P = 0.347$; Fig. 2d). After 19 days of colonisation (11 in the stream + 8 in the aquaria), the sporulation rate was on average 407.4 spores mg^{-1} leaf AFDM day^{-1} (±0.1 SE). Sporulation rate (log-transformed) was positively correlated with fungal biomass (Pearson = 0.384, $P = 0.003$, n = 56).

Twenty-nine different aquatic hyphomycete species were identified and four taxa remained unidentified ("Appendix"). Assemblages were dominated by four species that made up nearly 90% of the total pool of spores and, in order of abundance, these were *Tricladium chaetocladium*, *Flagellospora curvula*, *Alatospora acuminata* and *Articulospora tetracladia*.

The number of aquatic hyphomycete species was on average 7.8 (±0.2 SE) per sample and was not affected by sediment ($F_{1,48} = 0.58$, $P = 0.452$). In the first block, species richness was higher ($F_{2,48} = 4.10$, $P = 0.023$) than in the other blocks. Shannon index (H′) was slightly lower due to the presence of sediment ($F_{1,48} = 4.18$, $P = 0.046$), the mean value without sediment being H′ = 1.45 and with sediment H′ = 1.33 (Fig. 2e). The maximum value of the Shannon index was $H'_{max} = 3.37$ (with S = 29 species). Evenness (Pielou J′) was not statistically different between treatments (Sediment: $F_{1,48} = 1.81$, $P = 0.185$) and on average was J′ = 0.68 (±0.01 SE).

In the NMDS ordination plot of Bray–Curtis similarities based on relative abundances, no distinction of groups could be made according to the treatments. ANOSIM analyses were not significant for sediment (R = −0.012, $P = 0.587$, 999 permutations) nor for shredder treatments (R = 0.072, $P = 0.100$, 999 permutations). Cluster analysis of the same data showed a minimum of 33.5% similarity among samples. When the data matrix was transformed in order to give more weight to rare species, the significance level of the factors in the ANOSIM decreased, indicating that the more abundant species were responsible for the dissimilarities.

The presence/absence of the species, through the Jaccard index, showed significant differences for the shredder treatment (ANOSIM, Jaccard index, R = 0.122, $P = 0.022$, 999 permutations). A pairwise test between shredder treatments showed that differences were between the treatments without shredders and with *Gammarus* (R = 0.213, $P = 0.008$, 999 permutations).

Some fungal species were affected by the different treatments ("Appendix"). The relative sporulation rate of *Tetrachaetum elegans* was slightly lower with sediment (1.88%) than without sediment (3.16%) ($F_{1,48} = 4.31$, $P = 0.043$). With the presence of both shredders and sediment, the sporulation rate of *Clavatospora longibrachiata* was lower, of 0.07% respect to 0.24% on the other treatments ($F_{1,48} = 5.06$, $P = 0.029$), as well as *Anguillospora filiformis* that changed from 2.36 to 4.09% ($F_{1,48} = 5.19$, $P = 0.027$). *A. tetracladia* was more abundant in the treatments with *Gammarus* (21.98%) than in the other treatments (9.37%) ($F_{2,48} = 7.45$, $P = 0.002$). *A. acuminata* was less abundant in the shredder absence (14.27%) ($F_{1,48} = 6.32$, $P = 0.015$), and had the highest abundance with *Gammarus* (22.62%) ($F_{2,48} = 3.89$, $P = 0.027$). All of these species, except for *C. longibrachiata*, were among the six most abundant species of the assemblages, confirming that the dissimilarities were due to the dominant species.

Remaining leaf mass

During the first 11 days of colonisation in the stream, leaves lost 27.1% (±2.9 SE) of their mass while exposed in the fine mesh bags. There was no effect of sediment addition on the remaining AFDM (%) of leaves in aquaria ($F_{1,45} = 0.13$, $P = 0.723$) (Fig. 2f). The remaining AFDM was lower in the first block ($F_{2,45} = 14.45$, $P < 0.001$). As expected, remaining AFDM was higher in aquaria without shredders (91.27%) ($F_{1,45} = 180.97$, $P < 0.001$) and there

were significant differences between treatments with *Gammarus* (85.2%) and *Potamophylax* (53.5%) ($F_{2,45} = 185.40$, $P < 0.001$). When considering shredders' CR (Fig. 2g), *Gammarus* was a less efficient consumer than *Potamophylax* ($F_{1,20} = 38.87$, $P < 0.001$), both in the absence and presence of sediment. In control treatments without sediment (*C*), the % of leaf AFDM loss was 9.26% (±1.43 SE) and in controls with sediment (*CS*) it was 7.86% (±1.73 SE); note these values were used for the CR calculations.

Discussion

The main findings of our experiment were the lack of effects of sediment addition on leaf mass loss, as found by Schofield et al. (2004), although in disagreement with most of the literature (Herbst 1980; Bunn 1988; Benfield et al. 2001; Sponseller and Benfield 2001; Matthaei et al. 2010; Lecerf and Richardson 2010b). Even if the microbial community was not affected in general, species richness was lower under sediment and there was a tendency to a decrease in fungal biomass. A decrease in fungal biomass was observed by Schofield et al. (2004). Shredders' CR was not lowered by the sediment presence; whereas suspended solids increased due to their bioturbation action, as found by Gayraud et al. (2002) and Pringle et al. (1993). CR changes due to sediment on shredders have not been directly studied, although other effects as macroinvertebrates' biomass reduction or increased drift has been found (Quinn et al. 1992; Bilotta and Brazier 2008).

In general, our hypothesis was not supported by the results we found, although shredders removed the sediments from leaves as expected.

Sediment effects

From our initial hypothesis, we expected a decrease in the leaf mass loss when fine sediment was added, mediated by reduced colonisation and growth of aquatic fungi. Unexpectedly, sediment addition had no effect on leaf mass loss. With the presence of sediment, the microbial community remained largely unchanged, based on measures of microbial respiration, fungal biomass and the composition of fungal assemblages.

Interestingly, there was a slightly lower species richness (Shannon index) and a tendency towards lower fungal biomass in treatments with sediment (Schofield et al. 2004). Further, the relative sporulation rate of *T. elegans* was lower in response to sediment treatments.

In the literature, most studies of leaf decomposition show lower rates in the presence of sediment (Herbst 1980; Bunn 1988; Benfield et al. 2001; Sponseller and Benfield 2001; Lecerf and Richardson 2010b), including studies where the decomposition in the hyporheos was tested (Navel et al. 2010; Cornut et al. 2010). However, there are cases where leaf decomposition rates were not affected (Schofield et al. 2004) or even that decomposition rates increased (Matthaei et al. 2010) in the presence of fine sediments. So, even though the most common finding is that fine sediment would slow leaf decomposition; different trends in the results have been observed. In some studies, it was asserted that sediment was the factor causing the decrease in leaf decomposition, but sediment loads were not quantified and it is possible that other factors associated with sediments (e.g. agricultural chemicals or nutrients) were implicated in those results (Bunn 1988; Sponseller and Benfield 2001; Lecerf and Richardson 2010b) as Matthaei et al. (2006) pointed out in their paper.

In the study of Herbst (1980), the sediment cumulated on leaves was of 10–15 cm, and leaf decomposition rates decreased, whereas in the study of Matthaei et al. (2010) the cover was of 0.05 cm and decomposition rates increased, so the differences in the results are probably affected by the quantity of sediment.

The fungi species identified in our samples are all abundant (or highly abundant) in the leaf litter in southwest France in natural conditions (Chauvet 1991). Besides, the species richness, dominant species and fungal biomass were similar to the results found by Hieber and Gessner (2002) and Navel et al. (2010; only fungal biomass) on alder leaves. All these indicating that aquaria conditions did not bias fungal community structure or functioning.

The lack of a marked sediment effect on fungal biomass and fungal assemblages may be due to the high resilience of these organisms (Krauss et al. 2011), despite some particular species as *T. elegans*, which are likely more sensitive to sediment. This species' abundance was also found to be lower in the hyporheic zone (leaves buried 15–20 cm) versus the benthic zone (Cornut et al. 2010) and it disappeared downstream of a coal mine effluent (Bermingham et al. 1996) on alder leaves, indicating the sensitivity of this species to different impacts. Another reason for the lack of effects of sediment may be the initial colonisation of leaves that were exposed in the stream without the presence of sediment. The initial spore attachment phase is a critical first step, and once fixed on the leaf substrate, spore germinate in mere hours and mycelia solidly adhere to the leaves (Dang et al. 2007). Moreover, when sporulation rate was measured, leaves were rinsed for methodological reasons, so again the sediment was not present.

Interactions between shredders and sediment

Sediment can affect biomass, diversity and drift behaviour of benthic macroinvertebrates (Quinn et al. 1992; Wood and Armitage 1997) and, with similar stress indexes as in our study, these effects have been observed (Newcombe and Macdonald 1991; Bilotta and Brazier 2008). The only effect we might have observed in our experiment was a reduction in shredder feeding rates if sediments impaired foraging, but this did not occur, indicating that these species were resistant to short-term sediment impacts. The lack of a complete cover of aquaria glass bottom by sediments and leaves made the substrate somewhat artificial for invertebrates, although the only observed effect was that *Potamophylax* had slight difficulties to drag its case, while this did not seem to affect *Gammarus*. Continuous darkness during the trials could have had as well some effect on shredder behaviour, but the described effects are mainly based on drift rates (Holt and Waters 1967).

In the absence of shredders, fine sediments settled on the bottom and created a coating on leaves, apparently being integrated into the surface biofilms of leaves as previously reported from epilithic biofilms in streams (Kiffney et al. 2003; Pringle et al. 1993). Therefore, without shredders, leaf quality as a food supply could be reduced (Davies-Colley et al. 1992; on biofilm).

Turbidity and suspended particulates were indicators of bioturbation activities of shredders. All factors had a significant effect on turbidity, and the highest values (69.7 NTUs) were found in the presence of shredders and sediments. In aquaria with shredders, especially *Potamophylax*, suspended matter and turbidity were highly elevated due to the capacity of shredders to resuspend the fine sediments deposited on leaves. This result was very clear just looking at aquaria during the experiment. In absolute terms, *Potamophylax* suspended more sediment, although *Gammarus* was more efficient relative to its DM. This indicates that depending on the type and abundance of shredder present in the stream, sediment will be removed at different rates.

In natural conditions, one consequence of the resuspension of fine sediments caused by shredders is that sediments continue to be transported downstream and thus avoid their accumulation on leaf packs and on the streambed. From this point of view, shredders serve as ecosystem engineers. Other invertebrates have also been shown to serve as ecosystem engineers in different contexts, from crayfish disturbing sediments by digging burrows (Statzner et al. 2003) to net-building caddisfly larvae increasing bed stability by binding rocks together through construction of their silk nets (Takao et al. 2006). Although the mechanisms of engineering we predicted, i.e. enhancing the microbial processing of leaf litter by removing fine sediment, were not observed, their actions can reduce sediment deposition in areas where leaf litter settles. Thus, it is appropriate to apply the term allogenic ecosystem engineers to these shredders.

The experiment was a short-term study performed in microcosms, so we were not able to detect mechanisms potentially taking place in the longer term, which has logical limitations to transfer the results to natural streams. On the other hand, we had a high level of replication and there were no concomitant factors together with sediment. The concentration of sediment added in our experiment (400 mg L^{-1}) had some effects on leaf decomposition, mainly on the fungal assemblage. Nevertheless, our experiment points out other potential effects that could be important with a higher sediment concentration.

In our opinion, more research is needed in the laboratory, to elucidate the thresholds and duration of exposure at which sediment would have different kinds of effects, as for example Galbraith et al. (2006) did on salmon and Shaw and Richardson (2001) on rainbow trout. Another important factor to test would be the interaction between shredder diversity and the effect of sediment on leaf decomposition (McKie et al. 2009) together with field experiments adding controlled quantities of sediment to assess effects at ecosystem level (e.g. Suren and Jowett 2001) and species interactions.

To summarize, we found an interesting effect of shredders acting as ecosystem engineers by resuspending the sediment deposited on the leaves, although this effect did not have repercussions on leaf decomposition. Sediment addition at the concentration of 400 mg L^{-1} had effects on fungal richness and on some abundant fungal species, but not in leaf decomposition nor in the microbial community or shredders.

Understanding the effects of sediment on ecosystem functions and the mechanisms causing them is interesting to predict changes in these functions due to natural or anthropogenic changes and to give arguments justifying regulations about sediment loads in streams.

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Appendix

See Table 1.

Table 1 List of aquatic hyphomycete species found on alder leaves in the six treatments

Fungal species	*C*	*CS*	*G*	*GS*	*P*	*PS*
Alatospora acuminata Ingold[b]	15.3 (3.8)	13.2 (1.9)	20.4 (2.9)	25.5 (8.8)	16.5 (6.3)	20.1 (5.1)
Alatospora flagellata (Gönczöl) Marvanová	0.2 (0.1)				0.1 (0.1)	
Anguillospora filiformis Greathead[c]	3.1 (0.7)	4.1 (0.6)	3.2 (0.9)	1.3 (0.7)	7.6 (3.3)	3.1 (0.7)
Anguillospora furtiva Webster & Descals	0.5 (0.2)	0.1 (0.1)	2.7 (1.5)	0.5 (0.5)	0.6 (0.6)	2.5 (1.6)
Anguillospora longissima (Sacc. and Syd.) Ingold	0.5 (0.2)	0.3 (0.2)	0.6 (0.5)	0.7 (0.7)	1.4 (0.8)	2.6 (1.5)
Articulospora tetracladia Ingold[b]	12.0 (1.7)	9.7 (3.3)	20.3 (4.9)	24.2 (11.3)	7.4 (2.0)	5.8 (2.0)
Campylospora chaetocladia Ranzoni		0.1 (0.1)				
Casaresia sphagnorum Fragoso		0.1 (0.1)				
Clavariopsis aquatica De Wildeman	0.1 (0.1)	0.1 (0.1)		0.3 (0.1)		1.2 (1.2)
Clavatospora longibrachiata (Ingold) Marvanová & Nilsson	0.7 (0.5)			0.1 (0.1)		0.1 (0.1)
Crucella subtilis Marvanová & Suberkropp	0.3 (0.2)	0.1 (0.1)	0.1 (0.1)			0.1 (0.1)
Culicidospora aquatica Petersen	0.9 (0.3)	1.5 (0.5)	2.2 (1.3)	0.9 (0.7)	1.6 (0.9)	1.4 (0.7)
Dendrospora tenella Descals & Webster			0.1 (0.1)			
Flagellospora curta Webster		0.2 (0.2)				0.7 (0.7)
Flagellospora curvula Ingold[b]	18.1 (3.3)	21.4 (4.8)	12.3 (2.6)	17.0 (3.8)	21.8 (8.3)	11.8 (3.2)
Fontanospora eccentrica (Petersen) Dyko			0.1 (0.1)			
Heliscella stellata (Ingold and Cox) Marvanová & Nilsson						0.1 (0.1)
Heliscus lugdunensis Saccardo & Thérry	0.1 (0.1)	0.9 (0.5)	0.5 (0.2)		0.9 (0.5)	0.1 (0.1)
Isthmotricladia britannica Descals in Descals & Webster				0.1 (0.1)		
Lemonniera aquatica De Wildeman	0.1 (0.1)	[a]		0.1 (0.1)		
Lemonniera terrestris Tubaki		0.1 (0.1)				
Mycocentrospora sp. cf. *angulata* R.H. Petersen	[a]	0.1 (0.1)				
Mycofalcella calcarata Marvanová	0.1 (0.1)	[a]		0.1 (0.1)		
Stenocladiella neglecta (Marv. & Descals) Marvanová & Descals	[a]					
Sympodocladium frondosum Descals				0.2 (0.2)		
Taeniospora gracilis Marvanová	0.5 (0.2)		0.1 (0.1)	0.1 (0.1)	0.4 (0.3)	0.2 (0.2)
Tetrachaetum elegans Ingold[c]	3.1 (1.1)	2.9 (0.8)	3.0 (1.6)	0.5 (0.3)	3.6 (1.7)	1.1 (0.5)
Tricellula aquatica Webster		0.1 (0.1)				
Tricladium chaetocladium Ingold[b]	44.4 (4.2)	44.7 (5.1)	34.1 (4.9)	28.3 (6.2)	38.1 (8.3)	49.1 (5.8)
Filiform unidentified <60 μm	0.1 (0.1)	0.2 (0.2)				0.1 (0.1)
Filiform unidentified 60–120 μm					0.1 (0.1)	
Tricladiate unidentified		0.1 (0.1)				
Pluricladiate unidentified			0.4 (0.4)			

The values are the mean and standard error in parentheses (SE) of the relative contribution of species to the total production of spores in percentage. Blank cells indicate that the taxon was absent in the treatment

[a] Sporulation rates lower than 0.05%

[b] The four more abundant species (nearly 90% of the total production)

[c] The two following species in order of abundance

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