Science of the Total Environment 553 (2016) 330–339

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation

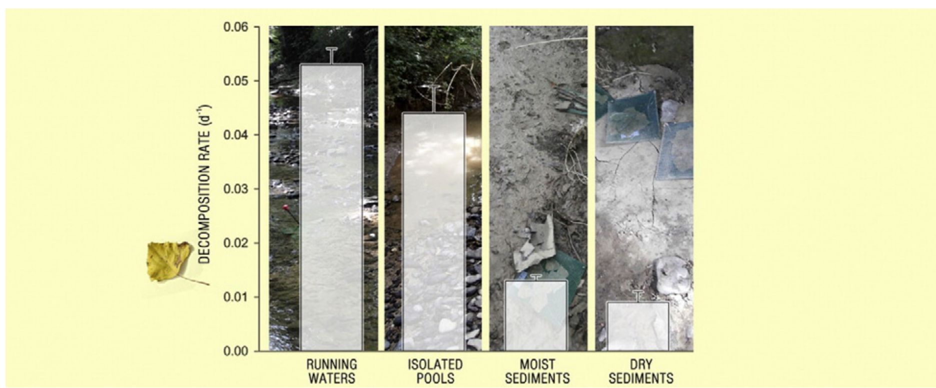
Meritxell Abril *, Isabel Muñoz, Margarita Menéndez

Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain

HIGHLIGHTS

- Temporary Mediterranean streams are characterized by high spatial and temporal hydrological variability.
- Flow fragmentation during the summer drought gives rise to a mosaic of aquatic and terrestrial habitat types.
- We assessed leaf litter decomposition in running waters, isolated pools, moist sediments and dry sediments.
- We found heterogeneous decomposition throughout the sites with implications to DOC utilization.
- Addressing environmental heterogeneity is crucial to improving our understanding of temporary streams.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 13 November 2015
Received in revised form 11 February 2016
Accepted 12 February 2016
Available online 27 February 2016

Editor: D. Barcelo

Keywords:
Drought
Flow fragmentation
Habitat heterogeneity
Black poplar
Microbial biomass
DOC release

ABSTRACT

In temporary Mediterranean streams, flow fragmentation during summer droughts originates an ephemeral mosaic of terrestrial and aquatic habitat types. The heterogeneity of habitat types implies a particular ecosystem functioning in temporary streams that is still poorly understood. We assessed the initial phases of leaf litter decomposition in selected habitat types: running waters, isolated pools and moist and dry streambed sediments. We used coarse-mesh litter bags containing *Populus nigra* leaves to examine decomposition rates, microbial biomass, macroinvertebrate abundance and dissolved organic carbon (DOC) release rates in each habitat type over an 11-day period in late summer. We detected faster decomposition rates in aquatic (running waters and isolated pools) than in terrestrial habitats (moist and dry streambed sediments). Under aquatic conditions, decomposition was characterized by intense leaching and early microbial colonization, which swiftly started to decompose litter. Microbial colonization in isolated pools was primarily dominated by bacteria, whereas in running waters fungal biomass predominated. Under terrestrial conditions, leaves were most often affected by abiotic processes that resulted in small mass losses. We found a substantial decrease in DOC release rates in both aquatic habitats within the first days of the study, whereas DOC release rates remained relatively stable in the moist and dry sediments. This suggests that leaves play different roles as a DOC source during and after flow fragmentation. Overall, our results revealed that leaf decomposition is heterogeneous during flow fragmentation, which has implications related to DOC utilization that should be considered in future regional carbon budgets.

* Corresponding author.
E-mail address: meritxell.abril@ub.edu (M. Abril).

http://dx.doi.org/10.1016/j.scitotenv.2016.02.082

1. Introduction

Temporary rivers and streams are defined as those watercourses that cease to flow at some point in space and time along their course (Arthington et al., 2014). Often overlooked in global inventories (Acuña et al., 2014), these ecosystems are widespread around the globe and are the dominant surface water type in Mediterranean climate regions (Bonada and Resh, 2013). Temporary Mediterranean streams are characterized by high hydrological variability governed by dry and wet periods throughout the year (Acuña et al., 2005). A dry period typically occurs in summer, when a decrease in precipitation combined with increases in evapotranspiration and water use drastically reduces water flow until the hydrological connectivity is lost (Bernal et al., 2013). This contraction phase implies the fragmentation of stream ecosystems and ultimately leads to the emergence of a changing and ephemeral mosaic of terrestrial and aquatic habitat types along the streambed (Larned et al., 2010). These habitat types include areas with running waters, isolated pools of different sizes and dry streambed sediments. The dynamics of this habitat mosaic are controlled by the frequency and duration of the dry period (Stanley et al., 1997; Bunn et al., 2006), which lasts until hydrological connectivity is restored (Tockner et al., 1999).

Flow variability is a determining factor in aquatic ecosystems (Richter et al., 2003), and in temporary streams the alternation between dry and wet periods influences all ecological processes (Sabater and Tockner, 2010). One of these processes is the decomposition of organic matter, a key ecosystem process that governs the entry of energy and nutrients into streams (Webster and Benfield, 1986). During dry periods, water stress may impact riparian vegetation by causing early leaf abscission that coincides with flow fragmentation (Sabater et al., 2001; Sanpera-Calbet et al., 2015). Then, leaf litter falls into the streambed and is primarily retained in dry streambed sediments and isolated pools (Acuña et al., 2007) where different factors affect its processing.

Decomposition rate is usually slower in dry streambed sediments than under aquatic conditions (e.g., Langhans et al., 2008; Schlief and Mutz, 2011), primarily because the absence of water limits the activity of decomposers. In dry sediments, invertebrates play a minor role in decomposition because aquatic shredders are inhibited by emersion (Datry et al., 2011; Riedl et al., 2013; Martínez et al., 2015) and terrestrial detritivores are scarce (Maamri et al., 1997; Corti et al., 2011). Microbial biomass and activity are also reduced in dry conditions (Boulton, 1991), although the importance of this factor seems to be closely linked to sediment moisture levels (Amalfitano et al., 2008; Gómez-Gener et al., 2015). In this regard, some studies have reported an increase in microbial decomposition when litter is partially rehydrated (Langhans and Tockner, 2006; Bruder et al., 2011; Foulquier et al., 2015). Nevertheless, little is known about the effect of moisture on decomposition and some authors have highlighted the importance of assessing this process at different stages of drying to better understand the mechanisms involved (e.g., Larned et al., 2010).

In isolated pools, decomposer communities are exposed to harsh physicochemical conditions. In these habitats, detritus accumulation increases nutrient concentrations and stimulates heterotrophic activity that causes a gradual decrease in oxygen levels and pH (Stanley et al., 1997; von Schiller et al., 2011). Moreover, the accumulation of leaf leachates in pools may be toxic for some decomposer communities (Schlief and Mutz, 2007; Canhoto et al., 2013). Though only a few studies have evaluated leaf litter decomposition in pools, they reported lower decomposition rates in comparison to running waters and related it to conditions unfavourable to the development of aquatic fungi and shredders (Baldy et al., 2002; Schlief and Mutz, 2009). However, studies of leaf litter decomposition in pools have been typically carried out in microcosms because the unpredictable dynamics of temporary streams make it difficult to develop a larger scale experimental framework.

This heterogeneity of detritus dynamics along fragmented streams may also have implications for other ecological processes that rely on the products of decomposition. Leaf litter leachates supply a large proportion of riverine dissolved organic carbon (DOC), an essential component of the carbon cycle that fuels stream metabolism (Meyer et al., 1998). Previous studies in temporary streams have found changes of the dynamics of DOC in relation to the hydrology (Vázquez et al., 2015; von Schiller et al., 2015); however, the contribution of leaf litter as a DOC source and its implications for the carbon cycle in these systems remains largely unexplored (but see Casas-Ruiz et al., 2016). Moreover, the retention of organic matter during flow fragmentation may be an important source of carbon and nutrients for downstream reaches when flow returns (Ylla et al., 2010). In this way, the different biotic and abiotic factors involved in organic matter decomposition during flow fragmentation may determine the availability of organic resources when flow connectivity is re-established, thereby influencing ecosystem's metabolism and related food webs (Riedl et al., 2013; von Schiller et al., 2015).

Despite the abundance of temporary streams and their predicted increase due to climate change (Larned et al., 2010), our knowledge of the dynamics of ecosystem processes such as litter decomposition in these systems is still limited. This limits our capacity to understand ecosystem processes in a large proportion of fluvial networks worldwide, hindering the accurate assessment of ecological conditions and preventing the effective management of these systems (Acuña et al., 2014; Arthington et al., 2014; Leigh et al., 2015).

The aim of our study was to assess the initial phases of leaf litter decomposition within different habitats resulting from flow fragmentation in a temporary Mediterranean stream: running waters, isolated pools and moist and dry streambed sediments. We used litter bags containing *Populus nigra* L. leaves to examine decomposition rates, carbon to nitrogen molar ratios, microbial biomass, macroinvertebrate abundance and DOC release rates associated with leaves in each habitat type over a period of 11 days in late summer. A short incubation period was set due to the importance of the first stages of decomposition in the release of DOC from the litter (Yoshimura et al., 2010) and to avoid a drastic shift in habitat conditions during the experiment. We hypothesized that higher decomposition rates would be observed in aquatic than in terrestrial habitats because microbial decomposers and detritivores would be more abundant under aquatic conditions. Regarding aquatic habitats, we expected lower decomposition rates in isolated pools than in running waters because the absence of flow in pools promotes harsh conditions for shredders and aquatic fungi. Regarding terrestrial habitats, we anticipated moisture level to be an important factor driving leaf litter decomposition, with higher microbial biomass and, thus, higher decomposition rates in moist than in dry sediments. Finally, we predicted a more pronounced decrease in the DOC release rate during the decomposition process in aquatic habitats compared to terrestrial habitats because of the utilization of DOC by microbial communities associated with leaf litter and the effect of leaching in aquatic habitats.

2. Material and methods

2.1. Study site

This experiment was conducted on the Fluvià River, located in the north-eastern Iberian Peninsula. Its watershed drains an area of 990 km^2 and has a mainstem that is 97 km long and flows into the Mediterranean Sea. The watershed is characterized by a Mediterranean climate, with dry, warm summers and scarce precipitation occurring primarily in the spring and autumn.

In the upper part of this watershed, we selected an experimental reach of approximately 2 km along a fourth-order stream (Strahler, 1957). The reach included both a permanent and a temporary section. The reach is situated between 42°8′33.61″N; 2°26′59.83″E and 42°7′35.54″; 2°26′59.83″E with the temporary section located in the upstream portion of this range. The permanent and temporary sections were selected as close as possible to minimize the potential interference of other environmental variables different from hydrology in our response variable. The land cover in the sub-watershed associated with the study reach is comprised primarily of forest (78%), with some agricultural (19%) and urban (3%) areas (Land Cover Map of Catalonia 2009, CREAF). The riparian vegetation along the reach is dense and dominated by *Populus nigra*, *Fraxinus angustifolia* and *Platanus hispanica*.

The experiment was carried out during the August − September 2013 summer drought, when the temporary stream section was fragmented into isolated pools of different sizes and exposed streambed sediments with different moisture levels. Along this section, we selected three replicate sites for each of the following habitat types: isolated pools, moist sediments and dry sediments. In the isolated pools, the wetted area ranged from 12 to 20 m^2 and the maximum depth from 30 to 80 cm, as measured on the first sampling date. At the streambed sediment sites, we identified three points that were completely dry and three points that were moist. We also selected three running water sites from the permanent stream section. Water flowed at a constant rate continuously during the experiment, with a discharge of 0.03 $m^3\ s^{-1}$, a maximum wetted width of 5 m and a maximum depth of 20 cm.

During the study period (29 August − 9 September 2013), the average daily air temperature was approximately 23 °C (min. 11 °C - max. 29 °C) and the accumulated precipitation was 17.3 mm (Meteorological Service of Catalonia, METEOCAT). This occurred in a single precipitation event just two days before the experiment ended.

2.2. Habitat characteristics

A WTW multi-parametric sensor (Weilheim, Germany) was used to measure water temperature (accuracy of ±0.1 °C), conductivity (accuracy of ±1 $\mu S\ cm^{-1}$), pH and the dissolved oxygen concentration (accuracy of ±0.1 $mg\ L^{-1}$) in the permanent section and isolated pools three times during the study period. Current velocity and discharge were also determined in situ. Water samples were taken in triplicate from each of these aquatic habitats on the third sampling day (after 8 days of leaf incubation) for nutrient analyses. Water was filtered through nylon membrane filters (0.45 μm pore size; Millipore, USA), transported to the laboratory under cool conditions, and stored at −20 °C in the dark until analysis. The concentrations of dissolved nitrite, nitrate, ammonium, soluble reactive phosphorus (SRP), chloride, sulphate, calcium and sodium were analysed using ionic chromatography (IC5000, DIONEX, USA) with an average accuracy of ±2.8% at 1 ppm. The dissolved organic and inorganic carbon concentrations in water (DOC and DIC, respectively) were measured using a total organic carbon analyser (TOC-V CSH, Shimadzu, Japan) that had an accuracy of ±4.4% at 5 ppm.

In the moist and dry sediments, soil temperature and moisture were measured in triplicate at each replicate site using portable sensors (ECH2O 10HS, Decagon, USA and Hi93500, Hanna, USA) on three sampling dates (4, 8 and 11 days of leaf incubation).

2.3. Leaf decomposition

Black poplar (*Populus nigra* L.) leaves were collected just after abscission in the fall of 2012. Leaves were air-dried to constant weight and stored at room temperature until needed. Portions of 3.27 ± 0.01 g (mean ± SE) of these leaves were weighed, moistened with distilled water using a garden atomizer, and enclosed in coarse-mesh nylon bags (15 × 20 cm, 5 mm mesh openings).

During the August–September 2013 summer drought, a total of 12 leaf bags were placed in each habitat type (4 bags × 3 replicate habitat type). At the running water and isolated pool sites, bags were tied with nylon lines to iron bars. At the streambed sediment sites, bags were put in contact with the substrate and secured using tent pegs and rocks. One litter bag was retrieved from each habitat replicate 1, 4, 8 and 11 days after the experiment started. The litter bags were then placed in individual plastic bags and transported in cool conditions to the laboratory, where they were immediately processed. Leaf material from each bag was rinsed with distilled water over a 500 μm sieve to remove invertebrates and inorganic particles. Invertebrates remaining on the sieve were preserved in 70% ethanol for later counting and identification to the lowest-feasible taxonomic level. Macroinvertebrate abundance was expressed as the number of individuals (Ind.) per unit of ash-free dry mass (AFDM) of leaf litter. Just after cleaning the leaves, 5 leaf discs from each bag (12 mm diameter) were cut with a cork borer to determine the DOC release rate (see below). On all sampling dates except day 1, another set of 3 discs per bag were obtained to determine bacterial biomass (see below). These discs were preserved in vials with 10 ml of distilled water and 0.5 ml of 37% formalin at 4 °C until analysed. On the last sampling date, one set of 10 discs from each bag was put into small plastic bags and frozen at −80 °C to obtain fungal biomass by ergosterol determination (see below).

The remaining material was oven-dried (60 °C, 72 h) and weighed to determine dry mass. An extra set of 5 leaf discs from each habitat type and for each sampling date was dried in the same way as the remaining material to estimate the mass used in the microbial biomass and DOC release determinations. Then, a subsample of each dried material sample was incinerated (450 °C, 5 h) to remove the inorganic components and to obtain the AFDM. The results were expressed as a percentage of the remaining initial AFDM. The initial AFDM was determined from an extra set of 5 leaf bags that were transported into the field and returned to the laboratory on the same day. These bags were processed as described above to create a conversion factor between the initial air-dry mass and the initial AFDM, taking into account manipulation losses.

Another subsample of dried material was ground into a fine powder (~1 mm pore size), and the nitrogen (N) and carbon (C) concentrations were analysed. Both elements were determined using a Perking Elmer series II CHNS/O elemental analysis. The results were expressed in terms of C:N molar ratios. We also obtained the C:N molar ratio from non-incubated leaves in the field.

2.4. Microbial biomass

2.4.1. Fungal biomass

To calculate the fungal biomass at each site, frozen leaf discs were lyophilized, weighed to determine the dry mass and used in the ergosterol analyses (Gessner, 2005). Lipid extraction and saponification were performed using KOH methanol 0.14 M (8 $g\ L^{-1}$) at 80 °C for 30 min in a shaking bath. Extracted lipids were purified using solid-phase extraction cartridges (Waters Sep-Pak®, Vac RC, 500 mg, tC18 cartridges, Waters Corp., Milford, MA, USA), and ergosterol was eluted using isopropanol. Ergosterol was detected and quantified via high pressure liquid chromatography (HPLC) by measuring absorbance at 282 nm. A Jasco HPLC system (USA) equipped with a Gemini-NX 5 μm C18 250 × 4.6 mm column (Phenomenex, UK) was used. The mobile phase was 100% methanol and the flow rate was set to 1.2 $ml\ min^{-1}$. Ergosterol was converted to fungal biomass using a conversion factor of 5.5 mg ergosterol per gram of fungal mycelium (Gessner and Chauvet, 1993). The results were expressed in mg of fungal biomass per unit of leaf litter AFDM.

2.4.2. Bacterial biomass

For bacterial biomass, one leaf disc of each fixed sample was transferred to a new glass vial filled with 10 ml of pure water previously filtered through 0.2-μm pore size nitrate cellulose membranes (Whatman, Germany). Samples were mixed with a vortex and then sonicated for 15 min at low power (10 W) using an ultrasonic homogenizer (Sonic Ruptor 250, Omni International) to detach bacteria from the leaves. During sonication, samples were kept on ice to minimize cell damage. After appropriate dilution, bacterial suspensions were stained with DAPI (4, 6-diamidino-2-phenylindole hydrochloride; Sigma-Aldrich, Germany) for 5 min in the dark to a final concentration of 2 μg ml^{-1}. Then, the suspensions were filtered through polycarbonate membranes (0.2 μm pore size; Whatman, Germany) and the filters were mounted on a slide between two drops of immersion oil. Bacteria were counted using an epifluorescence microscope (Olympus BX-60, 100× objective and UV excitation/long-pass filter set). From each filter, a minimum of 200 bacterial cells were counted in at least 20 random fields. The bacterial biomass was estimated in terms of carbon at 2.2×10^{-3} g C μm^{-3} (Bratbak and Dundas, 1984) and considering a bacteria cell biovolume in *Populus nigra* of 0.147 μm^3 (Gaudes et al., 2009). The results were expressed as mg of bacterial biomass per unit of leaf litter AFDM.

2.5. DOC release rate

Leaf discs were incubated in 100 ml Erlenmeyer flasks with 50 ml filtered stream water (0.45 μm pore size, Nylon membrane; Millipore, USA) in a shaker (60 rpm) for 48 h at the stream's water temperature. Flasks were covered with perforated aluminium foil to allow air exchange. After 48 h, 30 ml of 0.45-μm filtered water was taken from each microcosm, acidified and stored in pre-combusted vials at 4 °C for DOC determination using a total organic carbon analyser (TOC-V CSH, Shimadzu, Japan). The stream water used in the microcosms was collected from the running water habitat on each sampling date, during which time three 30 ml aliquots were also sampled for initial DOC determination. Obtained DOC release rates corresponded to the net release of DOC (production–consumption) in the water during the incubation time, as corrected using the initial DOC concentration in the stream water at the beginning of the incubation (Baldy et al., 2007). Values were expressed as mg of carbon produced per gram of leaf litter AFDM per day.

2.6. Data analyses

Physicochemical characteristics were compared within aquatic (running waters and isolated pools) and terrestrial (moist and dry sediments) conditions using Student's test.

Leaf litter decomposition rates were calculated assuming an exponential decay. Linear regressions between the ln-transformed proportion of AFDM remaining and time were used to estimate the decomposition rate given by the slope. To compare the slopes of these regressions between habitats, we performed an analysis of covariance (two-way ANCOVA) using the ln-transformed proportion of AFDM remaining as a dependent variable, time as a covariate and habitat as a categorical variable. Subsequent pair-wise comparisons were performed using Tukey's Honest Significant Difference (HSD) test.

Bacterial biomass, the C:N molar ratio, macroinvertebrate abundances and leaf litter DOC release rates were compared among treatments using a two-way analysis of variance (ANOVAs) with time and habitat as categorical variables. For macroinvertebrate abundance and DOC release rates, subsequent pair-wise comparisons were performed using Tukey's HSD test. For the C:N molar ratio and bacterial biomass two samples lost during processing unbalanced the data; therefore, we applied the Tukey–Kramer HSD post-hoc test to these data. To meet assumptions for normality and equality of variances, bacterial biomass data was ln-transformed and macroinvertebrate abundances were $\log_{10} + 1$ transformed. In the case of fungal biomass, the data were $\log_{10} + 1$ transformed and compared between habitats using a one-way ANOVA and Tukey's HSD test.

We used Pearson's correlation to test for potential relationships among variables and a simple linear regression to build predictive models of these relationships.

Before the statistical analysis, the distributional properties of the data were assessed to identify outliers. The Shapiro–Wilk test was applied to assess normality and the Bartlett's test to assess equality of variances. All statistical analyses were conducted using R version 2.15.3 (R Core Team, 2013), with a significance level set at $p < 0.05$ for all tests.

3. Results

3.1. Physical and chemical characteristics of habitats

In the streambed sediments, temperature remained stable at an average 17.9 ± 0.4 °C during the study period, without significant differences between the moist and dry sediments (*t*-test, $t = 0.61$, $p = 0.54$). By contrast, soil moisture differed between these habitats (*t*-test, $t = -5.07$, $p < 0.001$), with an average soil water content of 19.6 ± 2.5% in moist sediments and 4.3 ± 1.7% in dry sediments. In the dry sediments, soil water content reached a minimum value of 0% during the third sampling and a maximum of 13.1% on the last sampling date, which may have been related to a precipitation event (17.3 mm) that occurred just two days before the end of the experiment. In the moist sediments, the maximum moisture level (27.3%) was registered during the second sampling date, when the soil water content across all replicated sites averaged 25.0 ± 1.3% and we found the greatest difference for dry sediments (6.4 ± 3%).

Regarding the aquatic habitats (Table 1), water temperature differed between the running water and isolated pool sites (*t*-test, $t = 4.66$, $p = 0.01$), with slightly higher values in the isolated pools (17.8 ± 0.3 °C) than in the running waters (16.0 ± 0.3 °C). Dissolved oxygen concentrations were lower (*t*-test, $t = -3.0$, $p = 0.04$) in isolated pools (3.4 ± 1.3 mg l^{-1}) than in running waters (7.7 ± 0.5 mg l^{-1}). We found high variability in dissolved oxygen content between pools, with percent saturation ranging between 8% and 58%. No current was found in isolated pools, whereas running water sites had a permanent flow during the experiment. Nutrient levels differed sharply between aquatic habitats. DOC (*t*-test, $t = 25.2$, $p < 0.001$), nitrite (*t*-test, $t = 9.5$, $p < 0.001$), ammonium (*t*-test, $t = 328.1$, $p < 0.001$) and SRP (*t*-test, $t = 29.9$, $p < 0.001$) had significantly higher concentrations in isolated pools than in running waters. On the contrary, DIC (*t*-test, $t = -14.4$, $p < 0.001$), nitrate (*t*-test, $t = -144.9$, $p < 0.001$), chloride (*t*-test, $t = -14.1$, $p < 0.001$), sulphate (*t*-test, $t = -14.3$, $p < 0.001$), sodium (*t*-test, $t = -17.8$, $p < 0.001$) and calcium (*t*-test, $t = -6.0$, $p < 0.001$) concentrations were significantly lower in isolated pools than in running waters.

3.2. Decomposition rates

Decomposition dynamics differed significantly between habitats during the study period (ANCOVA, Time × Habitat, $F_{3,40} = 12.71$, $p < 0.0001$), with a clear distinction between aquatic and terrestrial habitats (Tukey's test, $p < 0.01$; Fig. 1A). After 24 h of incubation, the percentage of mass loss (as AFDM) in running waters was 13.7 ±

Table 1
Physicochemical characteristics of running waters and isolated pools during the study period (mean ± SE; $n = 3$).

	Units	Running waters	Isolated pools
Temperature	°C	16.0 ± 0.3	17.8 ± 0.3
Conductivity	$\mu S\ cm^{-1}$	718 ± 12	450 ± 122
pH		7.6 ± 0.1	7.3 ± 0.1
Dissolved O_2	mg L^{-1}	7.7 ± 0.5	3.4 ± 1.3
O_2 saturation	%	84 ± 6	38 ± 15
Water velocity	m s^{-1}	0.04 ± 0.01	0
DIC	mg C L^{-1}	75.5 ± 0.2	26.2 ± 3.4
DOC	mg C L^{-1}	0.8 ± 0.0	5.1 ± 0.2
Nitrite	mg N L^{-1}	0.02 ± 0.00	0.08 ± 0.01
Nitrate	mg N L^{-1}	6.6 ± 0.0	0.9 ± 0.0
Ammonium	mg N L^{-1}	0.01 ± 0.00	0.24 ± 0.00
SRP	mg P L^{-1}	0.03 ± 0.00	0.18 ± 0.01
Chloride	mg Cl L^{-1}	18.4 ± 0.1	9.5 ± 0.6
Sulphate	mg S L^{-1}	13.1 ± 0.0	3.8 ± 0.6
Sodium	mg Na L^{-1}	12.3 ± 0.0	6.9 ± 0.3
Calcium	mg Ca L^{-1}	83.2 ± 4.8	39.7 ± 5.4

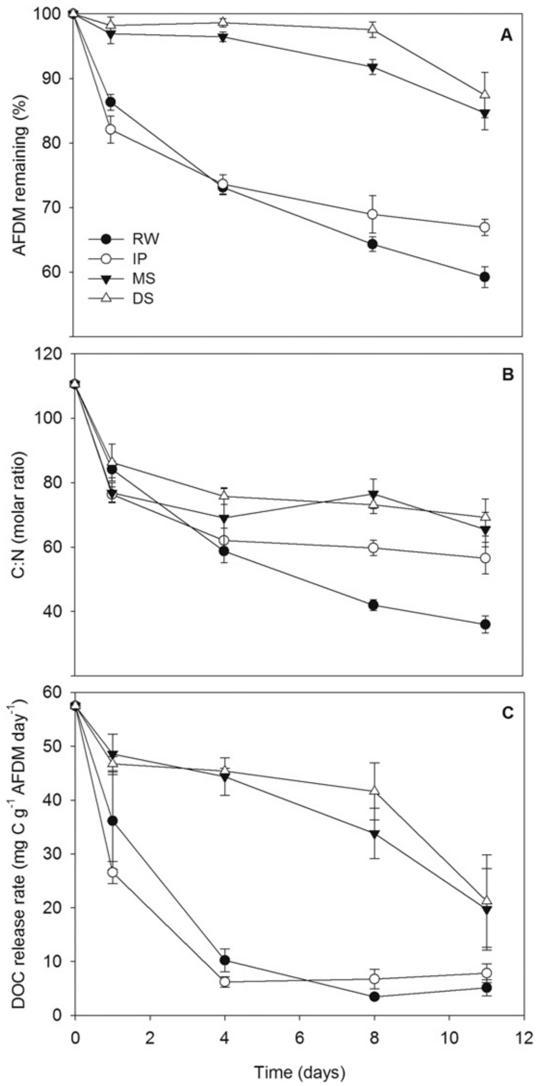


Fig. 1. Percentage of ash-free dry mass (AFDM) remaining (A), C:N molar ratio in leaf litter (B) and DOC release rate (C) from leaf litter in each habitat over time (mean ± SE, $n = 3$): running waters (RW), isolated pools (IP), moist sediments (MS) and dry sediments (DS).

1.2%, and in isolated pools it was 17.9 ± 2.1. By contrast, a mass loss of 3.1 ± 1.5% was measured in moist sediments on the first sampling date, and a mass loss of only 1.8 ± 0.9 was measured in dry sediments. On the following dates, mass loss in the aquatic habitats continued to be more pronounced than in sediments. Moist sediments presented a constant mass loss over time, with a final remaining AFDM percentage of 84.6 ± 2.6%. The mass loss from the dry sediments was practically non-existent during the first 8 days (2.4 ± 1.2% AFDM loss) but increased thereafter until reaching a remaining AFDM percentage of 87.4 ± 3.5%, which was probably related to the precipitation event. Running waters had a slightly higher decomposition rate (0.053 ± 0.003 d^{-1}; $R^2 = 0.95$, $p < 0.001$) than isolated pools (0.044 ± 0.005 d^{-1}, $R^2 = 0.88$, $p < 0.001$), although this difference was not statistically significant. As with aquatic habitats, no significant differences were found in the rates between streambed sediments, despite a higher decomposition rate in the moist (0.013 ± 0.001 d^{-1}, $R^2 = 0.89$, $p < 0.001$) than in the dry sediments (0.009 ± 0.002 d^{-1}, $R^2 = 0.66$, $p < 0.001$).

Taking into account decomposition dynamics across all habitats conforming the temporary section (isolated pools, moist and dry sediments), we obtained a global decomposition rate (0.021 ± 0.002 d^{-1}, $R^2 = 0.95$, $p < 0.001$) lower than that of the permanent section (running waters; 0.053 ± 0.003 d^{-1}, $R^2 = 0.95$, $p < 0.001$).

3.3. Microbial biomass on leaf litter

3.3.1. Fungal biomass

After 11 days of incubation, the amount of fungal biomass colonizing the leaves was significantly different between habitats (ANOVA, Habitat, $F_{3,8} = 7.98$, $p = 0.008$). Running waters presented the highest colonization rates, with an average value of 91.6 ± 21.9 mg of fungal biomass per g^{-1} AFDM, whereas isolated pools had the lowest values (1.5 ± 1.2 mg g^{-1} AFDM). Fungal biomass was higher in moist (15.9 ± 2.4 mg g^{-1} AFDM) than in dry (11.8 ± 6.1 mg g^{-1} AFDM) sediments. Subsequent post-hoc comparisons revealed that fungal colonization was significantly different from running waters only in isolated pools (Tukey's test, $p < 0.05$).

3.3.2. Bacterial biomass

Bacterial biomass on leaf litter varied significantly between habitats over time (ANOVA, Time × Habitat, $F_{6,22} = 8.80$, $p < 0.001$; Fig. 2). Bacterial colonization was much higher in aquatic than in terrestrial habitats (Tukey Kramer's test, $p < 0.001$), with a maximum value of 0.71 ± 0.22 mg g^{-1} AFDM at running waters and a minimum value of 0.02 ± 0.005 mg g^{-1} AFDM in dry sediments after 11 days of incubation. No significant differences in bacterial biomass were found between aquatic habitats during the process; however, bacterial colonization in isolated pools increased faster than in running waters, reaching a maximum value of 0.28 ± 0.03 mg g^{-1} AFDM after 8 days of incubation. In running waters, we found the highest bacterial biomass after 11 days of incubation. Regarding streambed sediments, post-hoc comparisons revealed significant differences in bacterial colonization between moist and dry sediments (Tukey's Kramer test, $p = 0.012$). These differences appeared clearly only after 4 days of incubation, when the bacterial biomass presented in moist sediments was 3 times higher than that in dry sediments. Both habitats had maximum colonization rates on the last sampling date (0.03 ± 0.004 mg g^{-1} AFDM in moist and 0.02 ± 0.005 mg g^{-1} AFDM in dry sediments).

After 11 days of incubation, bacterial biomass in isolated pools represented 12.9% of the total microbial biomass (fungal and bacterial biomass) associated with leaves. This value was 0.8% for running waters, 0.2% for moist sediments and 0.1% for dry sediments.

3.4. Macroinvertebrate abundance

Total macroinvertebrate abundance associated with leaf litter was significantly higher in aquatic than in terrestrial habitats (ANOVA, Habitat, $F_{3,32} = 56.99$, $p < 0.001$; Tukey's test, $p < 0.001$; Fig. 3). Macroinvertebrate

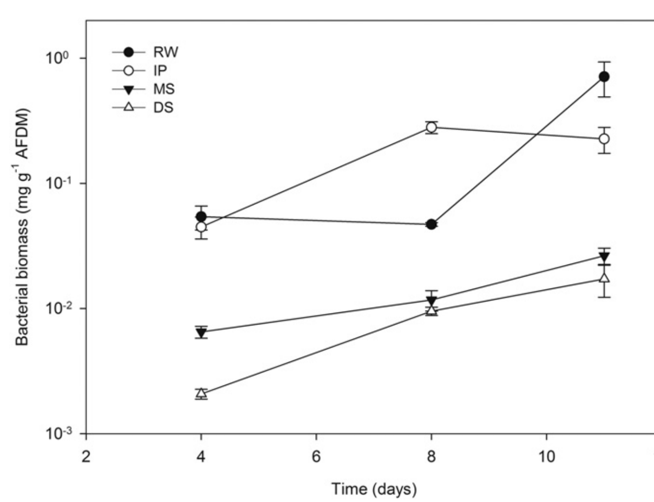


Fig. 2. Bacterial biomass associated with *Populus nigra* leaves in each habitat over time (mean ± SE, $n = 3$): running waters (RW), isolated pools (IP), moist sediments (MS) and dry sediments (DS).

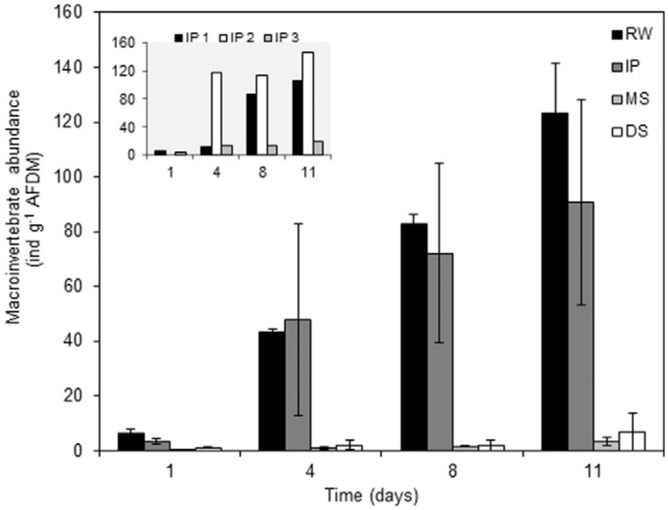


Fig. 3. Total macroinvertebrate abundance in leaf bags over time for all habitat types ($n = 3$, mean $\pm$ SE): running waters (RW), isolated pools (IP), moist sediments (MS) and dry sediments (DS). Insert: Total macroinvertebrate abundance in each isolated pool (IP1, IP2, IP3) at each sampling time (days).

abundance in aquatic habitats increased gradually until the end of the experiment. No significant differences were found in total macroinvertebrate density between isolated pools and running waters, but total abundance varied considerably between pools (Fig. 3, insert), a fact likely related to the marked differences in oxygen availability between sites. Approximately 90% of the macroinvertebrates in isolated pools were scrapers of the genus *Physa*, whereas this proportion was lower in running waters (41%). Shredders accounted for <1% to total macroinvertebrate abundance in both aquatic habitats.

3.5. C:N molar ratio

The elemental composition of the decomposing leaf litter varied significantly between habitats during the study period (ANOVA, Time x Habitat, $F_{9,30} = 2.83$, $p = 0.015$; Fig. 1B). The C:N molar ratio decreased over time in all habitats (ANOVA, Time, $F_{3,30} = 18.63$, $p < 0.001$) compared to the initial value of 110.5 $\pm$ 5.4 found on litter not incubated in the field, a result related to an increase in nitrogen while carbon concentrations remained constant. The lowest values were detected at running water sites (35.9 $\pm$ 2.6) after 11 days of incubation. In this habitat, leaf quality differed significantly from that in dry and moist sediments (Tukey Kramer's test, $p < 0.001$) but not from that in isolated pools (Tukey Kramer's test, $p = 0.076$). Significant differences in the C:N molar ratio were also found between isolated pools and dry sediments (Tukey Kramer's test, $p = 0.002$).

In aquatic habitats, we found a significant negative correlation between the percentage of AFDM lost and the C:N molar ratio (Pearson's correlation, $r = -0.92$, $p < 0.001$), which decreased in a significant linear relationship (linear regression, $R^2 = 0.85$, $p < 0.0001$; Fig. 4A) as decomposition progressed. This correlation was higher in running waters (Pearson's correlation, $r = -0.97$, $p < 0.001$) than in isolated pools (Pearson's correlation, $r = -0.81$, $p < 0.001$) and was not observed in dry or moist sediments (Pearson's correlation, $r = -0.27$, $p = 0.197$; Fig. 4B).

3.6. DOC release rate from litter

DOC release rates from leaf litter differed significantly between habitats over time (ANOVA, Time $\times$ Habitat, $F_{9,32} = 2.70$, $p = 0.018$; Fig. 1C). After 11 days of incubation, all habitats presented lower DOC release rates than the initial value of 57.5 $\pm$ 8.4 mg C g^{-1} AFDM day^{-1} 1 in litter not incubated in the field. However, the decrease in DOC release rates followed different patterns in aquatic and terrestrial habitats (Tukey's test, $p < 0.001$). A more pronounced decrease occurred in aquatic habitats, where the DOC release rate fell to 10.2 $\pm$ 2.2 mg C g^{-1} AFDM day^{-1} in running waters and 6.2 $\pm$ 0.9 mg C g^{-1} AFDM day^{-1} in isolated pools after only 4 days in the field. In terrestrial habitats, we observed a more constant decrease in the DOC release rate over time, without significant differences between moist and dry sediments. After 11 days of incubation, the DOC release rate was 19.7 $\pm$ 7.6 mg C g^{-1} AFDM day^{-1} in moist sediments and 21.2 $\pm$ 8.6 mg C g^{-1} AFDM day^{-1} in dry sediments. In the case of dry sediments, we observed a drastic decrease in the DOC release rate from litter on the last sampling date, which may be related to the precipitation event that occurred two days earlier.

Across all habitats, we found a negative correlation between DOC released rates and the proportion of AFDM lost (Pearson's correlation, $r = -0.89$, $p < 0.001$). This correlation followed a linear relationship with AFDM lost and explains 80% of the variation in DOC release rates (linear regression, $R^2 = 0.80$, $p < 0.001$; Fig. 5). At the same time, the DOC release rates in aquatic habitats correlated positively with the C:N molar ratio (Pearson's correlation, $r = 0.73$, $p < 0.001$). However, this correlation was found to be higher in running waters (Pearson's correlation, $r = 0.85$, $p < 0.001$) than in isolated pools (Pearson's correlation, $r = 0.61$, $p = 0.04$). This correlation was not significant in moist or dry sediments (Pearson's correlation, $r = 0.39$, $p = 0.055$).

4. Discussion

In temporary streams, the decomposition of organic matter tends to be a slower process than in perennial ones (e.g., Herbst and Reice, 1982;

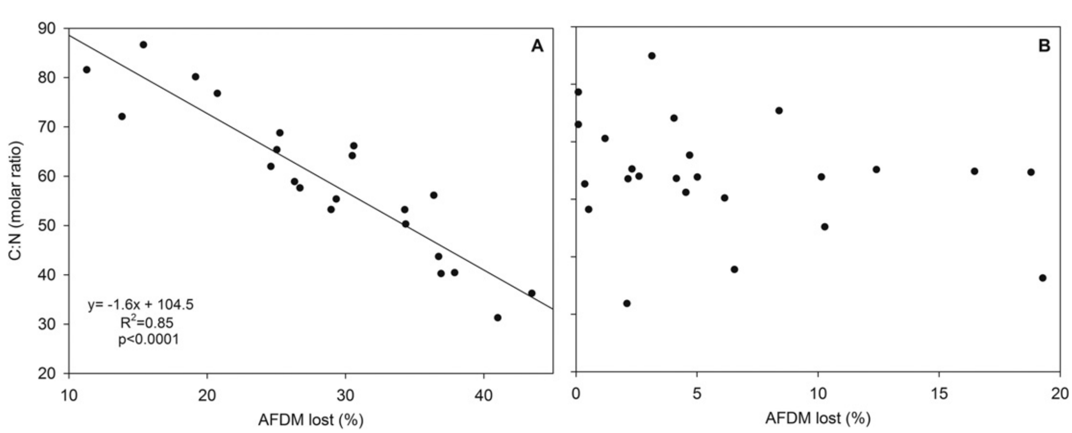


Fig. 4. Relationship between the leaf C:N molar ratio and the proportion of ash-free dry mass (% AFDM) lost in aquatic (A; $n = 22$) and terrestrial (B; $n = 24$) habitats.

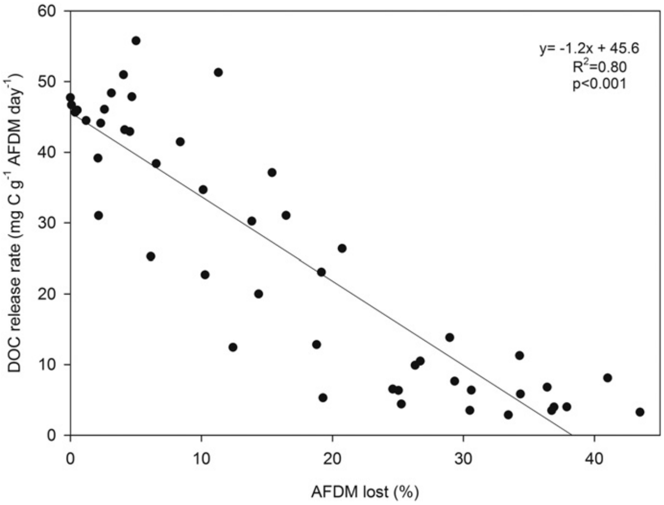


Fig. 5. DOC release rate from leaf litter related to the proportion of ash-free dry mass (% AFDM) lost in all habitats: running waters, isolated pools, moist sediments and dry sediments ($n = 48$).

Richardson, 1990) basically because processing efficiency is reduced during drought events (Maamri et al., 1997; Pinna and Basset, 2004). However, spatial and temporal habitat heterogeneity caused by flow fragmentation during these events creates disparate ecological conditions that may result in a highly heterogeneous decomposition process. To assess this hypothesis, we analysed the initial stages of leaf litter decomposition in different habitats resulting from flow fragmentation. After only 11 days of incubation, we detected widely different decomposition rates among habitats, distinguishing faster rates for leaves exposed to aquatic (isolated pools and running waters) than terrestrial (moist and dry sediments) conditions. These results are consistent with previous studies (Langhans et al., 2008; Datry et al., 2011) and can be primarily attributed to the fact that decomposer communities are negatively affected by emersion (Corti et al., 2011; Foulquier et al., 2015; Martínez et al., 2015). However, we also found differences in factors controlling leaf litter decomposition within aquatic and terrestrial conditions, suggesting a high heterogeneous decomposition process that is not detectable within general (i.e., per condition) decomposition rates.

In aquatic habitats, contrary to our expectations, isolated pools showed similar decomposition rates to running waters. Using *Populus nigra* leaves, Langhans et al. (2008) found an opposing trend, with higher rates in the river channel than in pools after three months of incubation in a floodplain. Along the same lines, Schlief and Mutz (2009) simulated isolated pools using mesocosms and found slower decomposition rates of *Alnus glutinosa* under reduced flow conditions. In these studies, a greater contribution of shredders to litter decomposition in streams than in stagnant waters was a key factor explaining these differences. In our study, however, macroinvertebrate abundance in litter bags was similar among aquatic habitats, and the relative abundance of shredders was insignificant. This lack of shredders in the study reach may be related to the fact that sampling was performed in late summer, when the presence of shredders is practically non-existent in Mediterranean streams (Muñoz, 2003; Sabater et al., 2006). Thus, shredder feeding did not appear to play an important role in leaf litter decomposition in our study. In contrast, our results were in line with Baldy et al. (2002), who found similar decomposition rates for *Populus nigra* at the river channel and in a floodplain pond despite differences in the microbial communities colonizing the leaves. Similarly, we found a much lower fungal biomass in pools than in running waters after only 11 days of incubation. As previous studies have already described (Langhans et al., 2008; Schlief and Mutz, 2009), the reduced presence of fungi in our isolated pools may be attributed to the absence of flow. A decrease in water flow limits fungal colonization because flow stimulates the sporulation process (Webster and Towfik, 1972; Maamri et al., 2001) and supplies a continuous source of fungal spores to detritus (Bärlocher, 1992). Furthermore, reduced flow also limits re-aeration and allows the accumulation of detritus in pools, causing a reduction in oxygen and an increase in leaf leachates that can hinder fungal development in these habitats (Schlief and Mutz, 2007; Medeiros et al., 2009; Canhoto et al., 2013). Similarly, our study pools exhibited high DOC concentrations, and the oxygen concentrations observed therein were lower than in running waters.

Based on our results, bacterial biomass was similar in running water and isolated pool sites, which is in accordance with the results described by Baldy et al. (2002). Physicochemical conditions in pools were likely not so unfavourable to bacteria, as in the case of fungi. For example, Pascoal and Cassio (2004) reported an increase in bacterial production in polluted sites, and Eiler et al. (2003) found that bacterial metabolism was stimulated by large amounts of DOC in batch cultures. Along these lines, a high availability of DOC and other nutrients could drive the rapid bacterial development observed in pools after just 8 days of incubation. This development may also be enhanced by the large abundance of scrapers found in pools because scrapers are able to stimulate microbial growth and activity through their feeding practices (Suberkropp, 1992).

Our results revealed a decrease in the C:N molar ratio in leaf litter during decomposition as a result of a gradual increase in nitrogen that occurred while carbon concentration remained practically constant. Other studies have found a similar pattern (e.g., Gulis and Suberkropp, 2003; Pascoal and Cassio, 2004; Menéndez et al., 2011) and have associated it with the accumulation of microbial biomass on leaves that uptake and immobilize nitrogen from the water column as carbon is mineralized (Melillo et al., 1984; Chauvet, 1987). The mineralized litter carbon is replaced by microbial cells, which explains the small changes observed in carbon concentration (Yoshimura et al., 2010). Along these lines, the mass loss during leaf decomposition was negatively related to the C:N molar ratio in aquatic habitats, suggesting that microbial decomposers played an active role in these habitats. However, a less pronounced decrease in the C:N molar ratio and a lower correlation with mass loss observed in isolated pools than in running waters may indicate that microbial development and activity was constrained in pools, a fact already apparent in the relatively low bacterial biomass observed at the end of the incubation period and in the low presence of fungi found in this habitat. This constraint also suggests that decomposition rates in isolated pools may have been lower than in running waters if a longer incubation time was allowed.

Terrestrial habitats showed litter decomposition rates up to four times slower than in aquatic habitats, as well as a much lower macroinvertebrate and bacterial biomass presence. Similar decomposition rate was recorded in exposed streambed sediments, with slightly faster rates observed in the moist sediments. However, bacterial biomass differed between habitats and reached higher values in leaves exposed in moist than in dry sediments. These differences were larger after four days of incubation coinciding with the highest levels of soil water content registered in the moist sediment sites. Previous studies have reported a positive effect of soil moisture on mass loss (Cortez, 1998; Lee et al., 2014), which has mainly been attributed to the more active role microbial decomposers play under wet conditions (Amalfitano et al., 2008; Manzoni et al., 2012). A decrease in moisture availability results in the physiological stress of microbial communities because it constrains their osmotic regulation and the diffusive transport of solutes in soil (Borken and Matzner, 2009). In contrast, we found similar fungal biomass on leaf litter in moist and dry sediments after 11 days of incubation with values in agreement with Langhans and Tockner (2006). These findings may be related to the fact that fungi are generally more resistant to desiccation than bacteria, likely because their hyphal development facilitates the search for water and nutrients (Yuste et al., 2011; Barnard et al., 2013). Nevertheless, and contrary to aquatic habitats, we did not find any relationship between the C:N molar ratio and mass loss in sediments, indicating the limited role microbial decomposers played in these habitats.

Thus, based on our results, the initial phase of leaf litter decomposition in exposed streambed sediments was primarily driven by abiotic factors, whereas biotic factors were probably not important at the time scale of our study. Steward et al. (2012) reviewed the ecology of dry streambeds and described an increase in the relative importance of abiotic mineralization processes in these systems. Austin and Vivanco (2006) also suggested the limited influence of biotic activity in leaf litter decomposition under semi-arid conditions and noted the relevance of photo-degradation as an important driver of decomposition. Leaves on the sediment surface are exposed to high solar radiation that promotes direct photochemical mineralization and also facilities litter biodegradability (Gallo et al., 2006; Wang et al., 2015; Almagro et al., 2015). Together with this process, the negligible mass loss observed in streambed sediments also could be attributed to the leaching of water-soluble compounds (Langhans et al., 2008). A high moisture level may have enhanced leaching in our study, causing the slightly higher mass loss observed in moist than in dry sediments.

By the action of these biotic and abiotic factors involved in decomposition, a significant part of leaf mass is transformed and released as DOC (Baldy and Gessner, 1997). In our microcosms, DOC release rates obtained at each sampling time represent the integration of all the processes of DOC production and loss from leaves occurring inside each microcosm during the 48 h incubation period. Rates are the net balance between the DOC produced by leaching and microbial degradation of leaves, and the DOC lost via microbial assimilation and physical adsorption (Baldy et al., 2007; Yoshimura et al., 2010). The importance of each of these processes during incubation in each microcosm was influenced by leaf preconditioning within each habitat type; and indeed, we observed clear differences in the DOC release rates obtained from leaves previously incubated under aquatic or terrestrial conditions. Under aquatic conditions, leaching promotes a substantial release of DOC just after immersion that could account for an important decrease (10–30%) in initial mass within the first days (Petersen and Cummins, 1974). As a result of this process, leaves exposed to running waters and isolated pools experienced an important reduction in their DOC release rate within a few days. Then, despite the fact that leaching presumably continued (Gessner et al., 1999), microbial processes likely mediated the DOC dynamics (Fischer et al., 2006) and the balance between DOC production and consumption in the microcosms maintained rates constant over time. By contrast, DOC release rates from leaves exposed to sediments remained high during the first week, suggesting that a small amount of DOC had been previously released or assimilated from leaves in the field. Contrary to the aquatic habitats, leaching under terrestrial conditions in the field was minimal over our timescale (Treplin and Zimmer, 2012), as already shown with the irrelevant decrease in initial leaf mass within the first days. The small differences observed between these rates and the initial DOC release rate obtained from leaves not incubated in the field could be due to an additional DOC release caused by rinsing the leaves with distilled water to remove invertebrates and inorganic particles after sampling. At the last sampling date, however, we observed a decline in the DOC release rate, which coincided with an increase in mass loss occurring in sediments after the precipitation event. This decrease was especially dramatic in dry sediments, in accordance with Dieter et al. (2011), who suggested that leaf desiccation promotes greater leaching losses at first water contact.

Summarizing all these processes, we found a negative relationship between the proportion of leaf mass lost in the field and the DOC release rate obtained in the microcosms across all habitats and times. This relationship evidences a decrease in the capacity to release DOC as leaves decompose, suggesting differences in the potential of leaves as a DOC source during flow fragmentation and, presumably, when flow is re-established. Previous studies have described an increase in DOC concentrations during the rewetting phase (e.g., von Schiller et al., 2015; Vázquez et al., 2015) due to the amount of organic matter retained in the stream bed during drought events. Along the same lines, we detected that the decomposition degree of this organic matter determines its remaining potential as a DOC source, which is higher for leaves exposed in dry streambeds.

5. Conclusions

When leaves fall into a streambed during flow fragmentation, the heterogeneity of habitats governs the differences in factors affecting the decomposition of this litter. Under aquatic conditions, we found that initial phases of decomposition of *Populus nigra* leaves were marked by an intense leaching just after immersion and early microbial colonization, which swiftly began to mineralize the litter. By contrast, under terrestrial conditions leaves were mainly affected by abiotic processes that caused small mass losses. As a result, leaves in aquatic habitats yielded faster decomposition rates than those in exposed streambed sediments. Despite this overall decomposition rate, the environmental heterogeneity within each condition type (aquatic or terrestrial) also implied differences in the decomposition factors affecting leaf litter. These results underline that in temporary streams decomposition is a heterogeneous process both in space and time and is primarily determined by the aquatic or terrestrial conditions that are consequence of the varying duration and frequency of droughts in the basin. The reduced scale of our experiment restricts to generalize about the decomposition process in temporary streams. However, our results contribute with new empirical evidences to build new hypothesis about this process and clearly indicate that it is indispensable to deal with the environmental heterogeneity of temporary streams to better understand their functioning. This heterogeneity also has implications for the utilization of carbon in streams, suggesting a specific carbon cycle during flow fragmentation with potential effects on the rewetting phase that should be considered in the carbon budgets of temporary streams, especially when permanent streams are currently becoming temporary as a result of warming and water abstraction activities.

Acknowledgements

We are grateful to JP. Casas-Ruiz, V. Ferreira, B. Obrador and Ll. Gómez-Gener for their comments on an earlier version of this manuscript. We also thank M. Felip and M. Llorente for their help with determining bacterial biomass and F. Oliva for their statistical advice. This study was funded by the Spanish Ministry of Economics and Competitiveness through project CGL2014-58760-C3-1-R and by the European Union's Seventh Programme under project Globaqua (603629).

References

Acuña, V., Muñoz, I., Giorgi, A., et al., 2005. Drought and post-drought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. J. N. Am. Benthol. Soc. 24, 919–933. http://dx.doi.org/10.1899/04-078.1.

Acuña, V., Giorgi, A., Muñoz, I., Sabater, F., Sabater, S., 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. J. N. Am. Benthol. Soc. 26, 54–69.

Acuña, V., Datry, T., Marshall, J., et al., 2014. Why should we care about temporary waterways ? Science 343, 1080–1082. http://dx.doi.org/10.1126/science.1246666.

Almagro, M., Maestre, F., Martínez-López, J., et al., 2015. Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. Soil Biol. Biochem. 90, 214–223. http://dx.doi.org/10.1016/j.soilbio.2015.08.006.

Amalfitano, S., Fazi, S., Zoppini, A., et al., 2008. Responses of benthic bacteria to experimental drying in sediments from Mediterranean temporary rivers. Microb. Ecol. 55, 270–279. http://dx.doi.org/10.1007/s00248-007-9274-6.

Arthington, A.H., Bernardo, J.M., Ilhéu, M., 2014. Temporary rivers: linking ecohydrology, ecological quality and reconciliation ecology. River Res. Appl. 30, 1209–1215. http://dx.doi.org/10.1002/rra.2831.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555–558. http://dx.doi.org/10.1038/nature05038.

Baldy, V., Gessner, M.O., 1997. Towards a budget of leaf litter decomposition in a first-order woodland stream. C. R. Acad. Sci. Paris Sér. III 320, 747–758. http://dx.doi.org/10.1016/S0764-4469(97)84824-X.

Baldy, V., Chauvet, E., Charcosset, J., Gessner, M., 2002. Microbial dynamics associated with leaves decomposing in the mainsteam and floodplain pond of a large river. Aquat. Microb. Ecol. 28, 25–36. http://dx.doi.org/10.3354/ame028025.

Baldy, V., Gobert, V., Guerold, F., et al., 2007. Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. Freshw. Biol. 52, 1322–1335. http://dx.doi.org/10.1111/j.1365-2427.2007.01768.x.

Bärlocher, F., 1992. Community organization. In: Bärlocher, F. (Ed.), The ecology of aquatic hyphomycetes. Springer-Verlag, Berlin, pp. 38–69 http://dx.doi.org/10.1007/978-3-642-76855-2.

Barnard, R.L., Osborne, C.A., Firestone, M.K., 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. ISME J. 7, 2229–2241. http://dx.doi.org/10.1038/ismej.2013.104.

Bernal, S., von Schiller, D., Sabater, F., Martí, E., 2013. Hydrological extremes modulate nutrient dynamics in Mediterranean climate streams across different spatial scales. Hydrobiologia 719, 31–42.

Bonada, N., Resh, V.H., 2013. Mediterranean-climate streams and rivers: geographically separated but ecologically comparable freshwater systems. Hydrobiologia 719, 1–29. http://dx.doi.org/10.1007/s10750-013-1634-2.

Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob. Chang. Biol. 15, 808–824. http://dx.doi.org/10.1111/j.1365-2486.2008.01681.x.

Boulton, A.J., 1991. Eucalypt leaf decomposition in an intermittent stream in South-Eastern Australia. Hydrobiologia 211, 123–136. http://dx.doi.org/10.1007/BF00037368.

Bratbak, G., Dundas, I., 1984. Bacterial dry matter content and biomass estimations. Appl. Environ. Microbiol. 48, 755–757.

Bruder, A., Chauvet, E., Gessner, M., 2011. Litter diversity, fungal decomposers and litter decomposition under simulated stream intermittency. Funct. Ecol. 25, 1269–1277. http://dx.doi.org/10.1111/j.1365-2435.2011.01903.x.

Bunn, S.E., Thoms, M.C., Hamilton, S.K., Capon, S.J., 2006. Flow variability in dryland rivers: boom, bust and the bits in between. River Res. Appl. 22 (2), 179–186. http://dx.doi.org/10.1002/rra.904.

Canhoto, C., Calapez, R., Gonçalves, A.L., Moreira-Santos, M., 2013. Effects of eucalyptus leachates and oxygen on leaf-litter processing by fungi and stream invertebrates. Freshw. Sci. 32, 411–424. http://dx.doi.org/10.1899/12-062.1.

Casas-Ruiz, J.P., Tittel, J., von Schiller, D., Catalán, N., et al., 2016. Drought-induced discontinuities in the source and degradation of dissolved organic matter in a Mediterranean river. Biogeochemistry 127, 125–139. http://dx.doi.org/10.1007/s10533-015-0173-5.

Chauvet, E., 1987. Changes in the chemical composition of alder, poplar, and willow leaves during decomposition in a river. Hydrobiologia 148, 35–44. http://dx.doi.org/10.1007/BF00018164.

Core Team, R., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna (http://www.R-project.org/).

Cortez, J., 1998. Field decomposition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. Soil Biol. Biochem. 30, 783–793. http://dx.doi.org/10.1016/S0038-0717(97)00163-6.

Corti, R., Datry, T., Drummond, L., Larned, S., 2011. Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river. Aquat. Sci. 73, 535–537. http://dx.doi.org/10.1007/s00027-011-0216-5.

Datry, T., Corti, R., Claret, C., Philippe, M., 2011. Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: the "'drying memory". Aquat. Sci. 73, 471–478. http://dx.doi.org/10.1007/s00027-011-0193-8.

Dieter, D., von Schiller, D., Garcıa-Roger, E., et al., 2011. Preconditioning effects of intermittent stream flow on leaf litter decomposition. Aquat. Sci. 73, 599–609. http://dx.doi.org/10.1007/s00027-011-0231-6.

Eiler, A., Langenheder, S., Bertilsson, S., Tranvik, L.J., 2003. Heterotrophic bacterial growth efficiency and community structure at different natural organic carbon concentrations. Appl. Environ. Microbiol. 69, 3701–3709. http://dx.doi.org/10.1128/AEM.69.7.3701.

Fischer, H., Mille-Lindblom, C., Zwirnmann, E., Tranvik, L.J., 2006. Contribution of fungi and bacteria to the formation of dissolved organic carbon from decaying common reed *Phragmites Australis*. Arch. Hydrobiol. 166, 79–97. http://dx.doi.org/10.1127/0003–9136/2006/0166–0079.

Foulquier, A., Artigas, J., Pesce, S., Datry, T., 2015. Drying responses of microbial litter decomposition and associated fungal and bacterial communities are not affected by emersion frequency. Freshw. Sci. 34 (4), 1233–1244. http://dx.doi.org/10.1086/682060.

Gallo, M.E., Sinsabaugh, R.L., Cabaniss, S.E., 2006. The role of ultraviolet radiation in litter decomposition in arid ecosystems. Appl. Soil Ecol. 34, 82–91. http://dx.doi.org/10.1016/j.apsoil.2005.12.006.

Gaudes, A., Artigas, J., Romaní, A.M., Sabater, S., Muñoz, I., 2009. Contribution of microbial and invertebrate communities to leaf litter colonization in a Mediterranean stream. J. N. Am. Benthol. Soc. 28, 34–43. http://dx.doi.org/10.1899/07-131.1.

Gessner, M.O., 2005. Ergosterol as a measure of fungal biomass. In: Graça, M., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition. A Practical Guide. Springer, The Netherlands, pp. 189–195 http://dx.doi.org/10.1007/1–4020-3466-0_25.

Gessner, M.O., Chauvet, E., 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. Appl. Environ. Microbiol. 59, 502–507.

Gessner, M.O., Chauvet, E., Dobson, M., 1999. A perspective on leaf litter breakdown in streams. Oikos 85, 377–384. http://dx.doi.org/10.2307/3546505.

Gómez-Gener, Ll, Obrador, B., von Schiller, D., Marcé, R., et al., 2015. Hot spots for carbon emissions from Mediterranean fluvial networks during summer drought. Biogeochemistry 125, 409–426. http://dx.doi.org/10.1007/s10533-015-0139-7.

Gulis, V., Suberkropp, K., 2003. Interactions between stream fungi and bacteria associated with decomposing leaf litter at different levels of nutrient availability. Aquat. Microb. Ecol. 30, 149–157.

Herbst, G., Reice, S.R., 1982. Comparative leaf litter decomposition in temporary and permanent streams in semi-arid regions of Israel. J. Arid Environ. 5, 305–318.

Langhans, S., Tockner, K., 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, Northeastern Italy). Ecosyst. Ecol. 147, 501–509. http://dx.doi.org/10.1007/s00442-005-0282-2.

Langhans, S., Tiegs, S., Gessner, M., Tockner, K., 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. Aquat. Sci. 70, 337–346. http://dx.doi.org/10.1007/s00027-008-8062-9.

Larned, S.T., Datry, T., Arscott, D.B., Tockner, K., 2010. Emerging concepts in temporary-river ecology. Freshw. Biol. 55, 717–738. http://dx.doi.org/10.1111/j.1365-2427.2009.02322.x.

Lee, H., Fitzgerald, J., Hewins, D.B., et al., 2014. Soil moisture and soil-litter mixing effects on surface litter decomposition: a controlled environment assessment. Soil Biol. Biochem. 72, 123–132. http://dx.doi.org/10.1016/j.soilbio.2014.01.027.

Leigh, C., Boulton, A.J., Courtwright, J.L., et al., 2015. Ecological research and management of intermittent rivers: an historical review and future directions. Freshw. Biol. http://dx.doi.org/10.1111/fwb.12646.

Maamri, A., Chergui, H., Pattee, E., 1997. Leaf litter processing in a temporary northeastern Moroccan river. Arch. Hydrobiol. 140, 513–531.

Maamri, A., Bärlocher, F., Pattee, E., Chergui, H., 2001. Fungal and bacterial colonisation of *Salix pedicellata* leaves decaying in permanent and intermittent streams in Eastern Morocco. Int. Rev. Hydrobiol. 83, 337–348. http://dx.doi.org/10.1002/1522-2632(200106)86:3<337::AID-IROH337>3.0.CO;2-N.

Manzoni, S., Schimel, J., Porporato, A., 2012. Responses of soil microbial communities to water stress : results from a meta-analysis. Ecology 93, 930–938. http://dx.doi.org/10.1890/11-0026.1.

Martínez, A., Pérez, J., Molinero, J., et al., 2015. Effects of flow scarcity on leaf-litter processing under oceanic climate conditions in calcareous streams. Sci. Total Environ. 503-504, 251–257. http://dx.doi.org/10.1016/j.scitotenv.2014.06.018.

Medeiros, A.O., Pascoal, C., Graça, M.A.S., 2009. Diversity and activity of aquatic fungi under low oxygen conditions. Freshw. Biol. 54, 142–149. http://dx.doi.org/10.1111/j.1365-2427.2008.02101.x.

Melillo, J.M., Naiman, R.J., Aber, J.D., Linkins, A.E., 1984. Factors controlling mass-loss and nitrogen dynamics of plant litter decaying in northern streams. Bull. Mar. Sci. 35, 341–356.

Menéndez, M., Descals, E., Riera, T., Moya, O., 2011. Leaf litter breakdown in Mediterranean streams: effect of dissolved inorganic nutrients. Hydrobiologia 669, 143–155. http://dx.doi.org/10.1007/s10750-011-0657-9.

Meyer, J.L., Wallace, J.B., Eggert, S.L., 1998. Leaf litter as a source of dissolved organic carbon in streams. Ecosystems 1, 240–249. http://dx.doi.org/10.1007/s100219900019.

Muñoz, I., 2003. Macroinvertebrate community structure in an intermittent and a permanent Mediterranean streams (NE Spain). Limnetica 22, 107–116.

Pascoal, C., Cassio, F., 2004. Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. Appl. Environ. Microbiol. 70, 5266–5273. http://dx.doi.org/10.1128/AEM.70.9.5266.

Petersen, R.C., Cummins, K.W., 1974. Leaf processing in a woodland stream. Freshw. Biol. 4, 343–368. http://dx.doi.org/10.1111/j.1365-2427.1974.tb00103.x.

Pinna, M., Basset, A., 2004. Summer drought disturbance on plant detritus decomposition processes in three River Tirso (Sardinia, Italy) sub-basins. Hydrobiologia 522, 311–319. http://dx.doi.org/10.1023/B:HYDR. 0000029984 0.9347 1.b5.

Richardson, W.B., 1990. A comparison of detritus processing between permanent and intermittent headwater streams. J. Freshw. Ecol. 5, 341–357. http://dx.doi.org/10.1080/02705060.1990.9665247.

Richter, B.D., Mathews, R., Harrison, D.L., Wigington, R., 2003. Ecologically sustainable water management: managing river flows for ecological integrity. Ecol. Appl. 13, 206–224. http://dx.doi.org/10.1890/1051–0761(2003)013[0206:ESWMMR]2.0.CO;2.

Riedl, H.L., Marczak, L.B., McLenaghan, N., Hoover, T.M., 2013. The role of stranding and inundation on leaf litter decomposition in headwater streams. Riparian Ecol. Conserv. 1, 3–10. http://dx.doi.org/10.2478/remc-2013-0002.

Sabater, S., Tockner, K., 2010. Effects of hydrologic alterations on the ecological quality of river ecosystems. In: Sabater, S., Barceló, D. (Eds.), Water Scarcity in the Mediterranean. The Handbook of Environmental Chemistry 8, pp. 15–19. http://dx.doi.org/10.1007/698_2009_24.

Sabater, S., Bernal, S., Butturini, A., et al., 2001. Wood and leaf debris input in a Mediterranean stream: the influence of riparian vegetation. Arch. Hydrobiol. 153, 91–102.

Sabater, S., Guasch, H., Muñoz, I., Romaní, A., 2006. Hydrology, light and the use of organic and inorganic materials as structuring factors of biological communities in Mediterranean streams. Limnetica 25, 335–348.

Sanpera-Calbet, I., Acuña, V., Butturini, A., Marcé, R., Muñoz, I., 2015. El Niño Southern oscillation and seasonal drought drive riparian input dynamics in a Mediterranean stream. Limnol. Oceanogr. http://dx.doi.org/10.1002/lno.10211.

Schlief, J., Mutz, M., 2007. Response of aquatic leaf associated microbial communities to elevated leachate DOC: a microcosm study. Int. Rev. Hydrobiol. 92, 146–155. http://dx.doi.org/10.1002/iroh.200510950.

Schlief, J., Mutz, M., 2009. Effect of sudden flow reduction on the decomposition of alder leaves (*Alnusglutinosa* [L.] Gaertn.) in a temperate lowland stream: a mesocosm study. Hydrobiologia 624, 205–217. http://dx.doi.org/10.1007/s10750-008-9694-4.

Schlief, J., Mutz, M., 2011. Leaf decay processes during and after a supra-seasonal hydrological drought in a temperate lowland stream. Int. Rev. Hydrobiol. 96, 633–655. http://dx.doi.org/10.1002/iroh.201111322.

Stanley, E.H., Fisher, S.G., Grimm, N.B., 1997. Ecosystem expansion and contraction in streams. Bioscience 47, 427–435. http://dx.doi.org/10.2307/1313058.

Steward, A.L., von Schiller, D., Tockner, K., et al., 2012. When the river runs dry: human and ecological values of dry riverbeds. Front. Ecol. Environ. 10, 202–209. http://dx.doi.org/10.1890/110136.
Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38, 913–920. http://dx.doi.org/10.1029/TR038i006p00913.
Suberkropp, K., 1992. Interactions with invertebrates. In: Bärlocher, F. (Ed.), The Ecology of Aquatic Hyphomycetes. Springer-Verlag, Berlin, pp. 118–134 http://dx.doi.org/10.1007/978-3-642-76855-2_6.
Tockner, K., Pennetzdorfer, D., Reiner, N., et al., 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshw. Biol. 41, 521–535. http://dx.doi.org/10.1046/j.1365-2427.1999.00399.x.
Treplin, M., Zimmer, M., 2012. Drowned or dry: a cross-habitat comparison of detrital breakdown processes. Ecosystems 15, 477–491. http://dx.doi.org/10.1007/s10021-012-9523-5.
Vázquez, E., Ejarque, E., Ylla, I., et al., 2015. Impact of drying/rewetting cycles on the bioavailability of dissolved organic matter molecular-weight fractions in a Mediterranean stream. Freshw. Sci. 34, 263–275. http://dx.doi.org/10.1086/679616.
von Schiller, D., Acuña, V., Graeber, D., et al., 2011. Contraction, fragmentation and expansion dynamics determine nutrient availability in a Mediterranean forest stream. Aquat. Sci. 73, 485–497. http://dx.doi.org/10.1007/s00027-011-0195-6.
von Schiller, D., Graeber, D., Ribot, M., et al., 2015. Hydrological transitions drive dissolved organic matter quantity and composition in a temporary Mediterranean stream. Biogeochemistry 123, 429–446. http://dx.doi.org/10.1007/s10533-015-0077-4.
Wang, J., Liu, L., Wang, X., Chen, Y., 2015. The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. Glob. Chang. Biol. 21, 2095–2104. http://dx.doi.org/10.1111/gcb.12812.
Webster, J.R., Benfield, E.F., 1986. Vascular plant breakdown in freshwater ecosystems. Annu. Rev. Ecol. Evol. Syst. 17, 567–594. http://dx.doi.org/10.1146/annurev.es.17.110186.003031.
Webster, J.R., Towfik, F.H., 1972. Sporulation of aquatic hyphomycetes in relation to aeration. Trans. Br. Mycol. Soc. 59, 353–364. http://dx.doi.org/10.1016/S0007-1536(72)80117-7.
Ylla, I., Sanpera-Calbet, I., Vázquez, E., et al., 2010. Organic matter availability during pre- and post-drought periods in a Mediterranean stream. Hydrobiologia 657, 217–232. http://dx.doi.org/10.1007/s10750-010-0193-z.
Yoshimura, C., Fujii, M., Omura, T., Tockner, K., 2010. Instream release of dissolved organic matter from coarse and fine particulate organic matter of different origins. Biogeochemistry 100, 151–165. http://dx.doi.org/10.1007/s10533-010-9412-y.
Yuste, J.C., Peñuelas, J., Estiarte, M., et al., 2011. Drought-resistant fungi control soil organic matter decomposition and its response to temperature. Glob. Chang. Biol. 17, 1475–1486. http://dx.doi.org/10.1111/j.1365-2486.2010.02300.x.