Annual patterns of litter decomposition in the stream channel and riparian area of an intermittent stream

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Abstract

Intermittent streams, dominant in arid and semi-arid regions, are suggested to be more representative of the global river network than perennial rivers. Even so, the impacts of constant changes in hydrological regime on the functioning of these streams and riparian areas remain to be elucidated. In this study, two native deciduous litter species were used to compare microbial-decomposition patterns between the channel of an intermittent stream and its riparian area over one year. Overall, the stream channel presented higher decomposition rates and fungal biomass than the riparian area, for both litter species. Despite a prolonged absence of streambed surface water (254 days), differences in hydrological conditions in the wetter seasons (autumn and winter) led to lingering effects, shaping and differentiating decomposition dynamics in both zones throughout the whole hydrological cycle. As the present results highlight the importance of the "hydrological imprint" for the leaves degradation process, long term studies seem to be advisable over short-term ones to better understand the functioning of intermittent streams.

Key-words: leaf processing, microbial activity, streambed, riparian floor, hydrological regime

Introduction

Intermittent streams designate watercourses that cease to flow for some time throughout the year in response to fluctuating hydrological cycles (Skoulikidis et al. 2017). Despite their high (>50%) representativeness in the global river network (Steward et al. 2012; Datry et al. 2014) these streams have historically attracted far less attention than their perennial counterparts. A bias of interest occurred, nonetheless, in the last decade in the face of climate changes and increased water demands, both concurring to regime alterations from perennial to temporary conditions. The growing proportion and geographical expansion of intermittent streams, even out of their dominant arid and semi-arid areas of occurrence (Schneider et al. 2017), presently strengthens the urgency of understanding their still poorly characterized ecological processes and services provided to humans (Datry et al. 2018).

The decomposition of dead organic matter is a key ecosystem process that plays a fundamental role in carbon and nutrient cycling globally (Raymond et al. 2013), since up to 90% of global terrestrial plant production escapes herbivory and enters the detrital pool (Cebrian 1999). In forested streams, where the food web is mainly based on the leaf litter inputs from surrounding ecosystems (Wallace et al. 1997), the water stimulates leaching of leaf soluble compounds (Gessner et al. 1999) and enhances the mechanical fragmentation of detrital material due to physical abrasion (Ferreira et al. 2006). This boosts the decomposer activity of microbial assemblages (Mora-Gómez et al. 2018; Niyogi et al. 2020) and invertebrate detritivores (Martínez et al. 2015; Abril et al. 2016). Therefore, ecosystems such as perennial streams, are more efficient in catabolizing detrital material than surrounding terrestrial ecosystems (Hutchens and Wallace 2002) or than intermittent streams due to the more or less elongated presence of the dry periods that characterize these systems (Pinna and Basset 2004; Datry et al. 2011; Martínez et al. 2015).

As intermittent streams dry out, streambeds becomes “terrestrialized” by acquiring structural and functional features of the nearby soils (Arce et al. 2019), the similarity likely depending on the duration of the dry phase and inundation frequency (Harms and Grimm 2012; Mori et al. 2017). Whether such convergence of conditions directs similar decomposition dynamics is largely unknown. A single study (Lohse et al. 2020), to our knowledge, compared microbial-mediated decomposition of leaves incubated in the streambed of an intermittent stream and its riparian floor with results suggesting divergent patterns ruled by water presence (rather than flow) in the streambed during the hydrological period. In fact, the effects of drought on leaf processing has consequences extending beyond the water scarcity period (Datry et al. 2011; Martínez et al. 2015). This “drought legacy” effect (Mora-Gómez et al. 2020) has been attributed to an alteration of the invertebrate community density and richness rather than to the microbial compartment (Acuña et al. 2005; Corti et al. 2011), since decomposers may resist to desiccation (Gonçalves et al. 2019) and persist in moist substrata (Sridhar and Bärlocher 1993) being able recover their activity when flow resumes (Langhans and Tockner 2006; Bruder et al. 2011; Gonçalves et al. 2019).

The main goal of this study was to compare leaf litter decomposition patterns, mediated by microbial activity, in the channel and its riparian area of an intermittent stream (running dry for 254 days) over one year. For this, leaf litter of two native deciduous tree species - *Castanea sativa* Mill. (chestnut) and *Quercus robur* L. (oak) - were used. We hypothesize faster decomposition rates and higher fungal biomass associated with leaf material conditioned in the stream channel *vs*. riparian area; differences will be, mainly related with the presence of water-- in the channel providing lotic, lentic and/or moist conditions to the incubating leaves.

Materials and methods

Study site and procedures

The study was conducted in a low-order intermittent stream and its riparian area located in Lousã Mountain (central Portugal; 40°03'38.0"N 8°12'26.9"W). The stream watershed is covered mainly by a mixed deciduous forest dominated by *C. sativa* and *Q. robur* . This area is located in the transitional area between Atlantic and Mediterranean climates, with hot and dry summers, and mild and rainy winters (European Environmental Agency 2002).

During the study period, temperature in the stream channel and riparian zone was continuously measured (every hour) using temperature data loggers (Hobo Pendant Datalogger UA-001-08; Onset Computer Corp., Cape Cod, MA, U.S.A.). Average monthly precipitation ranged from 1.3 mm in August 2018 to 286.7 mm in March 2018 (Fig. 1; data from the nearest meteorological station located in Santo António da Neve, Lousã). Stream flow condition was checked every two days by a remote-controlled photographic camera (GSM Digital Trail Camera HC-300M) – water flow was observed during 33 days, isolated pools during 78 days, and no superficial water was observed in the stream channel for the remaining 254 days of the year (Fig. 1). The riparian area was never flooded.

Leaves of the native species chestnut (*C. sativa*) and oak (*Q. robur*) were collected just after natural abscission, air-dried at room temperature and stored in the dark until use. Leaves of each species (4 ± 0.15 g) were enclosed in 96 fine mesh bags (10 x 12 cm, 0.5 mm mesh). An additional group of six samples per leaf species were oven-dried (60 ºC, 48 h), weighed, ashed (500 ºC, 4 h) and reweighed to estimate initial ash free dry mass (AFDM) in each bag. On the start of autumn 2017, half of the bags per species was randomly placed in the stream channel, and the other half was placed in the adjacent riparian zone. After 90, 180, 270 and 360 days of incubation, corresponding to seasonal periods,12 bags per location and species were randomly retrieved, placed in individual zip lock bags, and transported to the laboratory in a cooler for subsequent determinations. In the laboratory, leaf material from each bag was gently rinsed with distilled water through a 500 µm sieve to remove sediments. Then, five leaf discs were punched out with a cork borer (10 mm Ø) from six bags for each species, zone and sampling date to determine fungal biomass (see below). The remaining leaf material was oven-dried (60 ºC, 48 h), weighed, ashed (500 ºC, 4 h) and reweighed to obtain AFDM remaining (AFDMr).

For fungal biomass determination, punched discs were freeze-dried for 24 h (lyophilizer CHRIST, ALPHA 1-2 / LD Plus, Osterode am Harz, Germany) and weighed. Ergosterol was extracted by microwave exposure in methanol, separated by pentane (Canhoto et al. 2013) and quantified by high performance liquid chromatography (HPLC; Shimadzu Prominence UFLC, Kyoto, Japan) using a HPLC C18 column (Mediterranea sea18, 250 x 4.6 mm, 5 µm particle size; Teknokroma). Ergosterol concentration was converted into fungal biomass (5.5 µg ergosterol per mg fungal dry mass; Gessner and Chauvet 1993). Results were expressed as mg fungal biomass g^{-1} AFDMr.

Data treatment

Decomposition rates were estimated by the negative exponential model ($M_t = M_0 \times e^{-kt}$) where M_t is the remaining mass in terms of percentage at t time, and k is the decomposition rate. Degree-days were used rather than time in order to standardize the rates in view of the temperature differences among zones (Fig. 1). Decomposition rates from stream channel and riparian zone were compared independently for each leaf species by a one-way ANCOVA (fixed factor: incubation zone; covariate: degree-days). Differences in fungal biomass were tested also independently for each species by a two-way ANOVA (fixed factors: zone and sampling date) followed by Tukey's test.

Whenever necessary, data were log 10 (x+1) transformed to fulfill requirements for parametric analyses (normality and homogeneity of variances). Results of statistical analyses were considered significant when $p < 0.05$ and were analyzed with R statistical software (version 3.2.5; R Development Core Team 2016).

Results

After the incubation period, AFDMr of chestnut was 51.3 ± 3.4 % in the stream channel and 61.8 ± 2.0 % in the riparian zone, and that of oak was 57.1 ± 1.7 % in the channel, and 78.7 ± 1.6 % in the riparian zone. The decomposition dynamics of the two species showed a slowing-down during the last phase of the incubation period (coinciding with summer season) in the riparian zone (Fig. 2). Decomposition rates were higher in the stream channel than in the riparian zone for both chestnut ($F_{1,67} = 5.31$, $p = 0.024$) and oak ($F_{1,67} = 9.27$, $p = 0.003$; Fig. 2).

Fungal biomass associated with chestnut leaf litter ranged from 27.7 ± 4.0 mg g^{-1} AFDM in the riparian zone after 90 days of incubation, to 184.7 ± 14.4 mg g^{-1} AFDM in the stream channel after 180 days incubation (Fig. 3). Here, fungal biomass peaked after 180 days incubation (end of Winter), maintained this value until 270 days (end of Spring), and then decreased drastically at 360 days (end of summer) incubation. Meanwhile, in the riparian zone, fungal biomass accrual was slower, peaking clearly after 270 days (end of Spring) incubation; a clear decrease in chestnut leaf associated fungal biomass was observed by the end of the summer period (365 days incubation) (Fig. 3). Overall, fungal biomass was greater in the stream channel than in the riparian zone ($F_{1,40} = 49.40$, $p < 0.001$), except in the last sampling date (i.e., end of summer), where the leaf litter material from the two zones presented similar values (Tukey test $p = 0.996$, Fig. 3).

The maximum (109.1 ± 17.2 mg g^{-1} AFDM) and minimum (17.6 ± 4.7 mg g^{-1} AFDM) values of fungal biomass associated with oak leaves were registered in the stream channel after 270 and 360 days of incubation, respectively. In both incubation zones, fungal biomass progressively reached the peak after 270 days, decreasing at the last sampling date (Fig. 3). Although oak leaf litter from stream channel generally presented a higher fungal biomass than leaf litter incubated in the riparian zone ($F_{1,40} = 7.60$, $p = 0.009$), values were not different between incubation zones after 270 and 360 days incubation (Tukey test $p = 0.945$, and $p = 0.999$ respectively; Fig. 3).

Discussion

In this study we compared the dynamics of microbial-mediated decomposition of oak and chestnut leaf litter, throughout the year, in two zones: channel and *riparia.* As expected, environmental conditions were different between zones, inducing more accentuated mass loss in the channel, particularly evident in the less recalcitrant leaf (i.e. chestnut). Despite the lengthy (254 days) absence of water observed at the channel surface, differences in hydrological conditions between zones in the wetter seasons (autumn and winter) seem to cascade and shape decomposition dynamics for both leaf species across all seasons. The importance of an "hydraulic imprint" promoted by an even reduced water presence (rather than stream flow) in the stream channel, was also recognized by (Lohse et al. 2020) when comparing microbial decomposition rates of oak leaf litter on the channel *vs*. riparian and upland areas under distinct climatic conditions.

In our study, leaves incubated in the stream channel were stochastically subjected to flowing water, pools (originated from the loss of the longitudinal surface-water connectivity) and a moist substratum, which seem to have concurred to stimulate fungal biomass accrual and leaf decomposition. Flow and turbulence are important disruptive physical forces to leaf material in streams (Ferreira et al. 2006) and drivers of leaf degradation through stimulating effects on aquatic hyphomycetes' conidial production, leaf fungal imprint and colonization (Maamri et al. 2001; Kuehn 2016; Arias-Real et al. 2018). On the other hand, aquatic fungi have been referred to be able to remain active in lentic and moist organic (i.e. leaf litter) and inorganic (i.e. sediments) environments (Baldy et al. 2002; Chauvet et al. 2016; Gonçalves et al. 2019). It is also noteworthy that, along with streambed microhabitats, fine mesh bags, used in our experimental design, may have facilitated the retention of humidity within the contained leaves – refuge habitats (Romaní et al. 2017). Such water holding capacity may have favored mycelial viability, a rapid re-activation of the microbial metabolism upon flow resumption, and a potentially elongated microbial-mediated degradation in emerged leaves. Physical disruption, promoted by wet-dry-rewet cycles (Dieter et al. 2011; Gonçalves et al. 2016; von Schiller et al. 2017), may also promote leaf mesophyll accessibility and inner protection to decomposers, facilitating their activity beyond immersion periods (Bruder et al. 2011; Arroita et al. 2018).

Fungal biomass dynamics and concentration differed among the stream channel and riparian area; such differences were particularly evident in the case of chestnut. This may be the result of the friability and high nutritious quality of this leaf species, that facilitates its processing by fungi, namely aquatic hyphomycetes (Lecerf and Chauvet 2008; Bastias et al. 2018; Jabiol et al. 2019). Oak recalcitrance, namely its higher toughness – expression of leaf structural polysaccharides concentration and cuticular layer –, likely limited the chemical (i.e. leaching) and mechanical effects of flow on leaf integrity. While affecting microbial conditioning, this also concurred to closer (although distinct, $p < 0.05$) patterns of biomass accrual (and thereby mass loss) between zones, until spring.

It is noteworthy that fungal biomass associated with both leaf species peaked or maintained maximum levels on spring, in both environments. Along with lingering hydrological effects from the wet/colder seasons, mild temperatures in both zones (around 12 ºC) may have contributed to the stimulation of mycelial growth of mixed aquatic and terrestrial fungal assemblages (LeRoy et al. 2011), and leaf degradation, under dryer springtime conditions. In fact, previous studies point to optimal enzymatic activity around 10 ºC, for aquatic (Ferreira and Chauvet 2011; Gonçalves et al. 2015), and between 10-25 ºC for terrestrial (Graça and Ferreira 1995; Razavi et al. 2017) fungi. In addition, we cannot rule out the possibility that a stimulation of algal biomass production due to increased light in both areas, may have had a priming effect on leaf-associated fungi (Franken et al. 2005; Kuehn et al. 2014). Globally, results suggest that, for both litter species, annual decomposition in either the channel or the riparian area will result in different litter residual quality, endowed with a similar fungal biomass concentration.

Changes in fungal community composition are known to occur concomitantly with leaf degradation/changes in quality (Moorhead and Sinsabaugh 2006; Bhatnagar et al. 2018; Gionchetta et al. 2020; Mora-Gómez et al. 2020) or as a response to variations in environmental conditions (Kohl et al. 2020). Such changes in fungal assemblages may result in higher biomass evaluations due to species-specific ergosterol concentrations (proxy of fungal biomass; (Gessner and Chauvet 1993; Cornut et al. 2015) and/or species physiological alterations, involving ergosterol accumulation, as a response to desiccation in the warmer seasons (Dupont et al. 2012). This plausible difference in fungal assemblages' composition could contribute not only to higher (chestnut)/highest (oak) Spring biomass values, but also to marked differences in mass loss, among zones, during summer. During this season, a sharp converging decrease in fungal biomass observed in both leaf species was translated into a stabilization of leaves' mass loss in the terrestrial zone while accentuating, particularly on oak leaves, the mass loss in the channel. It seems likely that the remaining leaf material, particularly oak (remaining mass ~60%), may have suffered an increasing degradative effect promoted by photodegradation and photopriming (Brandt et al. 2010; Pieristè et al. 2019). No information was gathered in our study on bacteria or prokaryotic microorganisms, but both groups may also profit from less severe competition with aquatic fungi under non-flowing conditions and higher temperature, contributing to leaf litter decomposition (Romaní et al. 2017).

The present study elucidates that, despite zonal differences between the decomposition dynamics of each of the two used leaf species, the capacity of intermittent streams' channel to catabolize dead organic matter exceeds that of its riparian area. Differences may even occur when the former acquires terrestrial-like features as a consequence of surface water absence during an elongated period of the year (~70%). Considering the present results, and the importance of the “hydrological imprint” for the leaves degradation process, particularly in the channel, long term studies seem to be advisable over short-term approaches to a better understanding of the functioning of and management intermittent streams.

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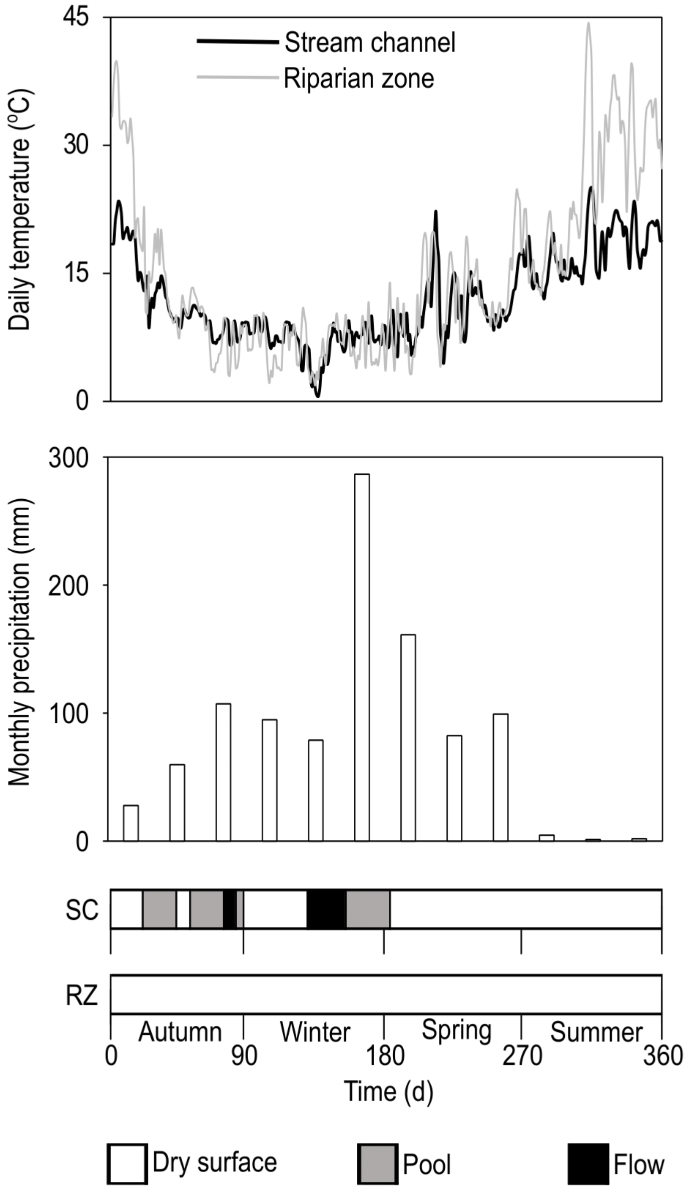

Fig. 1 Daily temperature, monthly precipitation and distribution of dry surface, pool or flow conditions in the stream channel (SC) and riparian zone (RZ) along the incubation period.

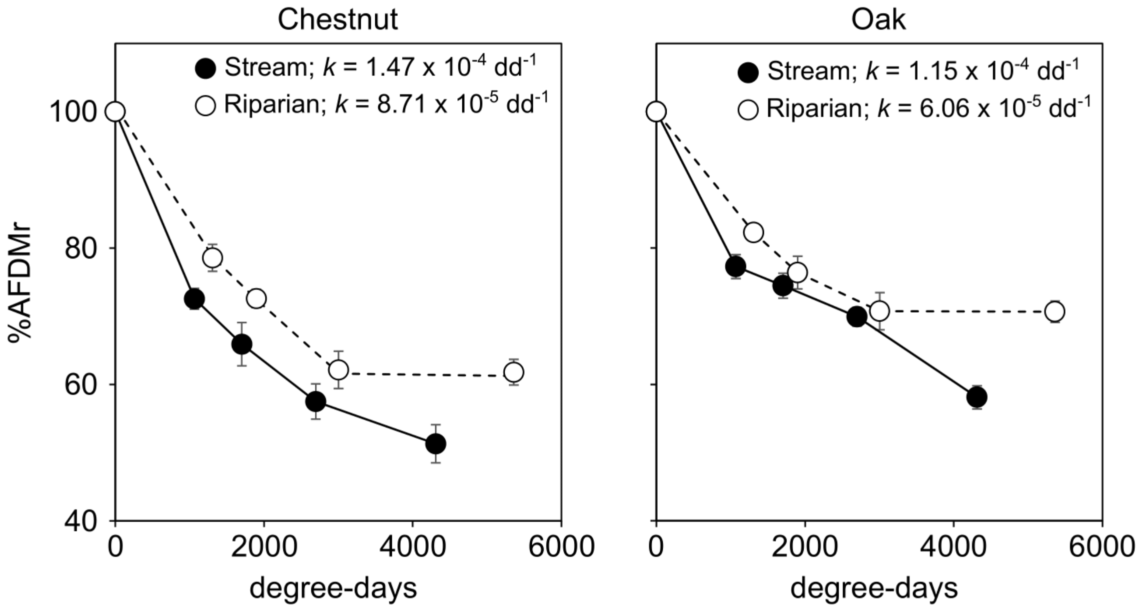

Fig. 2 Percentage of remaining ash free dry mass (%AFDMr) in relation to degree-days of decomposing leaves (mean ± SE) and decomposition rate (*k*) of chestnut and oak in the stream channel and riparian zone.

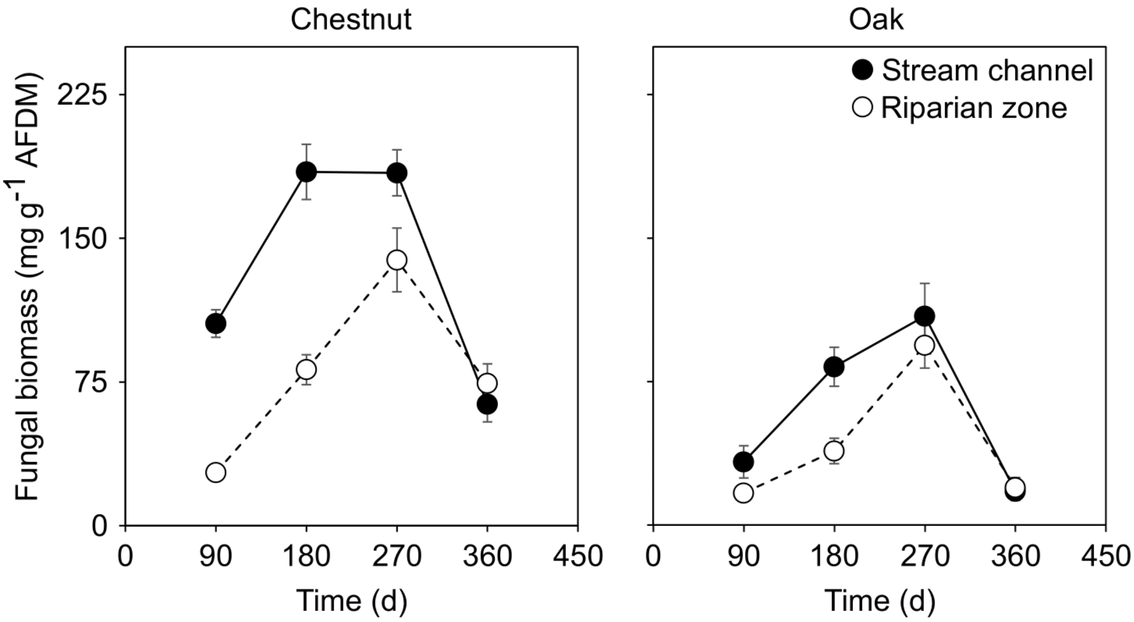

Fig. 3 Fungal biomass (mean ± SE) along the decomposition process on chestnut and oak in the stream channel and riparian zone.