

# Online Research @ Cardiff

This is an Open Access document downloaded from ORCA, Cardiff University's institutional repository: <https://orca.cardiff.ac.uk/138715/>

This is the author's version of a work that was submitted to / accepted for publication.

Citation for final published version:

Simoes, Sara, Martinez, Aingeru, Goncalves, Ana Lucia, Capela, Nuno, Alves, Joana, Alves da Silva, Antonio, Jones, Thomas Hefin, Sousa, Jose Paulo and Canhoto, Cristina 2021. Annual patterns of litter decomposition in the stream channel and riparian area of an intermittent stream. *Aquatic Ecology* 55 , pp. 519-526. 10.1007/s10452-021-09841-w file

Publishers page: <http://dx.doi.org/10.1007/s10452-021-09841-w>  
<<http://dx.doi.org/10.1007/s10452-021-09841-w>>

Please note:

Changes made as a result of publishing processes such as copy-editing, formatting and page numbers may not be reflected in this version. For the definitive version of this publication, please refer to the published source. You are advised to consult the publisher's version if you wish to cite this paper.

This version is being made available in accordance with publisher policies.

See

<http://orca.cf.ac.uk/policies.html> for usage policies. Copyright and moral rights for publications made available in ORCA are retained by the copyright holders.



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

3 Sara Simões<sup>1</sup>, Aingeru Martínez<sup>1\*</sup>, Ana Lúcia Gonçalves<sup>1</sup>, Nuno Capela<sup>1</sup>, Joana Alves<sup>1</sup>, António  
4 Alves da Silva<sup>1</sup>, Thomas Hefin Jones<sup>2</sup>, José Paulo Sousa<sup>1</sup>, Cristina Canhoto<sup>1</sup>

5 <sup>1</sup> *Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada*  
6 *Martim de Freitas, 3000-456 Coimbra, Portugal*

7 <sup>2</sup> *Cardiff School of Biosciences, Cardiff University, Wales, United Kingdom*

8

9 \* Corresponding author: Aingeru Martínez, Centre for Functional Ecology, Department of Life  
10 Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal;

11 email: [aingerumargom@gmail.com](mailto:aingerumargom@gmail.com)

12

13 **Abstract**

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

26

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

28

## 29 **Introduction**

30 Intermittent streams designate watercourses that cease to flow for some time throughout  
31 the year in response to fluctuating hydrological cycles (Skoulikidis et al. 2017). Despite their high  
32 (>50%) representativeness in the global river network (Steward et al. 2012; Datry et al. 2014)  
33 these streams have historically attracted far less attention than their perennial counterparts. A bias  
34 of interest occurred, nonetheless, in the last decade in the face of climate changes and increased  
35 water demands, both concurring to regime alterations from perennial to temporary conditions.  
36 The growing proportion and geographical expansion of intermittent streams, even out of their  
37 dominant arid and semi-arid areas of occurrence (Schneider et al. 2017), presently strengthens the  
38 urgency of understanding their still poorly characterized ecological processes and services  
39 provided to humans (Datry et al. 2018).

40 The decomposition of dead organic matter is a key ecosystem process that plays a  
41 fundamental role in carbon and nutrient cycling globally (Raymond et al. 2013), since up to 90%  
42 of global terrestrial plant production escapes herbivory and enters the detrital pool (Cebrian 1999).  
43 In forested streams, where the food web is mainly based on the leaf litter inputs from surrounding  
44 ecosystems (Wallace et al. 1997), the water stimulates leaching of leaf soluble compounds  
45 (Gessner et al. 1999) and enhances the mechanical fragmentation of detrital material due to  
46 physical abrasion (Ferreira et al. 2006). This boosts the decomposer activity of microbial  
47 assemblages (Mora-Gómez et al. 2018; Niyogi et al. 2020) and invertebrate detritivores (Martínez  
48 et al. 2015; Abril et al. 2016). Therefore, ecosystems such as perennial streams, are more efficient  
49 in catabolizing detrital material than surrounding terrestrial ecosystems (Hutchens and Wallace  
50 2002) or than intermittent streams due to the more or less elongated presence of the dry periods  
51 that characterize these systems (Pinna and Basset 2004; Datry et al. 2011; Martínez et al. 2015).

52 As intermittent streams dry out, streambeds becomes “terrestrialized” by acquiring  
53 structural and functional features of the nearby soils (Arce et al. 2019), the similarity likely  
54 depending on the duration of the dry phase and inundation frequency (Harms and Grimm 2012;  
55 Mori et al. 2017). Whether such convergence of conditions directs similar decomposition  
56 dynamics is largely unknown. A single study (Lohse et al. 2020), to our knowledge, compared

57 microbial-mediated decomposition of leaves incubated in the streambed of an intermittent stream  
58 and its riparian floor with results suggesting divergent patterns ruled by water presence (rather  
59 than flow) in the streambed during the hydrological period. In fact, the effects of drought on leaf  
60 processing has consequences extending beyond the water scarcity period (Datry et al. 2011;  
61 Martínez et al. 2015). This “drought legacy” effect (Mora-Gómez et al. 2020) has been attributed  
62 to an alteration of the invertebrate community density and richness rather than to the microbial  
63 compartment (Acuña et al. 2005; Corti et al. 2011), since decomposers may resist to desiccation  
64 (Gonçalves et al. 2019) and persist in moist substrata (Sridhar and Bärlocher 1993) being able  
65 recover their activity when flow resumes (Langhans and Tockner 2006; Bruder et al. 2011;  
66 Gonçalves et al. 2019).

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

74

## 75 **Materials and methods**

### 76 *Study site and procedures*

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

82 During the study period, temperature in the stream channel and riparian zone was  
83 continuously measured (every hour) using temperature data loggers (Hobo Pendant Datalogger  
84 UA-001-08; Onset Computer Corp., Cape Cod, MA, U.S.A.). Average monthly precipitation

85 ranged from 1.3 mm in August 2018 to 286.7 mm in March 2018 (Fig. 1; data from the nearest  
86 meteorological station located in Santo António da Neve, Lousã). Stream flow condition was  
87 checked every two days by a remote-controlled photographic camera (GSM Digital Trail Camera  
88 HC-300M) – water flow was observed during 33 days, isolated pools during 78 days, and no  
89 superficial water was observed in the stream channel for the remaining 254 days of the year (Fig.  
90 1). The riparian area was never flooded.

91 Leaves of the native species chestnut (*C. sativa*) and oak (*Q. robur*) were collected just  
92 after natural abscission, air-dried at room temperature and stored in the dark until use. Leaves of  
93 each species ( $4 \pm 0.15$  g) were enclosed in 96 fine mesh bags (10 x 12 cm, 0.5 mm mesh). An  
94 additional group of six samples per leaf species were oven-dried (60 °C, 48 h), weighed, ashed  
95 (500 °C, 4 h) and reweighed to estimate initial ash free dry mass (AFDM) in each bag. On the  
96 start of autumn 2017, half of the bags per species was randomly placed in the stream channel, and  
97 the other half was placed in the adjacent riparian zone. After 90, 180, 270 and 360 days of  
98 incubation, corresponding to seasonal periods, 12 bags per location and species were randomly  
99 retrieved, placed in individual zip lock bags, and transported to the laboratory in a cooler for  
100 subsequent determinations. In the laboratory, leaf material from each bag was gently rinsed with  
101 distilled water through a 500 µm sieve to remove sediments. Then, five leaf discs were punched  
102 out with a cork borer (10 mm Ø) from six bags for each species, zone and sampling date to  
103 determine fungal biomass (see below). The remaining leaf material was oven-dried (60 °C, 48 h),  
104 weighed, ashed (500 °C, 4 h) and reweighed to obtain AFDM remaining (AFDMr).

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

113

#### 114 *Data treatment*

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

123           Whenever necessary, data were  $\log_{10}(x+1)$  transformed to fulfill requirements for  
124 parametric analyses (normality and homogeneity of variances). Results of statistical analyses  
125 were considered significant when  $p < 0.05$  and were analyzed with R statistical software (version  
126 3.2.5; R Development Core Team 2016).

127

#### 128 **Results**

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

135           Fungal biomass associated with chestnut leaf litter ranged from  $27.7 \pm 4.0 \text{ mg g}^{-1}$  AFDM  
136 in the riparian zone after 90 days of incubation, to  $184.7 \pm 14.4 \text{ mg g}^{-1}$  AFDM in the stream  
137 channel after 180 days incubation (Fig. 3). Here, fungal biomass peaked after 180 days incubation  
138 (end of Winter), maintained this value until 270 days (end of Spring), and then decreased  
139 drastically at 360 days (end of summer) incubation. Meanwhile, in the riparian zone, fungal  
140 biomass accrual was slower, peaking clearly after 270 days (end of Spring) incubation; a clear

141 decrease in chestnut leaf associated fungal biomass was observed by the end of the summer period  
142 (365 days incubation) (Fig. 3). Overall, fungal biomass was greater in the stream channel than in  
143 the riparian zone ( $F_{1,40} = 49.40$ ,  $p < 0.001$ ), except in the last sampling date (i.e., end of summer),  
144 where the leaf litter material from the two zones presented similar values (Tukey test  $p = 0.996$ ,  
145 Fig. 3).

146 The maximum ( $109.1 \pm 17.2 \text{ mg g}^{-1} \text{ AFDM}$ ) and minimum ( $17.6 \pm 4.7 \text{ mg g}^{-1} \text{ AFDM}$ )  
147 values of fungal biomass associated with oak leaves were registered in the stream channel after  
148 270 and 360 days of incubation, respectively. In both incubation zones, fungal biomass  
149 progressively reached the peak after 270 days, decreasing at the last sampling date (Fig. 3).  
150 Although oak leaf litter from stream channel generally presented a higher fungal biomass than  
151 leaf litter incubated in the riparian zone ( $F_{1,40} = 7.60$ ,  $p = 0.009$ ), values were not different between  
152 incubation zones after 270 and 360 days incubation (Tukey test  $p = 0.945$ , and  $p = 0.999$   
153 respectively; Fig. 3).

154

## 155 **Discussion**

156 In this study we compared the dynamics of microbial-mediated decomposition of oak and  
157 chestnut leaf litter, throughout the year, in two zones: channel and *riparia*. As expected,  
158 environmental conditions were different between zones, inducing more accentuated mass loss in  
159 the channel, particularly evident in the less recalcitrant leaf (i.e. chestnut). Despite the lengthy  
160 (254 days) absence of water observed at the channel surface, differences in hydrological  
161 conditions between zones in the wetter seasons (autumn and winter) seem to cascade and shape  
162 decomposition dynamics for both leaf species across all seasons. The importance of an “hydraulic  
163 imprint” promoted by an even reduced water presence (rather than stream flow) in the stream  
164 channel, was also recognized by (Lohse et al. 2020) when comparing microbial decomposition  
165 rates of oak leaf litter on the channel vs. riparian and upland areas under distinct climatic  
166 conditions.

167 In our study, leaves incubated in the stream channel were stochastically subjected to  
168 flowing water, pools (originated from the loss of the longitudinal surface-water connectivity) and

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

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

193 It is noteworthy that fungal biomass associated with both leaf species peaked or  
194 maintained maximum levels on spring, in both environments. Along with lingering hydrological  
195 effects from the wet/colder seasons, mild temperatures in both zones (around 12 °C) may have  
196 contributed to the stimulation of mycelial growth of mixed aquatic and terrestrial fungal



197 assemblages (LeRoy et al. 2011), and leaf degradation, under dryer springtime conditions. In fact,  
198 previous studies point to optimal enzymatic activity around 10 °C, for aquatic (Ferreira and  
199 Chauvet 2011; Gonçalves et al. 2015), and between 10-25 °C for terrestrial (Graça and Ferreira  
200 1995; Razavi et al. 2017) fungi. In addition, we cannot rule out the possibility that a stimulation  
201 of algal biomass production due to increased light in both areas, may have had a priming effect  
202 on leaf-associated fungi (Franken et al. 2005; Kuehn et al. 2014). Globally, results suggest that,  
203 for both litter species, annual decomposition in either the channel or the riparian area will result  
204 in different litter residual quality, endowed with a similar fungal biomass concentration.

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

223         The present study elucidates that, despite zonal differences between the decomposition  
224 dynamics of each of the two used leaf species, the capacity of intermittent streams' channel to

225 catabolize dead organic matter exceeds that of its riparian area. Differences may even occur when  
226 the former acquires terrestrial-like features as a consequence of surface water absence during an  
227 elongated period of the year (~70%). Considering the present results, and the importance of the  
228 “hydrological imprint” for the leaves degradation process, particularly in the channel, long term  
229 studies seem to be advisable over short-term approaches to a better understanding of the  
230 functioning of and management intermittent streams.

231

### 232 **Acknowledgments**

233 This study was supported by FCT, within the POCH – Human Capital Operating Program,  
234 to SS (Fellowship Reference SFRH/BD/119133/2016), co-funded by the European Social Fund  
235 and MCTES national funds, is gratefully acknowledged. Also financed by a) project  
236 UID/BIA/04004/2013 co-funded by FCT/MEC through national funds and by FEDER, within the  
237 PT2020 Partnership Agreement, and COMPETE 2020; and b) project ReNATURE - Valorization  
238 of the Natural Endogenous Resources of the Centro Region (Centro 2020, Centro-01-0145-  
239 FEDER-000007), which also supported AM (fellowship reference ReNATURE – BPD11\_2).

240

241

242 **References**

- 243 Abril M, Muñoz I, Menéndez M (2016) Heterogeneity in leaf litter decomposition in a  
244 temporary Mediterranean stream during flow fragmentation. *Sci Total Environ* 553:330–  
245 339. doi: 10.1016/j.scitotenv.2016.02.082
- 246 Acuña V, Muñoz I, Giorgi A, et al (2005) Drought and postdrought recovery cycles in an  
247 intermittent Mediterranean stream: structural and functional aspects. *J North Am Benthol*  
248 *Soc* 24:919–933. doi: 10.1899/04-078.1
- 249 Arce MI, Mendoza-Lera C, Almagro M, et al (2019) A conceptual framework for understanding  
250 the biogeochemistry of dry riverbeds through the lens of soil science. *Earth-Science Rev*  
251 188:441–453
- 252 Arias-Real R, Menéndez M, Abril M, et al (2018) Quality and quantity of leaf litter: both are  
253 important for feeding preferences and growth of an aquatic shredder. *PLoS One*  
254 13:e0208272. doi: 10.1371/journal.pone.0208272
- 255 Arroita M, Flores L, Larrañaga A, et al (2018) Hydrological contingency: drying history affects  
256 aquatic microbial decomposition. *Aquat Sci* 80:31. doi: 10.1007/s00027-018-0582-3
- 257 Baldy V, Chauvet E, Charcosset J, Gessner MO (2002) Microbial dynamics associated with  
258 leaves decomposing in the mainstream and floodplain pond of a large river. *Aquat Microb*  
259 *Ecol* 28:25–36. doi: 10.3354/ame028025
- 260 Bastias E, Ribot M, Romaní AM, et al (2018) Responses of microbially driven leaf litter  
261 decomposition to stream nutrients depend on litter quality. *Hydrobiologia* 806:333–346.  
262 doi: 10.1007/s10750-017-3372-3
- 263 Bhatnagar JM, Peay KG, Treseder KK (2018) Litter chemistry influences decomposition  
264 through activity of specific microbial functional guilds. *Ecol Monogr* 1–16
- 265 Brandt LA, King JY, Hobbie SE, et al (2010) The role of photodegradation in surface litter  
266 decomposition across a grassland ecosystem precipitation gradient. *Ecosystems* 13:765–  
267 781. doi: 10.1007/s10021-010-9353-2
- 268 Bruder A, Chauvet E, Gessner MO (2011) Litter diversity, fungal decomposers and litter  
269 decomposition under simulated stream intermittency. *Funct Ecol* 25:1269–1277. doi:

270 10.1111/j.1365-2435.2011.01903.x

271 Canhoto C, Calapez R, Gonçalves AL, Moreira-Santos M (2013) Effects of Eucalyptus  
272 leachates and oxygen on leaf-litter processing by fungi and stream invertebrates. *Freshw*  
273 *Sci* 32:411–424. doi: 10.1899/12-062.1

274 Cebrian J (1999) Patterns in the fate of production in plant communities. *Am Nat* 154:449–468

275 Chauvet E, Cornut J, Sridhar KR, et al (2016) Beyond the water column: Aquatic hyphomycetes  
276 outside their preferred habitat. *Fungal Ecol* 19:112–127. doi:  
277 10.1016/j.funeco.2015.05.014

278 Cornut J, Ferreira V, Gonçalves AL, et al (2015) Fungal alteration of the elemental composition  
279 of leaf litter affects shredder feeding activity. *Freshw Biol* 60:1755–1771

280 Corti R, Datry T, Drummond L, Larned ST (2011) Natural variation in immersion and emersion  
281 affects breakdown and invertebrate colonization of leaf litter in a temporary river. *Aquat*  
282 *Sci* 73:537–550

283 Datry T, Boulton AJ, Bonada N, et al (2018) Flow intermittence and ecosystem services in  
284 rivers of the Anthropocene. *J Appl Ecol* 55:353–364. doi: 10.1111/1365-2664.12941

285 Datry T, Corti R, Claret C, Philippe M (2011) Flow intermittence controls leaf litter breakdown  
286 in a French temporary alluvial river: the “drying memory.” *Aquat Sci* 73:471–483

287 Datry T, Larned ST, Tockner K (2014) Intermittent rivers: A challenge for freshwater ecology.  
288 *Bioscience* 64:229–235. doi: 10.1093/biosci/bit027

289 Dieter D, von Schiller D, García-Roger EM, et al (2011) Preconditioning effects of intermittent  
290 stream flow on leaf litter decomposition. *Aquat Sci* 73:599–609. doi: 10.1007/s00027-011-  
291 0231-6

292 Dupont S, Lemetais G, Ferreira T, et al (2012) Ergostol biosynthesis: a fungal pathway for life  
293 on land. *Evolution (N Y)* 66:2961–2968. doi: 10.5061/dryad.pd28pm7n

294 European Environmental Agency (2002) Europe’s biodiversity - biogeographical regions and  
295 sea. The Mediterranean biogeographical region

296 Ferreira V, Chauvet E (2011) Synergistic effects of water temperature and dissolved nutrients  
297 on litter decomposition and associated fungi. *Glob Chang Biol* 17:551–564. doi:

298 10.1111/j.1365-2486.2010.02185.x

299 Ferreira V, Graça M a. S, de Lima JLMP, Gomes R (2006) Role of physical fragmentation and  
300 invertebrate activity in the breakdown rate of leaves. *Arch für Hydrobiol* 165:493–513.  
301 doi: 10.1127/0003-9136/2006/0165-0493

302 Franken RJM, Waluto B, Peeters ETHM, et al (2005) Growth of shredders on leaf litter  
303 biofilms: the effect of light intensity. *Freshw Biol* 50:459–466

304 Gessner MO, Chauvet E (1993) Ergosterol-to-biomass conversion factors for aquatic  
305 hyphomycetes. *Appl Environ Microbiol* 59:502–507

306 Gessner MO, Chauvet E, Dobson M (1999) A perspective on leaf litter breakdown in streams.  
307 *Oikos* 85:377–384

308 Gionchetta G, Oliva F, Romaní AM, Bañeras L (2020) Hydrological variations shape diversity  
309 and functional responses of streambed microbes. *Sci Total Environ* 714:. doi:  
310 10.1016/j.scitotenv.2020.136838

311 Gonçalves AL, Graça MAS, Canhoto C (2015) Is diversity a buffer against environmental  
312 temperature fluctuations? - A decomposition experiment with aquatic fungi. *Fungal Ecol*  
313 17:96–102. doi: 10.1016/j.funeco.2015.05.013

314 Gonçalves AL, Lírio A V., Graça MAS, Canhoto C (2016) Fungal species diversity affects leaf  
315 decomposition after drought. *Int Rev Hydrobiol* 101:78–86. doi: 10.1002/iroh.201501817

316 Gonçalves AL, Simões S, Bärlocher F, Canhoto C (2019) Leaf litter microbial decomposition in  
317 salinized streams under intermittency. *Sci Total Environ* 653:1204–1212. doi:  
318 10.1016/j.scitotenv.2018.11.050

319 Graça MAS, Ferreira RCF (1995) The ability of selected aquatic hyphomycetes and terrestrial  
320 fungi to decompose leaves in freshwater. *Sydowia* 47:167–179

321 Harms TK, Grimm NB (2012) Responses of trace gases to hydrologic pulses in desert  
322 floodplains. *J Geophys Res Biogeosciences* 117:

323 Hutchens JJJ, Wallace JB (2002) Ecosystem linkages between southern Appalachian headwater  
324 streams and their banks: Leaf litter breakdown and invertebrate assemblages. *Ecosystems*  
325 5:80–91. doi: 10.1007/s10021-001-0057-5

326 Jabiol J, Lecerf A, Lamothe S, et al (2019) Litter quality modulates effects of dissolved nitrogen  
327 on leaf decomposition by stream microbial communities. *Microb Ecol* 1–8. doi:  
328 10.1007/s00248-019-01353-3

329 Kohl L, Myers-Pigg A, Edwards KA, et al (2020) Microbial inputs at the litter layer translate  
330 climate into altered organic matter properties. *Glob Chang Biol* 1–19. doi:  
331 10.1111/gcb.15420

332 Kuehn KA (2016) Lentic and lotic habitats as templates for fungal communities: Traits,  
333 adaptations, and their significance to litter decomposition within freshwater ecosystems.  
334 *Fungal Ecol* 19:135–154. doi: 10.1016/j.funeco.2015.09.009

335 Kuehn KA, Francoeur SN, Findlay RH, Neely RK (2014) Priming in the microbial landscape:  
336 periphytic algal stimulation of litter-associated microbial decomposers. *Ecology* 95:749–  
337 762

338 Langhans SD, Tockner K (2006) The role of timing, duration, and frequency of inundation in  
339 controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento,  
340 northeastern Italy). *Oecologia* 147:501–509. doi: 10.1007/s00442-005-0282-2

341 Lecerf A, Chauvet E (2008) Intraspecific variability in leaf traits strongly affects alder leaf  
342 decomposition in a stream. *Basic Appl Ecol* 9:598–605. doi: 10.1016/j.baae.2007.11.003

343 LeRoy CJ, Fischer DG, Halstead K, et al (2011) A fungal endophyte slows litter decomposition  
344 in streams. *Freshw Biol* 56:1426–1433. doi: 10.1111/j.1365-2427.2011.02581.x

345 Lohse KA, Gallo EL, Meixner T (2020) Influence of climate and duration of stream water  
346 presence on rates of litter decomposition and nutrient dynamics in temporary streams and  
347 surrounding environments of southwestern USA. *Front Water* 2 571044 doi 103389/frwa

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

352 Martínez A, Pérez J, Molinero J, et al (2015) Effects of flow scarcity on leaf-litter processing  
353 under oceanic climate conditions in calcareous streams. *Sci Total Environ* 503:251–257

354 Moorhead DL, Sinsabaugh RL (2006) A theoretical model of litter decay and microbial  
355 interaction. *Ecol Monogr* 76:151–174. doi: 10.1890/0012-  
356 9615(2006)076[0151:ATMOLD]2.0.CO;2

357 Mora-Gómez J, Boix D, Duarte S, et al (2020) Legacy of Summer Drought on Autumnal Leaf  
358 Litter Processing in a Temporary Mediterranean Stream. *Ecosystems* 23:989–1003. doi:  
359 10.1007/s10021-019-00451-0

360 Mora-Gómez J, Duarte S, Cássio F, et al (2018) Microbial decomposition is highly sensitive to  
361 leaf litter emersion in a permanent temperate stream. *Sci Total Environ* 621:486–496. doi:  
362 10.1016/j.scitotenv.2017.11.055

363 Mori N, Simčič T, Brancelj A, et al (2017) Spatiotemporal heterogeneity of actual and potential  
364 respiration in two contrasting floodplains. *Hydrol Process* 31:2622–2636

365 Niyogi DK, Hu C-Y, Vessell BP (2020) Response of stream fungi on decomposing leaves to  
366 experimental drying. *Int Rev Hydrobiol* 105:52–58

367 Pieristè M, Chauvat M, Kotilainen TK, et al (2019) Solar UV-A radiation and blue light  
368 enhance tree leaf litter decomposition in a temperate forest. *Oecologia* 191:191–203. doi:  
369 10.1007/s00442-019-04478-x

370 Pinna M, Basset A (2004) Summer drought disturbance on plant detritus decomposition  
371 processes in three River Tirso (Sardinia, Italy) sub-basins. *Hydrobiologia* 522:311–319

372 R Development Core Team (2016) R: A language and environment for statistical computing. R  
373 Foundation for Statistical Computing, Vienna

374 Raymond PA, Hartmann J, Lauerwald R, et al (2013) Global carbon dioxide emissions from  
375 inland waters. *Nature* 503:355–359. doi: 10.1038/nature12760

376 Razavi BS, Liu S, Kuzyakov Y (2017) Hot experience for cold-adapted microorganisms:  
377 Temperature sensitivity of soil enzymes. *Soil Biol Biochem* 105:236–243. doi:  
378 10.1016/j.soilbio.2016.11.026

379 Romaní AM, Chauvet E, Febria C, et al (2017) The Biota of Intermittent Rivers and Ephemeral  
380 Streams: Prokaryotes, Fungi, and Protozoans. Elsevier Inc.

381 Schneider A, Jost A, Coulon C, et al (2017) Global-scale river network extraction based on

382 high-resolution topography and constrained by lithology, climate, slope, and observed  
383 drainage density. *Geophys Res Lett* 44:2773–2781

384 Skoulidakis NT, Sabater S, Datry T, et al (2017) Non-perennial Mediterranean rivers in Europe:  
385 status, pressures, and challenges for research and management. *Sci Total Environ* 577:1–  
386 18. doi: 10.1016/j.scitotenv.2016.10.147

387 Sridhar KR, Bärlocher F (1993) Aquatic hyphomycetes on leaf litter in and near a stream in  
388 Nova Scotia, Canada. *Mycol Res* 97:1530–1535. doi: 10.1016/S0953-7562(09)80229-3

389 Steward AL, Von Schiller D, Tockner K, et al (2012) When the river runs dry: Human and  
390 ecological values of dry riverbeds. *Front Ecol Environ* 10:202–209. doi: 10.1890/110136

391 von Schiller D, Bernal S, Dahm CN, Martí E (2017) Nutrient and organic matter dynamics in  
392 intermittent rivers and ephemeral streams. In: *Intermittent Rivers and Ephemeral Streams:  
393 Ecology and Management*. Elsevier Inc., pp 135–160

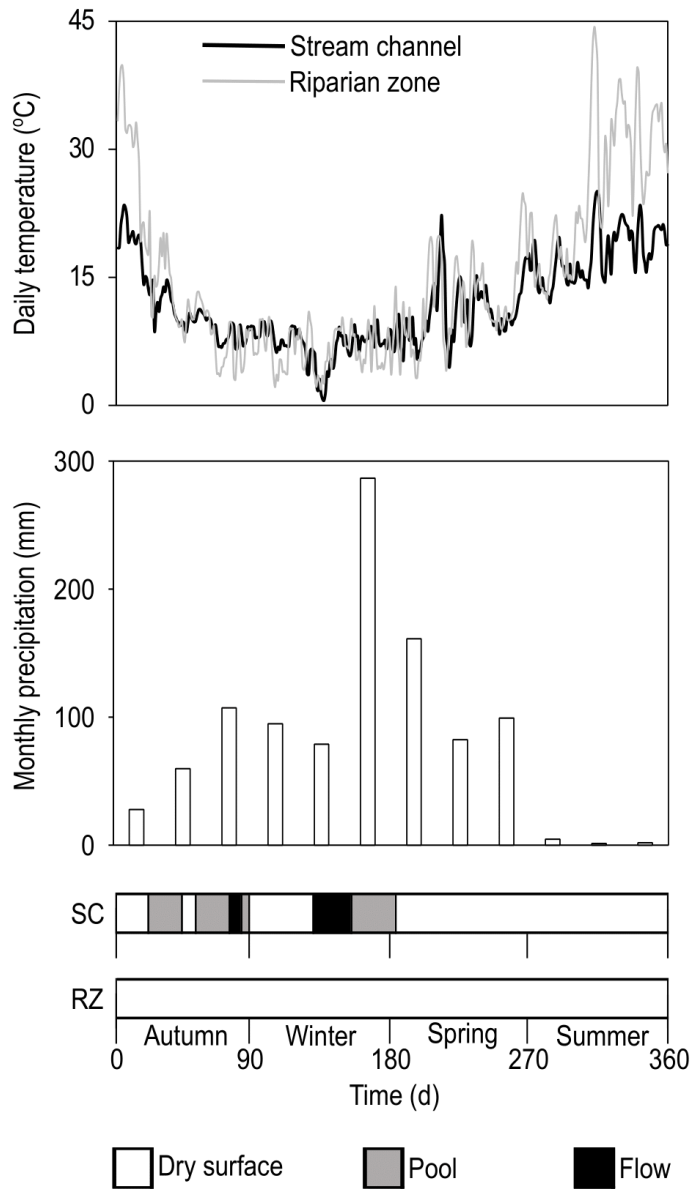
394 Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream  
395 linked to terrestrial litter inputs. *Science* (80- ) 277:102–104

396

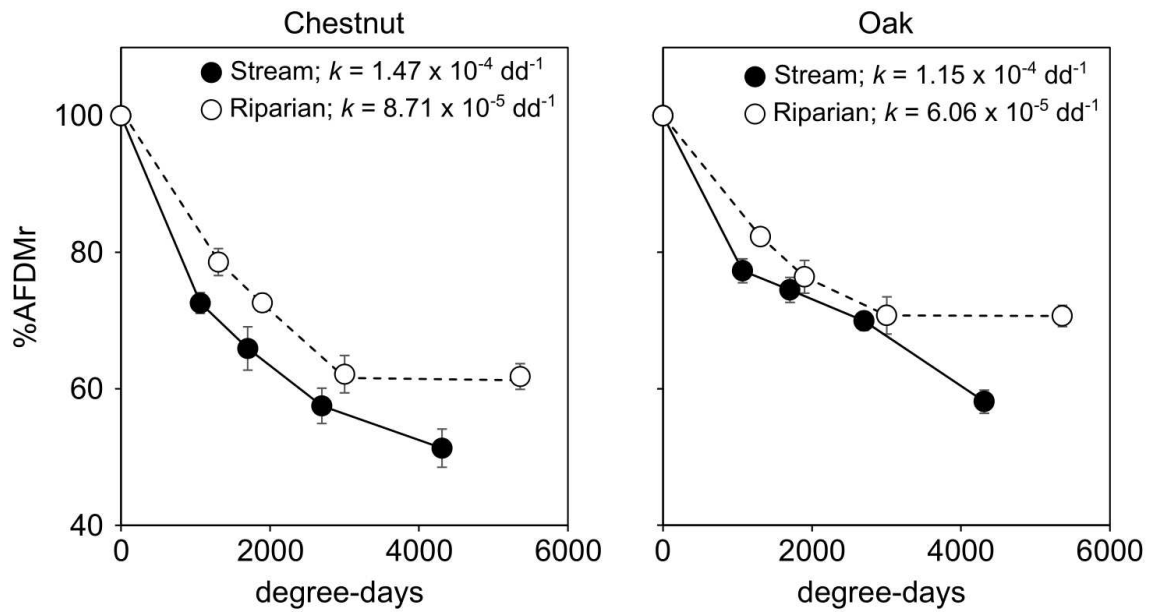
397

398

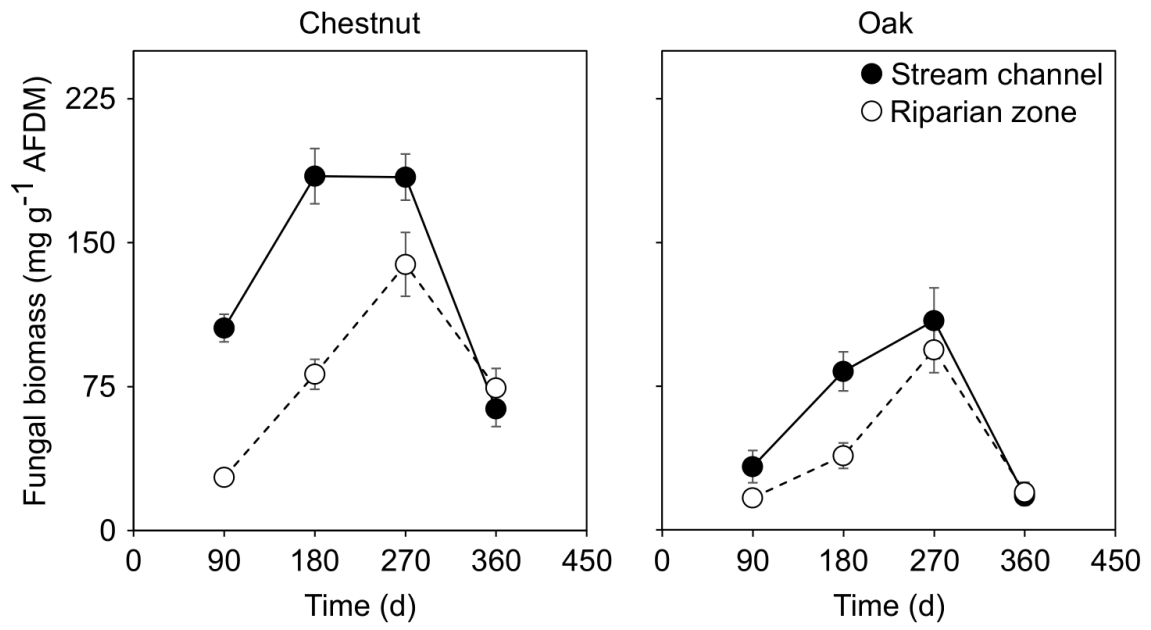




**Fig. 1** Daily temperature, monthly precipitation and distribution of dry surface, pool or flow conditions in the stream channel (SC) and riparian zone (RZ) along the incubation period.



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



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