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Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream

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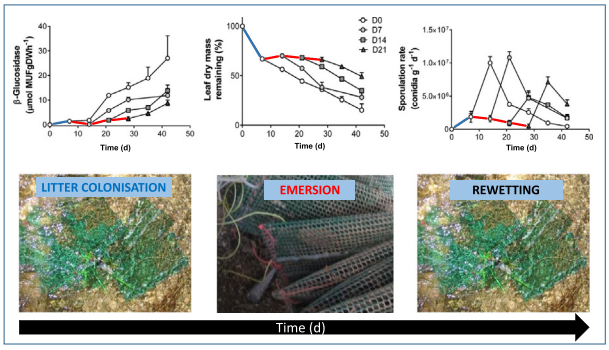
HIGHLIGHTS

- We evaluated the leaf litter emersion period effect on microbial decomposition.
- Emersion reduced EEA, decomposition rates, microbial biomass and fungal sporulation.
- Microbial assemblages were affected by emersion treatments.
- Variables changed with emersion time, either gradually or in a single step change.
- Despite sensitivity to emersion found, some microbial descriptors were resilient.

GRAPHICAL ABSTRACT



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ABSTRACT

Drought frequency and intensity in some temperate regions are forecasted to increase under the ongoing global change, which might expose permanent streams to intermittence and have severe repercussions on stream communities and ecosystem processes. In this study, we investigated the effect of drought duration on microbial decomposition of *Populus nigra* leaf litter in a temperate permanent stream (Oliveira, NW Portugal). Specifically, we measured the response of the structural (assemblage composition, bacterial and fungal biomass) and functional (leaf litter decomposition, extracellular enzyme activities (EEA), and fungal sporulation) parameters of fungal and bacterial communities on leaf litter exposed to emersion during different time periods (7, 14 and 21 d). Emersion time affected microbial assemblages and litter decomposition, but the response differed among variables. Leaf decomposition rates and the activity of β-glucosidase, cellobiohydrolase and phosphatase were gradually reduced with increasing emersion time, while β-xylosidase reduction was similar when emersion last for 7 or more days, and the phenol oxidase reduction was similar at 14 and 21 days of leaf emersion. Microbial biomass and fungal sporulation were reduced after 21 days of emersion. The structure of microbial assemblages was affected by the duration of the emersion period. The shifts in fungal assemblages were correlated with a decreased microbial capacity to degrade lignin and hemicellulose in leaf litter exposed to emersion. Additionally, some resilience was observed in leaf litter mass loss, bacterial biomass, some enzyme activities and structure of fungal assemblages. Our study shows that drought can strongly alter structural and functional aspects of microbial decomposers. Therefore, the exposure of leaf litter to increasing emersion periods in temperate streams is expected to affect decomposer communities and overall decomposition of plant material by decelerating carbon cycling in streams.

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1. Introduction

In a context of climate change, drier climatic conditions are forecasted in some temperate regions (Beniston et al., 2007; IPCC, 2013). Increased air temperature, reduced precipitation and intensive water usage (e.g. irrigation, drinking water) is expected to affect stream hydrology by increasing the frequency, intensity and duration of droughts (Andersen et al., 2006; Meyer et al., 1999). Although drought is a natural disturbance in streams from semi-arid regions, such as the Mediterranean one, it will become more frequent in many temperate streams under ongoing global change scenarios (Acuña et al., 2014). In those streams, biological communities are not evolutionarily adapted to drought, which threatens stream ecological integrity (Dieter et al., 2013; Schlief and Mutz, 2011).

In streams, drought results in decreased flow, thus reducing habitat availability and longitudinal connections (Larned et al., 2010), a contracting process that depends on local hydrological regimes (Humphries and Baldwin, 2003). The complex hydrological dynamics, typical of intermittent streams, structure biological communities and stream ecosystem processes (Abril et al., 2016; Datry et al., 2011; Ylla et al., 2010). However, there is still little information on the biological responses occurring when permanent streams become intermittent due to increased water scarcity.

Leaf litter decomposition has a fundamental role in the carbon cycle and in sustaining detritus-dependent food webs in headwater forested streams (Richardson, 1991; Tank et al., 2010; Wallace et al., 1999). Both microbial and invertebrate communities drive biological degradation of submerged leaves (Gessner and Chauvet, 1994; Graça et al., 2001; Hieber and Gessner, 2002). Microbes colonize and degrade leaf compounds through their enzymatic capabilities (Chamier, 1985; Romaní et al., 2006; Sinsabaugh et al., 2002), and are sensitive to disturbances, such as drought, which can affect leaf litter decomposition (Corti et al., 2011; Dieter et al., 2011; Mora-Gómez et al., 2016).

Drought can have both long-time and short-time effects on leaf litter breakdown. For example, it has been reported that sites submitted to long dry periods and high frequency of drought episodes exhibit reduced leaf litter decomposition rate, mainly related to a reduction of shredders abundance (Datry et al., 2011; Pinna and Basset, 2004). In addition, short-time effects can be observed as consequence of both: i) exposure of leaf litter to dried streambed affecting litter quality with effects on decomposition once the flow is resumed (Mora-Gómez, 2014); and ii) litter immersion and emersion cycles, which might also reduce decomposition rates by direct effects on microbial decomposers and invertebrate detritivores (Corti et al., 2011; Riedl et al., 2013).

Permanent streams recently subjected to flow reduction might be affected by litter exposure to emersion-immersion cycles. The response of aquatic biota to rewetting will be determined by the length of the emersion and the resistance/resilience of the communities (Lake, 2003). Although only few studies have examined the direct effects of drought on litter decomposition, evidence suggests that the duration of drought is more important than the frequency of drought events, with the decomposition rate being controlled by the time spent by leaves under water, as litter processing is slower under terrestrial conditions (Bruder et al., 2011; Langhans and Tockner, 2006; Riedl et al., 2013). Furthermore, growth and activity of microbial decomposers might be reduced due to emersion (Bruder et al., 2011; Inkley et al., 2008; Langhans and Tockner, 2006), although fungal biomass seems to recover rapidly after rewetting (Langhans and Tockner, 2006). Also, invertebrates have shown to be highly sensitive to desiccation of decaying leaves (Corti et al., 2011; Inkley et al., 2008).

Research on effects of drought in the functioning of freshwaters has been mainly carried out in systems already exposed to these environmental conditions, such as intermittent streams. In contrast, in this study we aimed to evaluate the responses of microbial decomposers to leaf emersion in a permanent stream, in a transition area between Mediterranean and temperate region, to examine the impacts of drought under current climate change scenarios. Our specific aims were to assess to what extent the duration of emersion (7, 14 and 21 d) influences: i) microbial decomposition of leaf litter and microbial attributes (microbial biomass, enzymatic activities and microbial diversity) and ii) the resilience of microbial communities once leaves are rewetted. Previous studies on drought effect on leaf litter decomposition did not monitor the microbial community nor tested their resilience ability. To better understand how non-adapted communities respond to drought duration, we included structural and functional responses of microbial communities. We hypothesized that longer emersion periods would reduce microbial decomposer activity, decelerating leaf litter decomposition; however, after re-immersion of leaf litter, the responses of microbial communities would depend on its resistance and resilience (Allison and Martiny, 2008). Therefore, if the communities were resistant, no emersion effect would be observed. If the communities were resilient to emersion two possible scenarios could be observed: i) microbial decomposer descriptors would change, but after a short period the communities might return to their initial state, or ii) if the microbial communities were functionally redundant, assemblages would change but not the decomposer activity. Finally, if all descriptors were affected, the communities would be very sensitive to drought further compromising leaf litter decomposition.

2. Materials and methods

2.1. Study site

The study was conducted in May–June 2012 at Oliveira stream, located in the Northwest of Portugal (41°58′63.00″N, −8°22′51.30″W). Oliveira is a low-order stream belonging to the Ave River basin and presenting low human impact (Geraldes, 2011). Riparian vegetation is dominated by *Alnus glutinosa* (L.) Gaertn., *Quercus robur* L., *Castanea sativa* Mill. and *Populus nigra* L. and the bedrock is composed of boulders and pebbles.

2.2. Experimental design

Populus nigra leaves were collected immediately after abscission in October 2011, air-dried for 15 days and stored in dark and dry conditions until the onset of the experiment. For the experiment, portions of 3 g (±0.1 g) of leaves were enclosed in plastic litterbags (5 mm mesh size). Coarse mesh bags were chosen to simulate natural conditions, allowing the access of detritivores and minimising artefacts resulting from unnatural moisture retention in fine mesh bags during simulated dry conditions (Bruder et al., 2011). To assess the effect of emersion duration on litter decomposition, we used four treatments in which leaves were subject to emersion as follows: 0 days i.e. immersed over the entire experiment (E0), 7 days of emersion (E7), 14 days of emersion (E14) and 21 days of emersion (E21) (Fig. 1).

All sets of bags were first immersed for seven days in Oliveira stream on 10th May 2012 to allow microbial colonization. After this period, three sets (E7, E14 and E21) were collected from the stream in separate plastic bags and transferred to the laboratory within 1 h. Once in the laboratory, bags were exposed to controlled drying conditions in mesocosms that simulated dry parafluvial areas, and consisted of sediment previously collected from the same stream placed in plastic boxes (100 × 50 × 50 cm). Boxes had no water, and were protected with black plastic bags to limit sunlight or rainfall, but permit aeration. During the emersion treatment temperature in the simulated parafluvial area ranged from 7.7 to 40.7 °C. Litterbags were re-immersed in the stream after 7, 14 or 21 days of emersion, according to the defined treatments. The decomposition process was planned to be monitored weekly for all treatments including both emersion and immersion phases of the experiment; however, the sampling of E7 after 21 days of re-immersion was discarded due to the loss of some bags by vandalism (Fig. 1). Four replicates per sampling date per treatment were