Soil Biology & Biochemistry 86 (2015) 17–23

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Litter-type specific microbial responses to the transformation of leaf litter into millipede feces

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ARTICLE INFO

Article history:
Received 2 October 2014
Received in revised form
12 March 2015
Accepted 16 March 2015
Available online 30 March 2015

Keywords:
Soil fauna
Glomeris marginata
Litter decomposition
Litter quality
Microbial decomposers

ABSTRACT

The transformation of leaf litter into fecal pellets by saprophagous macroarthropods has long been suggested to play an important role in litter decomposition by altering microbial processes. However, conflicting results are reported in the literature, and it is currently not clear to what extent varying initial litter quality contributes to distinct microbial responses to the transformation of litter into feces. Here we performed a screening test using a wide range of distinct leaf litter from 26 tree species. We fed these litters to the macroarthropod species *Glomeris marginata* during one week under controlled conditions, and compared microbial responses in uningested leaf litter with that of feces produced from the 26 different leaf litter types. We assessed substrate induced respiration (SIR) as an integrative measure of microbial responses. We found that litter SIR was highly variable across species and well related to initial litter quality. However, variability in feces SIR was strongly reduced and only weakly related to initial litter quality. Moreover, the difference between feces and litter SIR decreased with increasing litter SIR as a result of higher microbial stimulation in litter with low associated litter SIR. Our data clearly showed that the direction and magnitude of microbial stimulation in feces depend strongly on the litter type. Therefore, the consequence of litter transformation into macroarthropod fecal pellets for microbial decomposers and possibly for subsequent decomposition of feces is specific to litter species.
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1. Introduction

In terrestrial ecosystems, litter-feeding macroarthropods are key regulators of plant litter decomposition as they consume large amounts of leaf litter, most of it being transformed into fecal pellets. Feeding activities of these organisms directly affect decomposition through their own metabolism and indirectly through interactions with microbial decomposers (Wolters, 2000; Lavelle and Spain, 2001; Coleman et al., 2004). Although indirect effects of soil fauna on microbial decomposition are generally considered to be more important than direct effects (Lavelle and Spain, 2001), many of them are not well understood. In particular, it is unclear whether the abundance and activity of microbial communities is higher or lower in feces of litter-feeding macroarthropods than in the leaf litter animals were feeding on (David, 2014).

Significant progress has been made in the understanding of the fate of microorganisms during the transformation of leaf litter into feces. Many bacteria, yeasts and fungi that colonize leaf litter are digested and assimilated, while others are little affected by digestion (Byzov et al., 1998; Byzov, 2006; Inhen and Zimmer, 2008). Ultimately, because fungal hyphae are more susceptible than bacteria to litter fragmentation by animals (Anderson and Ineson, 1984; Visser, 1985) and because the hindgut of macroarthropods is a natural fermenter, in which conditions are favorable for bacterial growth (Zimmer and Topp, 1998; Frouz et al., 2003; Byzov, 2006), the bacteria:fungi ratio generally increases in fresh feces compared to leaf litter (Hassall et al., 1987; Maraun and Scheu, 1996; Byzov et al., 1998). Microbial development in feces is also affected by the changes in physical and chemical characteristics of

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http://dx.doi.org/10.1016/j.soilbio.2015.03.014
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the ingested litter. The physical structure of the litter is highly modified by the transformation, as plant tissues are disintegrated, cells are broken and the surface area available for microbial colonization increases (Webb, 1977; Kheirallah, 1990). Also, the chemical characteristics of the feces do not exactly track those of the litter, as a part of the organic matter is digested and subsequently assimilated during animal gut passage (Scheu and Wolters, 1991; Gillon and David, 2001; Rawlins et al., 2006). Collectively, these changes alter the microbial abundance and/or community structure in feces compared to original litter material and may ultimately influence microbial activity and the decomposition of this material (Ineson and Anderson, 1985).

Previous studies that specifically assessed how microbial activity in macroarthropod feces changes compared to intact leaf litter reported contrasting results. Increased microbial respiration in fresh feces was observed in some studies (Hassall et al., 1987; Maraun and Scheu, 1996; Frouz and Šimek, 2009), but unchanged or even reduced microbial respiration in fresh feces compared to leaf litter was also reported (Maraun and Scheu, 1996; Frouz and Šimek, 2009; Suzuki et al., 2013; Špaldoňová and Frouz, 2014). Several different explanations can be put forward for these apparently contradictory results. First, the direction and extent of effects are known to vary substantially with the age of feces, i.e. the time elapsed after egestion (Maraun and Scheu, 1996; Frouz and Šimek, 2009; Suzuki et al., 2013). Moreover, Frouz and Šimek (2009) showed that the results can vary depending on the detritivore species studied. Finally, a large variety of food sources were used in the studies mentioned above and food quality is likely to have a major influence on microbial activity in feces. For example, Hassall et al. (1987) and Maraun and Scheu (1996) fed macroarthropods on leaf litter at different stages of decomposition and found that microbial activity was much more stimulated in feces derived from relatively fresh litter than in those derived from more decomposed litter. Changes in litter quality may explain these litter age related differences, and Maraun and Scheu (1996) pointed to the depletion of carbon sources in older litter material as a potentially significant factor. Similarly, because different litter species have different chemical, physical and microbial characteristics, their transformation into feces by detritivores may result in a variety of effects on the activity of decomposer microorganisms. However, a comparative analysis of microbial activity in macroarthropod feces produced from a wide range of plant species has not been published so far.

In this study, we aimed at filling this gap of knowledge by assessing microbial responses to the transformation of leaf litter into feces using litter from a wide range of 26 tree species. We did this by using the macroarthropod species *Glomeris marginata*, a common European species that readily consumes leaf litter of a large variety of plant species. Substrate induced respiration (SIR) was chosen as microbial parameter in order to assess the potentially active microbial biomass, taking advantage of the fact that SIR accounts for changes in both the biomass and composition of microbial communities (Fanin et al., 2011). Hence, SIR provides an integrated measure of the overall microbial changes, feasible across a large number of samples. Depending on the relative stimulation or inhibition of microorganisms in feces compared to intact leaf litter, we may expect four different general relationships between SIR rates in tree species-specific leaf litter and in the corresponding fecal pellets. First, as a null hypothesis we stated that gut passage of leaf litter material does not affect microbial decomposers leading to unchanged SIR rates between litter and feces (Fig. 1, Scenario a). Second, microorganisms in feces may be stimulated compared to leaf litter, with the simplest case of constant relative stimulation (Fig. 1, Scenario b). Third, microorganisms in feces may be inhibited compared to leaf litter, again with the simplest case of constant relative inhibition (Fig. 1, Scenario c). In a fourth scenario we hypothesized that gut passage homogenizes initial differences in leaf litter SIR rates leading in its most extreme case to a slope of zero when feces SIR are plotted as a function of leaf litter SIR rates (Fig. 1, Scenario d).

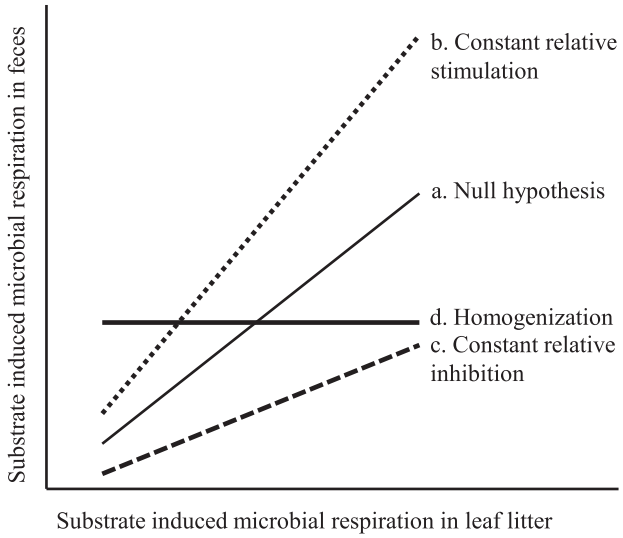

Fig. 1. Different potential relationships between feces and litter substrate induced respiration (SIR).

2. Material and methods

2.1. Animal and litter collection

We chose the millipede *Glomeris marginata* (Villers) for our experiment, because it is a widespread detritivore across European forests, locally abundant and feeding on leaf litter from a large range of tree species. Around 900 individuals were collected from a Holm oak (*Quercus ilex* L.) dominated forest in the surroundings of Montpellier (43°39′ N, 3°40′ E), and kept until use in large plastic boxes filled with decomposing litter from their site of origin. With the collection of a standard population of animals exposed to a common litter, we avoided potential confounding effects due to population-specific microbial gut communities or to adaptations to specific litter types. The latter may only partly hold for the litter from *Q. ilex ilex* L. and *Q. ilex rotundifolia* L., since we collected *G. marginata* in a holm oak forest of Southern France. However, *Q. ilex* is a species of extremely high genetic diversity, and the *Q. ilex ilex* litter from Italy and the *Q. ilex rotundifolia* litter from Spain are likely as different from *Q. ilex* in the forest of Southern France as for some other species included in our test.

Leaf litter from 26 tree species collected in seven European forests differing in species composition and geographic locations were used (Appendix 1). Leaf litter was collected at tree species-specific peak of leaf litter fall, between October 2011 and November 2012, except for *Alnus glutinosa* (L.) Gaertn. and *Fraxinus angustifolia* Vahl. for which litter was collected during the fall of 2006. For most species, fresh leaf litter was collected in suspended litter traps, except for eight species for which we collected leaf litter either on the forest floor (*Betula pendula* Roth.) a few days after litter fall, or directly from trees by gently moving branches to shake off leaf litter (*Acer monspessulanum* L., *Celtis australis* L., *Cercis siliquastrum* L., *Fraxinus ornus* L., *Ginkgo biloba* L., *Robinia pseudoacacia* L., *Tamarix* sp. L.) from a minimum of 5 individuals per species. As detritivores prefer feeding on leaf litter that has already started to

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