Soil Biology & Biochemistry 93 (2016) 119–130

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Mechanisms linking fungal conditioning of leaf litter to detritivore feeding activity

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ARTICLE INFO

Article history:
Received 5 June 2015
Received in revised form
26 October 2015
Accepted 30 October 2015
Available online 18 November 2015

Keywords:
Cell wall structural compounds
Decomposition
Litter
Saprotrophic fungi
Microbes
Millipedes
Nutrients

ABSTRACT

Saprotrophic fungi are one of the primary groups of organisms responsible for decomposition and nutrient cycling processes. Aside from their direct effects on litter decomposition, these organisms may indirectly affect litter invertebrate activity via fungal-mediated conditioning (i.e. ‘priming’) of litter substrates. While this priming effect is generally assumed to take place, this assumption is based on correlative observations and feeding preference trials rather than experimental discrimination of the mechanisms driving the process. We used a microcosm experiment of brown-rot (*Fistulina hepatica*, *Fomitopsis lilacinogilva*) and white-rot (*Pycnoporus coccineus*) fungi on two sclerophyllous leaf litters (*Eucalyptus loxophleba* and *Acacia acuminata*) to test if a fungal-mediated change in plant litter increased the nutritive value of the food source, and if a change in cell-wall (structural) compounds reduced the toughness of leaves, resulting in increased feeding activity by invertebrates. Brown- and white-rot fungal colonization had significant and diverse effects on the total nutrient concentrations and proportions of cellulose, lignin and hemicellulose of the leaf litter—fungi complex. However, significant decreases in leaf toughness and increases in mass loss and leaf fragmentation associated with detritivorous millipede (*Ommatoiulus moreletii*) activity only occurred in white-rot primed microcosms relative to the control. The mechanisms by which the white-rot fungus affected both leaf toughness and millipede feeding activity differed between leaf litters. In *E. loxophleba* microcosms, reduced leaf toughness and increased millipede grazing were mediated by relative changes in litter inorganic chemistry, rather than structural compounds, whereas in *A. acuminata* microcosms the effects of fungal priming were not mediated by either. These results suggest that, in the early stages of decomposition, fungal priming effects on leaf litter nutrients are a more important determinant of litter—invertebrate interactions than changes to litter structural compounds. Furthermore, different species of fungi interact with different litter types and invertebrates in functionally different ways.

1. Introduction

Decomposition processes have been studied extensively (Cadisch and Giller, 1997; Bardgett and Wardle, 2010), yet our understanding of the interactions between microorganisms and litter invertebrates is continually evolving (Coulis et al., 2013; Suzuki et al., 2013). It is well established that all plant-derived nutrients in detritus are moved through either bacterial- or fungal-based energy channels, and thus saprotrophic fungi and bacteria are the primary organisms responsible for nutrient processing and recycling (Hattenschwiler et al., 2005; Abbot et al., 2008). Litter invertebrates contribute to nutrient cycling through litter comminution, the digestion of litter material and microorganisms, and the excretion of excess ingested nutrients which sometimes enhance microbial growth (Lavelle et al., 1997). Historically, research on interactions between litter invertebrates and microorganisms has focused on the effects of litter transformers on

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http://dx.doi.org/10.1016/j.soilbio.2015.10.021

microbial populations (Anderson and Bignell, 1980). Very few studies have considered the effects of microbial priming of leaf litter on litter invertebrate activity (Zimmer et al., 2003; Ihnen and Zimmer, 2008), and this is the topic we address in this paper.

It has been suggested that fungal conditioning (hereafter called priming) of woody litter through enzyme activities, improved carbon to nutrient ratios, and the breakdown of inhibitory compounds may be necessary for subsequent colonization of saprophagous invertebrates (Wardle and Lavelle, 1997). Thus there are several mechanisms by which fungi may prime leaf litter for litter feeding invertebrates. First, fungal activity may reduce the physical resistance of leaf litter for comminution by degrading plant cell wall (structural) compounds, particularly lignin, cellulose, and hemicellulose. Second, leaf litter nutrient characteristics may change through fungal colonization and decay, and this process may result in a food source that has a higher nutritive value than the dead leaf itself. These potential mechanisms may be particularly important during the decomposition of sclerophyllous plant litter which is characterized as being both physically tough (Choong et al., 1992) and nutrient poor (Maisto et al., 2011) compared with mesophyllous plant litter.

Basidiomycetous fungi are important degraders of woody tissue in terrestrial environments (Eriksson et al., 1990), and contain two functionally different classes of saprotrophs: white-rot and brown-rot fungi. White-rot fungi produce both cellulases and ligninases to decompose most plant structural compounds, whereas brown-rot fungi have enzymatic systems that breakdown cellulose and hemicelluloses leaving behind partly modified lignin (Eriksson et al., 1990; Tanesaka et al., 1993). The patterns and properties of enzymatic production differ between fungal species, and pathways of degradation likely depend not only on the enzymes and substrates involved, but also reaction conditions (Grinhut et al., 2007). Hence, a complex interaction between substrate chemistry and abiotic conditions affects the secretion of enzymes, immobilization of nutrients in fungal tissue, fungal growth, and interactions between litter invertebrates and microorganisms.

The mechanical resistance of sclerophyllous leaves has important consequences for leaf litter decomposition through plant species-specific effects and nutrient cycling (Diaz et al., 2004). A significant negative correlation between leaf tensile strength and rates of litter mass loss has been demonstrated (Cornelissen et al., 1999). Several authors have suggested that litter with high phenol, tannin, and lignin content may experience a time lag between abscission and time of attack by soil invertebrates due to the toughness of the undecomposed tissues (e.g. Anderson, 1975; Dighton, 1995). Lavelle et al. (1997) proposed that the fibrous components of plant cell walls, including cellulose, hemicelluloses and lignin, are not accessible to litter transformers unless they have been conditioned by microorganisms. The relative proportions of these plant cell structural compounds fall into several classes of compounds related to litter quality, including (1) sugars and starches which are easily digested, (2) tannins, lignins, and other polyphenol-rich substrates which are recalcitrant, and (3) cellulose and hemicelluloses which are intermediate in terms of digestibility (Coleman et al., 2004). Thus litter quality can be thought of in terms of both nutrient content and plant cell wall structural polymers (Gallardo and Merino, 1993).

The carbon: nitrogen (C:N) ratio has been well established as a general index of litter quality (Cadisch and Giller, 1997), and diplopod feeding preferences (Loranger-Merciris et al., 2008) and biomass (Warren and Zou, 2002) have been shown to be significantly correlated with leaf N content. Litter transformers also require many macronutrients and trace elements, particularly phosphorus, calcium, magnesium, and manganese (Cromack et al., 1977; Jennings and Rayner, 1984; Scheu and Schaefer, 1998; Zimmer, 2002; Danger et al., 2013). Likewise, the concentration of sulphur in litter has been shown to be a good predictor of isopod and diplopod abundance in decomposer food webs (Kaspari and Yanoviak, 2009), and may be an important nutrient for litter invertebrates. Studies of fungi have shown there are fungal species that restrict the uptake of various nutrients, some that transport those same nutrients, and others that accumulate them (Chudzyński and Falandysz, 2008; Lavola et al., 2011). Fungus–litter complexes with lower carbon to nutrient ratios, particularly N, P, Ca, Mg, Mn, and S, may be more edible than leaf litter not colonized by fungi. As it is difficult to separate the fungal mycelia that penetrate the cellular structures in leaf litter from the leaf litter itself, in the following text the nutrient characteristics of the entire litter–fungus complex are discussed.

To our knowledge there are no published studies that explicitly address, from a mechanistic perspective, the priming effect of fungal mediated changes to litter–fungus complex chemistry and structure on litter transformer activity in terrestrial systems. In this paper, we present an experimental microcosm study in which we test if a fungal-mediated change in plant litter increased the nutritive value of the food source, and if a change in cell wall structural compounds reduced the toughness of leaves, resulting in increased feeding activity by invertebrates. We discriminated between these two potential central mechanisms by experimentally determining the effects of fungal colonization on the nutrient concentrations, proportions of cellulose, hemicellulose, and lignin, the mechanical properties of the leaf litter, and the causal relationships between these potential mediating variables and subsequent millipede feeding activity using structural equation modelling.

2. Materials and methods

2.1. Experimental protocols

We used a two-phased approach in this experiment (Fig. 1) in order to separate the effects of fungal colonization on leaf litter nutrients, structural compounds (lignin, cellulose, hemicellulose), and mechanical strength (Phase 1) from the effects of millipedes on

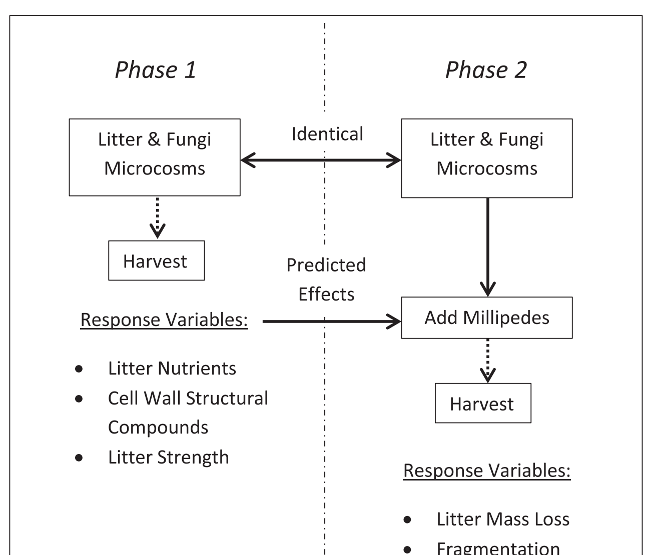

Fig. 1. The experimental protocol depicting the two-phased approach we used to separate the effects of fungal colonization on (1) leaf chemistry and mechanical strength, and (2) millipede feeding activity.