



Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web



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ABSTRACT

An increasing number of empirical studies are challenging the central fundamentals on which the classical soil food web model is built. This model assumes that bacteria consume labile substrates twice as fast as fungi, and that mycorrhizal fungi do not decompose organic matter. Here, we build on emerging evidence that points to significant consumption of labile C by fungi, and to the ability of ectomycorrhizal fungi to decompose organic matter, to show that labile C constitutes a major and presently underrated source of C for the soil food web. We use a simple model describing the dynamics of a recalcitrant and a labile C pool and their consumption by fungi and bacteria to show that fungal and bacterial populations can coexist in a stable state with large inputs into the labile C pool and a high fungal use of labile C. We propose a new conceptual model for the bottom trophic level of the soil food web, with organic C consisting of a continuous pool rather than two or three distinct pools, and saprotrophic fungi using substantial amounts of labile C. Incorporation of these concepts will increase our understanding of soil food web dynamics and functioning under changing conditions.

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1. Introduction

It has long been acknowledged that interactions in the soil food web are crucial for processes of soil carbon (C) and nitrogen (N) cycling. In the first complete soil food web, Hunt et al. (1987), identified the presence of a separate fungal and bacterial energy channel, as well as a root energy channel, formed by saprotrophic fungi and their consumers, bacteria and their consumers, and mycorrhizal fungi and root-feeding nematodes and their consumers, respectively. While the fungal and bacterial energy channels can be considered 'brown' because the bottom trophic levels—fungi and bacteria—obtain their energy from dead organic matter (detritus), the root energy channel can be considered 'green' because mycorrhizal fungi and root-feeding nematodes obtain their energy directly from living plants. Both modelling and empirical studies have consistently found more efficient C and N cycling in the fungal energy channel than in the bacterial energy channel (Hunt et al., 1987; De Ruiter et al., 1993; De Vries et al., 2011; Holtkamp et al., 2011; De Vries et al., 2012a). In addition,

theoretical and empirical work has shown that the presence of a 'slow' fungal energy channel with weak interactions strengths, and coupling of the two energy channels by higher-level consumers, confers stability to the soil food web (Rooney et al., 2006; De Vries et al., 2012b; Rooney and McCann, 2012). Shifts in the ratio between the fungal and bacterial energy channel (often measured as the shift in fungal/bacterial biomass ratio) are generally attributed to changes in agricultural management and plant community composition, and consequently in the quantity and quality of organic substrates, which primarily consist of plant inputs, i.e. leaf and root litter and root exudates (Bardgett and McAlister, 1999; Wardle et al., 2004; Bardgett and Wardle, 2010; De Vries et al., 2012d).

Despite its conceptual advances, some of the fundamental assumptions in the classical food web model that support these modelled and observed patterns are now being challenged by an increasing number of experimental and theoretical studies. In particular, evidence is mounting that feeding interactions in the soil are not restricted to the traditional energy channels (e.g. de Boer et al., 2005; Heidemann et al., 2011; Geisen et al., 2015). In addition, the original assumption that mycorrhizal fungi do not decompose organic matter has been revised in recent years by

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evidence that, in particular, ectomycorrhizal (EM) fungi can decompose organic matter (Read and Perez-Moreno, 2003; Phillips et al., 2013). However, the classical soil food web does not distinguish between arbuscular mycorrhizal (AM) and EM fungi. Moreover, the classical soil food web distinguishes between a labile and a recalcitrant pool of organic matter, and assumes that “bacteria use labile substrates twice as fast, per unit biomass, as do fungi and that (saprotrophic) fungi use resistant substrates twice as fast per unit biomass as do bacteria” (Hunt et al., 1987). This concept of different pools of organic matter has been challenged recently by the argument that soil organic matter forms a continuum of states and pools (Lehmann and Kleber, 2015). Here, we will focus on emerging evidence that challenges the traditional model of C inputs and their use by the bottom trophic levels, and the implications these may have for the traditional soil food web model.

2. C flow in soil food webs

The first food web models assumed that the C that fuels the detrital fungal and bacterial energy channels, consisting of a labile and a recalcitrant pool, predominantly originated from above-ground inputs such as leaf litter. This view was updated by Pollierer et al. (2007), who showed that soil fauna predominantly derived their C from root litter and exudates and not from leaf litter. At the time, the prevailing hypothesis was that only bacteria used labile C, and that it was unlikely that the highly labile C in root exudates would contribute energy to the fungal energy channel and higher trophic levels. However, recent work shows that root exudates constitute a major pathway of belowground C inputs (Nguyen, 2009) and are fundamental to food web controls on C and N cycling in response to climate change (Phillips et al., 2011). Moreover, recent evidence shows that both bacteria and fungi rapidly consume and respire root exudate C (De Deyn et al., 2011; Rousk and Frey, 2015), thus challenging the view that fungi primarily consume recalcitrant litter. Supporting these findings, Eissfeller et al. (2013) found root-derived recent photosynthate C in higher trophic levels of both the fungal and the bacterial energy channel.

Another important source of belowground labile C inputs is the transfer of recent plant photosynthate C to mycorrhizal fungal hyphae, which can occur extremely quickly (De Deyn et al., 2011; Hannula et al., 2012). Although it is assumed that the ability of AM fungi to decompose organic matter is limited, EM fungi have been shown to be able to decompose or cleave organic substrates to meet their nutrient demand (Read and Perez-Moreno, 2003; Talbot et al., 2008; Cheng et al., 2012). Recent work shows that this ability of EM fungi to decompose organic matter can increase soil C pools through competition for organic N between EM fungi and the decomposer community, supposedly resulting in a reduction in soil organic matter nutrient concentrations and increased soil C inputs through greater plant growth (Orwin et al., 2011; Averill et al., 2014). While empirical mechanistic research into the exact mechanisms underlying this increase in soil C pools is sorely needed, EM decomposition of organic matter also has the potential to increase the availability of labile substrates for bacteria and fungi and the energy channels they support (sensu Moore et al., 2004). In addition, AM fungi can prime the decomposition of organic matter by supplying plant-derived C to saprotrophic fungi and bacteria (Herman et al., 2012). Thus, the root energy channel can contribute to the labile C pool that is used by fungi and bacteria via two mechanisms: decomposition of organic matter by EM fungi, and direct transfer of recent root-derived photosynthate C by AM fungi. Importantly, this root-derived C in AM hyphae can enter this labile litter pool relatively quickly, for example when hyphae are pierced by fungal-feeding nematodes, similar to bacteria and fungi leaking their internal solutes as a waste product of grazing (Hunt et al.,

1987; Koller et al., 2013). Therefore, AM fungi can connect the three energy channels at the bottom of the soil food web, providing a rapid pathway through which recently photosynthesised C enters the soil food web.

3. A new central role for labile C and its consumption in soil food webs

Despite its relatively small pool size, fluxes of labile (dissolved organic) C are large because of continuous production (through decomposition and root exudation) and consumption (van Hees et al., 2005; Boddy et al., 2007). For example, van Hees et al. (2005) estimated that heterotrophic respiration of root exudate C constitutes 10–20% of total soil respiration. Despite slight modifications in soil food web models to represent the complex role of C inputs (e.g. the inclusion of a water soluble sugar pool in Holtkamp et al. (2008)), current food web models do not represent the importance of this C pool, and its consumption by the bottom trophic levels of the soil food web. Here, we propose the following modifications to existing food web models:

1. Despite the usually small standing pool size of labile C, inputs of labile C are the dominant source of C for the bottom trophic levels in the soil food web on short to medium timescales (hours to seasons) (Bardgett et al., 2005).
2. Saprotrophic fungi use more labile C than previously assumed. Using the model from Moore et al. (2004) (Fig. 1a), we show that fungal and bacterial populations can coexist in a stable state with large inputs into the labile C pool, a high fungal use of labile C, and high fungal mediated transfer of C from the recalcitrant to the labile pool (Fig. 1, Supplementary Methods). By increasing inputs into the labile C pool and the consumption of this pool by fungi (Fig. 1b), we show that fungi can achieve high consumption of the labile pool while also consuming the recalcitrant pool. Our model shows that both fungi and bacteria increase with increased input to the labile pool and increased rates of fungal mediated transfer of labile C (Fig. 1c, e).
3. In addition to their well-established role in protecting soil C through increasing soil aggregation (Rillig and Mummey, 2006; Wilson et al., 2009), EM fungi can decompose organic matter to meet their nutrient demands, thereby potentially increasing the amount of labile substrate available for saprotrophic fungi and bacteria.
4. The role of labile C is enhanced further through the contribution of mycorrhizal fungi to this C pool, through EM fungal organic matter decomposition by extracellular enzymes, and through AM fungi supplying saprotrophic fungi and bacteria with recent photosynthate.

This proposed role of labile C as a major C input into the soil food web has important implications for our understanding of soil C cycling and the role of the soil food web. Intuitively, the high use of labile C by saprotrophic fungi and bacteria might result in higher microbial turnover and respiration, priming of the decomposition of soil organic matter, and lower soil C pools. However, following the Microbial Efficiency-Matrix Stabilization (MEMS) framework by Cotrufo et al. (2013), labile C substrates are used more efficiently by microbes than recalcitrant litter, and are thus the most important source of microbial products and the main precursor of stable soil organic matter. Our proposed modifications are in line with the MEMS framework and suggest a higher microbial C use efficiency of labile C substrates than previously assumed. In particular, EM decomposition of organic matter would increase the availability of labile C, and high labile C use by fungi would increase soil organic matter formation because of their intrinsically higher substrate use

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