



## Points of View

# Dinner in the dark: Illuminating drivers of soil organic matter decomposition

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## ABSTRACT

Soil organic matter (SOM) dynamics plays a crucial role in soil ecosystem functioning and global warming. SOM is normally degraded slowly, but its decomposition rate can change substantially after addition of easily decomposable C sources. This process, known as “the priming effect”, has already been described in 1926 but is still poorly understood. Priming can be positive (extra decomposition of SOM) or negative (reduction of SOM decomposition), depending on the amount and physicochemical characteristics of added compounds, the composition of SOM and the metabolic abilities of responding microorganisms. We propose that the understanding of priming effects can be greatly advanced by investigating the level of convergence between the chemical characteristics of the added compound and SOM fractions, and the functional potential of microbial communities. This can be achieved by combining two different disciplines—microbial ecology and biogeochemistry. Such knowledge will deliver information under which conditions sequestration of soil carbon can be expected and provide possibilities to steer soil carbon dynamics in sustainable agricultural systems.

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## 1. Introduction

In terrestrial ecosystems, large quantities of carbon (1500 Gt in the first meter) are held in soil organic matter (SOM) (Jobbágy and Jackson, 2000). Its turnover plays a crucial role in soil ecosystem functioning and global warming. SOM is critical to the stabilization of soil structure, retention of plant nutrients and maintenance of water-holding capacity. Furthermore, the decomposition of SOM releases mineral nutrients thereby making them available for plant growth (Johnston et al., 2009). SOM formation results from microbial and geochemical processes that convert carbon (C) mainly comprised of plant litter and microbial biomass into stabilized, potentially long-lived materials (Kögel-Knabner, 2002). Whereas SOM is often thought to be mainly composed of degraded plant litter, microbial exudates and necromass are themselves also important components of SOM (Clemmensen et al., 2013; Liang and Balseer, 2011). Long turnover times of organic compounds are not only explained by anaerobic conditions such as in peats, but also by incorporation into aggregates after the attachment of organic

matter to protective mineral surfaces and the intrinsic biochemical properties of SOM (Lehmann and Kleber, 2015; Schmidt et al., 2011). This physical and chemical stabilization of SOM hinders microbial decomposition via restricted mobility of microbes, diffusion of water, enzymes and oxygen (von Lütow et al., 2007). In addition, it requires a broad range of microbial enzymes to degrade the insoluble macromolecules that comprise SOM (Wallenstein and Weintraub, 2008). SOM stabilization can thus provide a possibility for long-term storage of carbon. However, intensive soil management practices can disrupt soil aggregation and soil organisms that contribute to aggregation, thereby enhancing release of carbon to the atmosphere (Powlson et al., 2011). Recently, the French government proposed ahead of COP21 (Conference of Parties on climate change) to sequester annually an additional 0.4% of the current soil carbon stock to combat global warming, and sustainable agricultural practices are seen as valuable options to reach this target.

One of the crucial processes in ecosystem carbon balances is the “priming effect” on SOM decomposition. This effect is defined as the increase in decomposition of soil carbon stocks as a result of addition of easily degradable compounds (Bingeman et al., 1953). However, negative priming, e.g. a decrease in SOM decomposition, can also occur. Priming is not yet considered in current carbon-

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cycle-climate models (Perveen et al., 2014) as the underlying mechanisms are not well understood (Heimann and Reichstein, 2008; Zhu et al., 2014). Yet, priming effects can have dramatic impacts on ecosystem carbon budgets. For instance, exudation of carbon compounds by living roots can suppress 50% or stimulate up to 400% of SOM decomposition (Zhu et al., 2014).

## 2. Current view

To date, the most widely held explanation for positive priming effects is the theory of co-metabolism, i.e. the addition of easily degradable organic compounds serves as an energy source for microorganisms to synthesize extracellular enzymes capable of degrading SOM. Direct and indirect co-metabolism have been suggested to be responsible for the priming effect. It has been shown that the addition of labile C first stimulates the growth of pioneering micro-organisms (Kuzyakov, 2010). After a slight lag phase, these opportunistic responders are followed by bacteria and fungi that utilize more recalcitrant C (e.g. the necromass of the pioneers) and increase their enzyme activity leading to a co-metabolic decomposition of SOM (Fontaine et al., 2003; Blagodatskaya et al., 2014). Direct co-metabolism has also been shown; addition of ryegrass induced a priming effect whereas glucose did not (Wu et al., 1993). It was suggested that the enzymes produced by the microorganisms degrading the ryegrass, were also capable of decomposing fractions of SOM. However, supply of carbon compounds to soil resulted in a huge variation of priming effects, ranging from large – and small positive, to no or even negative priming effects (Hamer and Marschner, 2002; Kuzyakov et al., 2007; Blagodatskaya et al., 2007; Rousk et al., 2015). Nitrogen (N) limitation has also been proposed as an additional factor regulating priming effects by stimulating microbes that mine for N in SOM (Fontaine et al., 2011). Negative priming effects occur less often than positive priming effects (Kuzyakov et al., 2000), and are often explained by the result of “preferential substrate utilization”. After addition of easily degradable compounds, soil microorganisms prefer to utilize the added substrate to SOM (Fontaine et al., 2004a). This leads to a temporary decrease of SOM decomposition. In spite of all publications on priming effects, a clear mechanism remains elusive. We propose to combine two important disciplines –microbial ecology and biogeochemistry–to unravel the mechanisms driving priming effects with the purpose to provide possibilities to steer soil carbon dynamics.

## 3. Perspectives and implications

Major observations that may lie at the basis of understanding priming effects are:

1. The supply of different carbon compounds to soils induces priming effects that vary greatly in direction and magnitude (Dalenberg and Jager, 1989; Wu et al., 1993; Shen and Bartha, 1997).
2. The extent and direction of priming is influenced by the amount of added carbon compounds (Blagodatskaya and Kuzyakov, 2008; Guenet et al., 2010).
3. Similar carbon compounds can trigger different priming effects in different soils (Hamer and Marschner, 2005).

Thus, priming effects depend on the amount and physico-chemical characteristics of the added substrate and the properties of the receiving soil. The latter could involve both the composition of SOM and that of the responding micro-organisms. Fontaine et al. (2003) suggested that the degree of physicochemical similarity between the added carbon substrate and SOM is an important

factor explaining the extent of the priming effect. If added compounds trigger the production of extracellular enzymes by microbes, then these enzymes will also decompose fractions of SOM resembling the added compounds. For example, it has been shown that cellulose addition can stimulate two types of microbes: soil C decomposing microbes that also use cellulose, and specialized microbes that exclusively decompose cellulose (Fontaine et al., 2004b). However, the link between physicochemical properties of SOM and added substrates, and the extent of the priming effect has not yet been investigated.

Elaborating on the suggestion by Fontaine et al. (2003), we propose that the understanding of priming effects can be greatly advanced by investigating the level of convergence between the components involved, namely the physicochemical characteristics of the 1) added compound and 2) SOM fractions, and 3) the functional potential of microbial communities (Fig. 1). The functional potential of microbial communities can be grouped based on specific characteristics, such as extracellular enzyme profiles or ability to decompose hydrophobic compounds (Allison, 2012; Krasowska and Sigler, 2014). We hypothesize that a high degree of physicochemical similarity between added compounds and SOM fractions will result in a positive priming effect provided that indigenous soil microbes adapted to decompose SOM are well represented (Fig. 1A, hypothesis A). Adding a substrate that is chemically similar to SOM fractions, but with immediate access for microorganisms since it is not occluded in SOM aggregates (Lützow et al., 2006), will provide an extra source of energy to spark decomposition of SOM. Alternatively, a high degree of physicochemical dissimilarity between added compounds and SOM fractions will stimulate groups of microbes that decompose the added substrate without affecting SOM (“preferential substrate utilization” theory). This results in no or even negative priming effects (Fig. 1B, hypothesis B). An alternative explanation for this scenario is that microbes decomposing the added compounds have antagonistic effects against the SOM-degrading microbes resulting in decreased SOM decomposition. For instance, bacteria that grow on easily degradable compounds do often have antifungal activities to prevent fungi from using these substrates, including production of antibiotics, lytic enzymes and volatiles (De Boer et al., 2015). In addition, it has been shown that opportunistic fungi can delay the growth of specialized lignin-degrading fungi (Greaves, 1971; Van der Wal et al., 2007). A third possibility is that during negative priming, microorganisms grow on the added C (preferential substrate utilization), and their exudates increase SOM protection via greater reactivity towards mineral surfaces and incorporation into aggregates (Lehmann and Kleber, 2015). No or negative priming effects can also be expected when substrates are added that resemble fractions of the SOM but without the presence of microbial communities that are able to degrade these substrates and/or SOM fractions. This can for instance be the case in soils that have been contaminated with organic pollutants (Fig. 1C, hypothesis C). Biostimulation of microbes by addition of compounds that chemically resemble the pollutant may only lead to increased pollutant degradation after the microbial communities have adapted to decompose the organic pollutants in the soil (Kowalchuk, 2012).

We expect that hypotheses A and B will be especially applicable to soils where microbial communities are strongly adapted to breakdown of plant-specific compounds that are preserved in SOM fractions, such as cutin, suberin, lignin-derived molecules and tannins (Spielvogel et al., 2010; Kononova, 1966). It has been shown that saprophytic fungal communities are, to a certain degree, specialized on different litter – and wood types (Osono, 2007; Van der Wal et al., 2013). Since plant litter provides the primary source of SOM formation, it is likely that SOM-degrading microbes are, to some extent, also specialized on their substrate. This idea

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