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Priming effects: Interactions between living and dead organic matter

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ABSTRACT

In this re-evaluation of our 10-year old paper on priming effects, I have considered the latest studies and tried to identify the most important needs for future research. Recent publications have shown that the increase or decrease in soil organic matter mineralization (measured as changes of CO_2 efflux and N mineralization) actually results from interactions between living (microbial biomass) and dead organic matter. The priming effect (PE) is not an artifact of incubation studies, as sometimes supposed, but is a natural process sequence in the rhizosphere and detritusphere that is induced by pulses or continuous inputs of fresh organics. The intensity of turnover processes in such hotspots is at least one order of magnitude higher than in the bulk soil. Various prerequisites for high-quality, informative PE studies are outlined: calculating the budget of labeled and total C; investigating the dynamics of released CO_2 and its sources; linking C and N dynamics with microbial biomass changes and enzyme activities; evaluating apparent and real PEs; and assessing PE sources as related to soil organic matter stabilization mechanisms. Different approaches for identifying priming, based on the assessment of more than two C sources in CO_2 and microbial biomass, are proposed and methodological and statistical uncertainties in PE estimation and approaches to eliminating them are discussed. Future studies should evaluate directions and magnitude of PEs according to expected climate and land-use changes and the increased rhizodeposition under elevated CO_2 as well as clarifying the ecological significance of PEs in natural and agricultural ecosystems. The conclusion is that PEs – the interactions between living and dead organic matter – should be incorporated in models of C and N dynamics, and that microbial biomass should regarded not only as a C pool but also as an active driver of C and N turnover.

1. Introduction

It is amusing that our highly cited review on the mechanisms of priming effects (Kuzyakov et al., 2000) originated from a *rejected* research proposal designed to investigate interactions between carbon (C) pools in soil. In preparing the proposal, we – Jürgen Friedel, Karl Stahr and myself – thoroughly reviewed the available literature on priming effects (PEs), summarized earlier suggested mechanisms, and developed some new hypotheses. The topic was exciting and we were convinced that it was important and would provide a new direction of research. In other words, it had the potential to initiate a new way of thinking about the interactions between biotic and abiotic components, living and dead organic matter. We overcame our disappointment after the rejected proposal and decided to extend what started out as a conventional literature review and discuss suggested approaches to priming effect (PE) quantification and methods for identifying mechanisms.

1.1. Why the high citation?

The paper's citation success is a result of a number of factors and not just because of the sexy word 'priming'. Looking back it is clear that we achieved at least some of the prerequisites necessary to generate an appealing (and therefore highly cited) paper.

1) The review was timely – as shown by the fact that the next development step in PE studies was at least partly based on approaches suggested and opinions expressed in our paper. Despite the fact that the phenomenon was discovered 84 years ago (Löhnis, 1926) by studying the effect of legume green manure on mineralization of humus N and that the term 'priming effect' was suggested by Bingemann et al. in 1953, it remained largely unrecognized until the 1980s and 1990s. The review by Jenkinson et al. (1985) raised the importance of the inter-relationships between the pools in soil, but was focused on N and mainly related to abiotic processes of isotopic exchange with added mineral ^{15}N. As described below, the new view expressed in our 2000 paper on the interactions between biotic and abiotic pools challenged the conservative picture on

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independent turnover of individual pools (including microbial biomass), which at that time had been incorporated into most models of C and N dynamics (reviewed by Molina and Smith, 1998; Smith et al., 1997, 1998; Manzoni and Porporato, 2009). To us, the phenomenon of PE suggested new and alternative explanations for the many reports of changes in SOM decomposition after modifications in the pool composition.

2) The paper was of interest to a large number of soil biologists, ecologists and biochemists. This is because many research groups, both then and now, investigate C and N dynamics, nutrient availability for plants, turnover of SOM pools, C availability and stability, and the dependence of C dynamics and turnover on microbial biomass. A review linking these topics, therefore, was appealing and (rewardingly for us) stimulated studies related to understanding the mechanisms of soil functioning for C sequestration and N provision for plants.
3) The isotopic approaches recommended to study PEs were becoming available to a broad research community. We stated that using isotopes was necessary to unambiguously measure the priming effect. This is because it is the only way to separate C and N from various sources. Isotopes were first applied in soil science in the 1940s but even back then studies focused on the *interactions* between added and already existing pools (Broadbent, 1947; Bingeman et al., 1953; Halam and Bartholomew, 1953). In the early 1990s isotopes began to be applied more widely in soil science and the approaches suggested in our review could be adopted easily by many groups.

Last, but not least, our paper not only provided an overview, summary and systematization of studies up to 2000 but also went beyond the 'state of the art' and suggested PE mechanisms as well as providing an outlook on further development. The stimulation of further research has been the most exciting outcome of our paper.

In the last ten years studies on priming effects have become an important (and often controversial) part of soil ecology research, especially in Germany (e.g. Hamer and Marschner, 2005; Blagodatskaya et al., 2007; Dilly and Zyakun, 2008), France (Fontaine et al., 2004; Guenet et al., 2010), the USA (Cheng, 2009; Rasmussen et al., 2007), the UK (Bol et al., 2003a; Nottingham et al., 2009; Paterson et al., 2009) and Italy (Mondini et al., 2006). More than 300 papers have discussed the topic and *Soil Biology & Biochemistry* is home to a high number of these studies. We reviewed recently the mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure (Blagodatskaya and Kuzyakov, 2008). Therefore, in this article I have elected to look back over the decade since the review was published and suggest directions for future studies.

2. Background

2.1. Is priming a real process in natural soils or is it an artifact of adding glucose?

Some doubt the existence of priming effects in what they call 'real soil'. They are sceptical and believe that PEs are merely artifacts arising when we add glucose (or other easily-degraded C sources). In fact, the decomposition of most natural polymers releases monomeric sugars into the soil, and the addition of soluble bioavailable substances is, therefore, not artificial. In other words, as polysaccharides (and especially cellulose) are the most common polymer in plant litter (reviewed by Kögel-Knabner, 2002), adding its decomposition product – glucose – is a frequently used (and perfectly logical) approach. Glucose is also the most often released sugar in rhizodeposits (Derrien et al., 2004) and its microbial transformation parallels, and is therefore representative of, that of other monosaccharides (Derrien et al., 2007).

As the PE is the response after C input into the soil a comparison with a control soil without the addition of substrate is necessary in order to measure PE. In incubation experiments, we simulate the input of organics that occurs in natural ecosystems. Therefore, as stated by Nottingham et al. (2009): "*Evidence suggests that, rather than a rare phenomenon, real priming effects commonly occur in most plant–soil systems*." So, those soil biologists who neglect the priming effect actually neglect a fundamental process: the contribution of microbial biomass and its activity to the SOM turnover.

2.2. Types of C input into soil

In temporal terms there are two kinds of inputs of organics into soil: (i) one-time or occasional (i.e. as a pulse), as described in our original review or (ii) permanent (continuous). The *pulse* inputs are typical for the breakdown of microbial, root and animal cells, decomposition of above-ground litter with subsequent leaching of dissolved organic matter (DOM), and root exudation. Because of the ready availability of soluble organics, such inputs produce hotspots of microbial activity in which the turnover rates are much higher than they are outside of these zones. The lifetime of such hotspots is estimated at a few days (Pausch and Kuzyakov, in press). Most priming studies have simulated single-pulse inputs and only a few have investigated repeated pulses (Hamer and Marschner, 2005; Chigineva et al., 2009).

The *continuous* input (which was not considered in 2000 paper) is typical for the slow decomposition of dead roots, leaf and shoot residues, and for some rhizodeposits. In all these cases, the substrates are less immediately metabolisable and, therefore, utilized slowly and over longer periods. Because of the low availability, it is likely that the array of extracellular enzymes generated to degrade these organics may be more efficient at decomposing SOM in comparison with the largely intracellular enzymes that breakdown the easily-available substrates (Fontaine et al., 2003). Only a few studies have examined the effects of continuous input on the decomposition of organics (Kuzyakov et al., 2007) leading to increase of microbial biomass, its activity and SOM turnover.

For the rhizosphere, whether the input is pulsed or continuous depends on the rooting density. Because of the continuously moving root tip, the presence of zones with different rhizodeposition types (Kuzyakov, 2002), and the short lifetime of the hotspots (Pausch and Kuzyakov, in press) there is a pulse input for only a small soil volume around the root. However, if the soil is very densely rooted (e.g. upper few cm in grassland soil), the input by rhizodeposition is more or less continuous and the individual hotspots are joined to form large zones of high activity (i.e. gross rhizosphere). A special case of long-term continuous input is the increase of rhizodeposition of plants grown at elevated CO_2 conditions (Paterson et al., 1997, 2008).

2.3. Location and duration of the priming effect: the importance of hotspots

Microbial hotspots in the soil are important locations for the PE. These are found mainly in the rhizosphere and the detritusphere, but also the drillosphere and some other biopores (Nannipieri et al., 2003). The rhizosphere is the most important of these with regard to PEs and many have shown accelerated SOM decomposition and nutrient release in the presence of growing plants (Blagodatskaya et al., 2009; Cheng, 2009). These studies have been summarized and potential mechanisms involved in priming effects in the rhizosphere suggested (Kuzyakov, 2002; Cheng and Kuzyakov, 2005; Blagodatskaya and Kuzyakov, 2008). One general conclusion is that