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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

studies of SOM turnover should always include the effects of living roots (Cheng, 2009; Frank and Groffman, 2009). The other large group of PE studies have simulated the detritusphere and investigated the effects of plant compounds (Fontaine et al., 2007) or plant residues on SOM decomposition. It is difficult to draw a general conclusion on the priming effects in the detritusphere, partly because of wide differences in the availability and composition of plant residues and their components. To my knowledge, very few studies have been conducted on PEs in the drillosphere (Brown, 1995).

The duration of PEs remains an open and important question. Although many earlier studies (and in fact our review) stated that PEs arise immediately after substrate addition, it has now been accepted that the onset of what we call the 'real' PE may be delayed for days or even weeks (Fontaine et al., 2004; Blagodatsky et al., 2010). Linking experiments with modeling has revealed that, shortly after the input of easily-available substrates, the microbial turnover increases (termed the 'apparent' PE), and only later does the turnover of SOM change to a significant extent (the real PE) (Blagodatsky et al., 2010). Thus, even after the substrate is exhausted, some microorganisms remain active and the extracellular enzymes produced during the period of high activity remain in the soil and contribute to SOM decomposition. Accordingly, once arisen, hotspots affect microbial activity for longer periods and SOM turnover remains high even after exhaustion of the initial priming substrate(s).

2.4. Turnover intensity in hotspots

Priming effects are exemplified by intensified SOM turnover in hotpots of microbial activity stimulated by rhizodeposition or other substrate inputs (e.g. organic fertilizers, dead microbial biomass). However, in conventional experiments the hotspots are much smaller than the volume of soil filling the incubation vessel or the pot in which the plants are grown. Even in Ah or Ap horizons the rhizosphere usually occupy less than 10% of the soil volume (for example the zone of P depletion around the roots amounts between 0.5 and 3% of soil volume: Ge et al., 2000; Hinsinger et al., 2005). In addition, it is difficult to evenly distribute added substrates because much remains at the drop points. Even gentle mixing of the soil fails to disperse the added substrates: most of them remain on aggregate surfaces. Therefore, the actual concentration of the added substrates in these hotspots is much higher than that calculated for the whole soil volume. Notwithstanding, when calculating PE intensity, the change of SOM turnover is related to the whole soil volume and disregarded the turnover in the microsites. This dilutes the actual process intensity in the hotspots by large soil volume, in which the process rates are the same as in the control soil. If we accept that the rhizosphere makes up less than 10% of soil volume then the intensity of the PE in the rhizosphere is actually more than 10 times higher than that calculated for the whole soil volume. So, the 2–3-fold increase in SOM turnover due to growing plants (e.g. Cheng, 2009) actually means a microsite increase in the rhizosphere at least 20–30 times! Only few studies have estimated the intrinsic turnover intensity in such hotspots (Hill et al., 2008; Fischer et al., in press) because we lack suitable methods to evaluate the intensity of these and other processes at this scale (Frank and Groffman, 2009). We must always bear in mind however, that PEs occur at much higher local intensities than calculated.

2.5. What is the driver?

Most previous studies, and nearly all models of C and N dynamics (Molina and Smith, 1998; Smith et al., 1998), assume independent decomposition and turnover of the pools based on 1st order kinetics (i.e. decomposition depends solely and directly on pool size). Our review was among the first to give a clear indication that the decomposition of individual pools is not independent and is actually driven by microbial biomass activity stimulated by available substrates. By introducing PEs we suggested that microbial biomass is not only a pool but also a driver of the turnover (Blagodatsky et al., 2010). The decomposition and turnover of SOM pools are (micro) biologically driven processes whose rates may be modified by abiotic factors (see recent controversial discussions about the limitation of SOM decomposition by biotic and abiotic factors: Kemmitt et al., 2008; Kuzyakov et al., 2009a; Brookes et al., 2009; Paterson, 2009).

2.6. Which microorganisms prime SOM decomposition?

The question as to which microbes are responsible for SOM degradation is still an open one and is very closely connected with PE mechanisms: do bacteria, fungi and/or other microbial groups prime SOM decomposition? As shown by ^{13}C incorporation in PLFA, bacteria are the first group to trap and metabolize most of the easily-available organics after their input into the soil (Paterson et al., 2007; Moore-Kucera and Dick, 2008). This, in turn, accelerates the turnover of bacterial biomass, especially of *r*-strategists, triggering apparent PE (Blagodatskaya et al., 2007; Nottingham et al., 2009) (Fig. 1). The responsibility for the further steps remains an open question. Fontaine et al. (2003) suggested that other groups of microorganisms, that preferentially utilize poorly-available substrates (such as SOM), benefit from bacterial necromass remaining after the easily-available organics was exhausted. One such group may well be the fungi: they specialize in accessing and degrading substrates that are poorly available to most bacteria and, in contrast to bacteria, can grow through low nutrient zones to the distantly-located substrates using their hyphae (Otten et al., 2001). Such organisms, which are predominantly *K*-strategists (Fontaine et al., 2003; Blagodatskaya et al., 2007), are stimulated by moribund bacteria and their lysates, which increases SOM decomposition and thus real PE. However, as shown recently by ^{13}C-PLFA, Gram-negative bacteria may also contribute to real PE (Nottingham et al., 2009). So, the statement that *only* fungi are responsible for priming is probably incorrect. This is because *r*- and *K*-strategists are represented within the bacteria and fungi, and in both groups various species are specialized with regard to

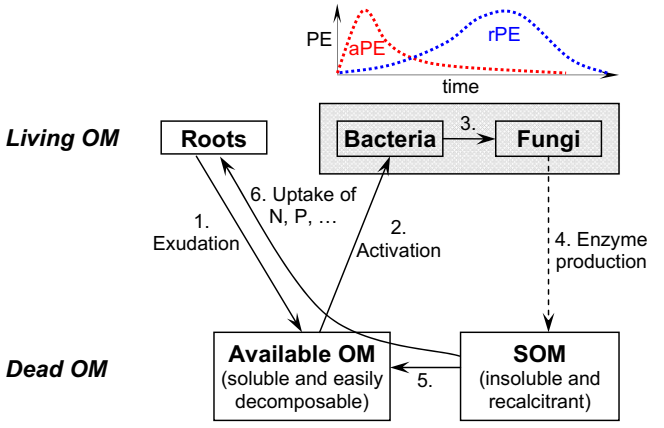

Fig. 1. Sequence of processes inducing apparent (aPE) and real (rPE) priming effects: 1. Input of available organics by rhizodeposition (Exudation). 2. Activation of microorganisms (mainly *r*-strategists) by available organics (Activation). 3. Activation of *K*-strategists. 4. Production of extracellular enzymes that degrade SOM by *K*-strategists (Enzyme production). 5. SOM decomposition and production of available organics and mineral nutrients. 6. Uptake of nutrients by roots. The dynamics and sequence of individual processes are described in detail in Blagodatskaya and Kuzyakov (2008). → fluxes; — — → effects; ····· dynamics of apparent priming effects (aPEs) and real priming effects (rPEs).

decomposing substrates of different availabilities (and even may switch their preferences depending on the substrate present). Note also that other microbial groups (e.g. actinomycetes, protozoa, archaea) have not been investigated in priming experiments. Furthermore, most priming studies are short term (a few weeks to 2–3 months) and only a very few (Blagodatskaya et al., 2007; Marx et al., 2007; Paterson et al., 2008) have examined the dynamics and activity of microbial groups over an extended period. We just don't know how long real PEs last and which microbial groups are responsible for them at different stages.

The proposed succession of mechanisms (Fig. 1) may be relevant for rhizosphere PEs but it is not obvious that it applies to the detritusphere. Because the generally higher molecular mass and many structural compounds plant residues are less bioavailable than rhizodeposits, the release of soluble organics by decomposition is typically slower. Therefore, the sequential processes typical for pulse inputs (Fontaine et al., 2003; Cheng and Kuzyakov, 2005; Kuzyakov and Bol, 2006; Blagodatskaya and Kuzyakov, 2008) overlap, at least partly, and the involvement of microbial groups at different stages is less obvious. As fungi are strongly concerned with plant residue decomposition (Chigineva et al., 2009), we can expect that their contribution to PEs induced in the detritusphere to be higher than in the rhizosphere. Mycorrhizal fungi, in particular, can access distantly-located substrates and stimulate SOM decomposition (Chalot and Brun, 1998) and some are able to switch to a saprophytic diet (Dabire et al., 2007). This combination of properties makes fungi a highly important microbial group for real PEs.

3. Requirements for priming effect experiments

I expect the topic of PE to be highly relevant to future studies in basic and applied soil biology, ecology, and C and N cycling. PE mechanisms, the drivers and the microbial groups involved are important in recognizing how interactions function between living and dead organic matter. In applied studies, this emphasizes the importance of comparing the processes of C stabilization, SOM turnover, and nutrient release under natural and agricultural ecosystems, and especially nutrient acquisition by plants in organic agriculture.

The number of PE studies will increase, but to be of real value these investigations must meet certain requirements. Some of these were already suggested in our original review but based on the progress in the last ten years (and the many errors), I have outlined below the most important requirements for future research.

3.1. Budget of C and N

The budget of added C (in most cases labeled C) should always be presented and compared with the amount of C released from SOM. This means reporting not only the amount of added C released from soil as CO_2 (as in most studies) but also the amount of C remaining in the soil and that incorporated into microbial biomass and other pools. Such remaining labeled C (and N) should be compared with the amounts of extra CO_2 released from SOM and microbial biomass (Dalenberg and Jager, 1989; Dijkstra and Cheng, 2007a; Cheng, 2009; Nottingham et al., 2009). This calls for presenting the full mass balance between the C added to the system and that which is released. Based on positive PEs, some studies have stated losses of SOM as CO_2 and argued that this makes a contribution to the CO_2 increase in the atmosphere. This is unjustified unless the complete C budget is presented. The increased turnover (higher input + higher output) does not necessarily mean decrease of the C stock (Dalenberg and Jager, 1989). In fact most studies that have presented C budgets state a net increase of C stock despite positive PEs.

3.2. Accounting for microbial biomass by calculating priming effects

All previous studies have estimated PEs based on changes of unlabeled CO_2 flux in treatments with and without substrate addition. This is certainly the correct approach, but altered SOM decomposition is reflected not only by CO_2 efflux changes but also in microbial biomass. Therefore, the increase of microbial biomass C from the unlabeled substrate should also be accounted for and added to the changes in CO_2 efflux (Nottingham et al., 2009). This will undoubtedly present a more complex but more correct picture of PE and, additionally, will help separate the real from the apparent.

3.3. Separation of apparent and real priming effects

As the extra CO_2 released by priming may originate from SOM and/or from microbial biomass turnover, it is crucial to estimate C fluxes from individual sources. Unfortunately, it is not possible to uniformly label microbial biomass without labeling SOM or *vice versa*. This prevents disentangling real and apparent PEs based on isotopes. Nonetheless, the PE dynamics and the amount of the released extra CO_2 give important hints about the sources (Nottingham et al., 2009; Blagodatsky et al., 2010) and therefore, reflect whether the PEs are apparent or real. Note here that experimental errors cannot be considered as apparent PE (as some have reported!). Apparent PEs are due to additional CO_2 released from the increased turnover of microbial biomass and not extra CO_2 from SOM (Blagodatskaya and Kuzyakov, 2008).

According to PE dynamics, the initial flush of extra CO_2 occurring within the first 0–3 days mainly (or at least partly) reflects accelerated turnover or pool substitution in microbial biomass (Fig. 2).

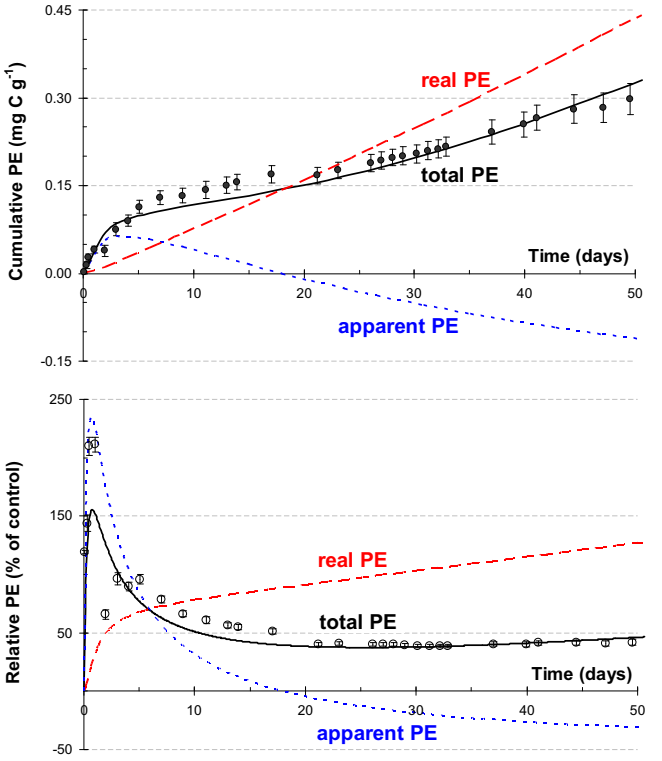

Fig. 2. Dynamics of apparent and real PEs and their contribution to total PE after addition of ^{14}C glucose to Ah of loamy Haplic Luvisol. The PEs are presented as the absolute amount (top) and as percentage of each flux in the control soil without glucose addition (bottom). Apparent PE was calculated by acceleration of microbial biomass turnover after glucose addition, and real PE presents accelerated decomposition of insoluble SOM. Points present measured PE (±SEM). After Blagodatsky et al. (2010).

This is the apparent PE. The contribution of apparent PE to the overall total PE probably increases with substrate availability. On the other hand, the real PE in the first 2–3 days is small but increases over time, completely replacing the apparent PE after several days (Fig. 2).

The amount of released extra CO_2 should be compared with microbial biomass C (Dalenberg and Jager, 1989). Clearly, if the released additional CO_2 exceeds the C in microbial biomass, at least some of that CO_2 must have originated from SOM. According to the percentage of microbial biomass that is active at any one-time – about 2–3% of the total (Anderson and Domsch, 1978) or even less (Blagodatsky et al., 2000) – at least this portion of extra CO_2 originates from accelerated microbial biomass turnover. The concepts regarding accelerated microbial turnover and its connection with active microbial biomass or with the activation of the usually passive microorganisms are open and urgently need further investigation.

3.4. Dynamics of the priming effects, microbial biomass and related parameters

The dynamics of additional CO_2 production are much more informative than merely the cumulative CO_2 recorded at the end of the experiment. PE dynamics allow tracing changes over time, recognizing the distinction between apparent and real PEs (Nottingham et al., 2009; Rasmussen et al., 2007), and determining possible compensation of negative and positive PEs during different periods (Blagodatsky et al., 2010). Such dynamics are also important to decide how long an experiment should last in order to take into account the decline and eventual termination of the PE. Even though many studies have measured PE dynamics, only a few have looked at this overall picture. Of course, PE dynamics should be linked with that of the microbial biomass and nutrient release.

Because microbial biomass drives PEs, a knowledge of its dynamics is a prerequisite for evaluating the underlying mechanisms (this was stated in our 2000 paper). Information about the dynamics of other parameters related to SOM decomposition and to the initial and subsequent changes in microbial community structure would also be very helpful (Blagodatskaya and Kuzyakov, 2008). Critical among these are: microbes and enzyme activities responsible for SOM breakdown (Fontaine et al., 2004); initial and changing amounts of easily-available C and of soluble C (Blagodatsky et al., 2010); and the bacterial/fungal ratio (for methods see Joergensen and Wichern, 2008). Measurements of the microbial biomass must go beyond presenting only total amounts. Additional factors which reflect microbial functions are: the incorporation of the label into microbial biomass or into specific microbial groups (e.g. by ^{13}C-PLFA, Paterson et al., 2007; Nottingham et al., 2009); changes in community structure including the ratio of *r*- and *K*-strategists (Blagodatskaya et al., 2007; Chigineva et al., 2009); utilization preferences for specific substrates (CLPP, Salome et al., 2010); and activity of microbial biomass. The last mentioned may be estimated by substrate induced growth respiration (SIGR) (Blagodatsky et al., 2000), rRNA (Anderson and Parkin, 2007), CLPP (Insam et al., 1996; Williamson and Wardle, 2007), ATP (Wen et al., 2005), Wright and Hobbie's approach (Wright and Hobbie, 1966; Panikov et al., 1992; Blagodatskaya et al., 2009), ^{13}C-PLFA (Denef et al., 2009) and other techniques (Nannipieri et al., 2003).

3.5. Availability of C and nutrients

Many studies have explained the differences in the PEs between soils with reference to nutrient availability (e.g. Cheng, 2009) and various PE mechanisms have been related to the C/N ratio in microbially-available pools (Kuzyakov, 2002). One of the most common explanations for a positive PE after adding substrates with a high C/N ratio is that microorganisms are mining for N from SOM and thus increase its decomposition and the evolution of CO_2. The released additional nutrients during these processes are used by microorganisms and later by roots (Fig. 1). This calls for considering the changes of available N (and probably other nutrients), and its occurrence in microbial biomass and plants (if present) in order to better understand the underlying mechanisms.

3.6. Continuous and repeated input

The questions related to the impacts of repeated and continuous inputs remain unanswered, even though in soils under field conditions both situations are frequent (see above). Hamer and Marschner (2005) showed a repeated priming response following four pulse additions of substrate. However, the effects were less pronounced when the substrates were added continuously (Kuzyakov et al., 2007). This calls for studies of both continuous and repeated inputs to evaluate the periodicity and intensity of PEs and whether the microbial community adapts to repeated additions and stabilizes the turnover at a new steady state. Such studies will strongly contribute to our understanding of the mechanisms driving PEs under elevated CO_2.

3.7. Identification of more than two C sources

Until now, most studies have been based on identifying only two C (or N) sources: 1) added C (or N) labeled by ^{14}C or ^{13}C (or ^{15}N), and 2) unlabeled C (or N) present in the soil before substrate addition. These two C sources were identified in released CO_2 and, in a few cases, in microbial biomass and DOM (Nottingham et al., 2009). In order to identify the SOM pools responsible for priming as well as to distinguish real and apparent PEs, more than two C sources should be detected. This is possible either by using one C isotope and a combination of treatments (Subke et al., 2004; Kuzyakov and Bol, 2004, 2006) or by applying two C isotopes: labeling by ^{13}C and ^{14}C at natural abundance level (Fontaine et al., 2007), or combining ^{13}C natural abundance with ^{14}C labeling – a method that we are using currently (Blagodatskaya et al., unpublished). Such three-source partitioning could prove especially effective if the identification involved not only CO_2, but also microbial biomass and DOM. Such an identification of SOM pools responsible for priming is crucial for PE modeling and for evaluating the stability of SOM in future land-use and climate change scenarios.

3.8. Reverse approaches for priming effect estimation

Nearly all previous studies of priming involved adding labeled substrates to unlabeled soil. A *vice versa* approach – adding unlabeled substrates to labeled SOM – would decrease statistical errors because PE would be estimated in one step. Moreover, applying unlabeled substrates to labeled soil may help identify SOM pools. Complementary approaches could use naturally labeled (Dalenberg and Jager, 1981), artificially synthesized, labeled humic substances (Kappler et al., 2000; Ji et al., 2000) or even very stable C pools such as labeled black carbon (Kuzyakov et al., 2009b). The use of differently labeled precursors for synthesizing humic substances would allow placing the ^{14}C or/and ^{13}C label in groups with contrasting availability (Kappler et al., 2000). Applying unlabeled substances to these synthesized, specifically labeled humic substances, would elucidate sources of priming and help clarify the mechanisms (Dalenberg and Jager, 1981).

3.9. Priming effects and SOM stabilization mechanisms

Organic matter is stabilized (i.e. becomes non-bioavailable) in soils by various mechanisms (Sollins et al., 1996; von Lützow et al., 2006). Up to now, only a few studies have evaluated the contribution of individual stabilization mechanisms to the extra CO_2 released during

PE (Ohm et al., 2007; Salome et al., 2010). Surely the mechanisms that reduce the accessibility of organics for decomposers (e.g. occlusion in aggregates, intercalation, hydrophobicity) are completely different from those responsible for releasing the organics bound to mineral surfaces (sesquioxides, phyllosilicates) and metal ions (Rasmussen et al., 2007). PEs can strongly accelerate the decomposition of very stable C pools such as black carbon (Hamer et al., 2004; Kuzyakov et al., 2009b). The first steps in clarifying such destabilization and its subsequent mineralization are urgently needed and will contribute strongly to clarifying PE mechanisms.

3.10. Statistical errors of measured priming effects

The priming effect is commonly calculated in two steps (Kuzyakov et al., 2000): (i) subtraction of labeled CO_2 from total CO_2 in the treatment following substrate addition; and (ii) subtraction of unlabeled CO_2 in treatments with and without addition. Because of there being two steps, the statistical error of the estimated PE is higher than that of measured CO_2. Also it should be noted that the second step is based on the means of CO_2 between the treatments. This prevents the traditional calculation of the SD (or SE) based on individual replications, requiring instead the use the SD of the means (Kuzyakov and Bol, 2004).

The uncertainties of estimated PEs are especially high when using ^{13}C natural abundance approaches (e.g. C_3–C_4 vegetation change, FACE, labeling by depleted CO_2). This reflects the: (i) high variation of $\delta^{13}C$ of the end-members and of the mixed pool; (ii) utilization of individual substances with different $\delta^{13}C$ from one C source with different rates; (iii) frequently unaccounted isotopic fractionation and certain other problems (Hobbie and Werner, 2004; Bowling et al., 2008; Werth and Kuzyakov, in press). Especially in PE studies, this calls for using those end-members with maximal difference of $\delta^{13}C$ and for considering the $\delta^{13}C$ variation of the end-members in the calculations, for example by using the IsoError model (Phillips and Gregg, 2001). Only PEs significantly different from zero should be accepted.

4. Future needs and research questions

4.1. Field experiments

It is important to relate PE studies, most of which have been done under controlled laboratory conditions, to the conditions prevailing in the field. This is the complicated issue of scale-up and there is no doubt that compiling budgets of added labeled substrates (a prerequisite for PE calculations) or any other C inputs to the soil under field conditions are much more difficult than under controlled conditions. The 'artificial' addition of easily-available substrates can, of course, be done under field conditions, but the options of changing C availability in soils without any such addition must also be considered.

In the presence of plants, root exudation is likely to be changed by altering photosynthesis (Paterson et al., 2009; Kuzyakov and Gavrichkova, 2010). Photosynthesis can be decreased not only by shading or cutting the above-ground plant parts (Craine et al., 1998; Kuzyakov and Cheng, 2001, 2004) but also by water stress. Another approach to reduce the C allocation to the living roots involves mechanical (Högberg et al., 2001) or physiological girdling (Johnsen et al., 2007) and then evaluating the components of the CO_2 efflux from soil (Subke et al., 2004). Both approaches – reducing photosynthesis and C allocation to below-ground – must be connected with labeling in order to separate SOM decomposition from root-derived CO_2. Similar studies under field conditions that have manipulated below-ground C input showed a strong effect of root exudates on decomposition (Subke et al., 2004). Manipulating above-ground C input from litter is an efficient alternative for inducing priming in the detritusphere (Crow et al., 2009).

Another possibility to induce PEs under field conditions is to change nutrient availability. This can be done by N fertilization, but should be linked with a separation of root-derived and SOM-derived CO_2 efflux. For such studies, and especially when calculating N mineralization, added nitrogen interactions should be considered (Jenkinson et al., 1985).

4.2. Incorporation in models

As described above, PEs are interactions between, on one hand, the organic pools of various availabilities and, on the other, living and dead organic matter. Such interactions must be included as components of models of C and N dynamics. To date, most models are based on the decomposition of individual C pools described by 1st order kinetics. The decomposition rate depends only on environmental parameters (mainly soil temperature and moisture), but not on the presence and state of the other C pools. This means that the interactions between the pools are not considered (Wutzler and Reichstein, 2008; Blagodatsky et al., 2010). Accordingly, most models neglect the presence and activity of microbial biomass in the decomposition of dead organics. This nonsense demands immediate attention!

First, the decomposition rate of individual pools must be related to the microbial biomass and its activity. This would represent a small but significant improvement to the models and involve an additional modifier of the rate constant. Another, probably more powerful and promising approach, is to construct the models based, not on the decomposition of individual pools, but on their utilization by microorganisms (Fontaine and Barot, 2005; Blagodatsky et al., 2010). This means that the microbial biomass feeds on the pools and that the rate of this depends on the amount and activity of microbial biomass. The availability of individual SOM pools, probably based on various stabilization mechanisms (von Lützow et al., 2006), should be considered also and will no doubt affect the microbial biomass activity. Even though parameter estimation in such an approach is more difficult than the commonly used 1st order kinetics, these linkages will reflect the real situation in soil. Similar approaches are already incorporated in some models (Blagodatsky and Richter, 1998; Gignoux et al., 2001; Fang et al., 2005; Fontaine and Barot, 2005; Neill and Gignoux, 2006) and allow PE simulations but, to my knowledge, only one model has been proven experimentally (Blagodatsky et al., 2010).

The new models should also consider the fact that microorganisms may utilize exclusively the soluble substances. Therefore, the DOM pool is crucial in soil not because of possible C and N losses by leaching as is frequently stated in studies but because only DOM contains substances that are directly available for microbial metabolism. Depolymerizing extracellular enzymes (glycosidases, phenoloxidases, glucosaminidases, peptidases, etc.) breakdown the many polymers and generate soluble dimers and monomers. Therefore, it is essential that the model parameterization considers the depolymerases' activities and DOM availability. In summary, microbial biomass and its activity must be incorporated in the models not as a pool but as a driver (Blagodatsky et al., 2010).

4.3. Elevated CO_2: changes of C input by plants into the soil and rhizosphere

Many FACE studies emphasized that more C will be allocated into the soil by plants grown at elevated CO_2 (Paterson et al., 1997; Cheng, 1999; Zak et al., 2000; De Graaff et al., 2006). The turnover of fine roots (Pregitzer et al., 1995) and microbial biomass (Blagodatskaya et al., 2010) will be accelerated leading to higher

production of root-derived CO_2 from soil (Martens et al., 2009). Because of this continuous input of additional available substrates in the rhizosphere the importance of the hotspots for microorganisms and their activities should increase under elevated CO_2 (Table 1). This will promote faster turnover and faster utilization of both easily- and poorly-available C pools; will compensate for higher C input by rhizodeposition (Blagodatskaya et al., 2010), and may even decrease the stock of sequestered C in the soil (Hoosbeek et al., 2004; Heath et al., 2005). It is scientifically challenging and urgently important to clarify mechanisms of SOM turnover in a high CO_2 world, the contribution of rhizosphere PEs to accelerated turnover (Billings et al., 2010), and to determine if *the sinks become the sources* and the *pools are converted to fluxes*?

Furthermore, the quality of plant residues under elevated CO_2 will be shifted towards increasing amounts of structural compounds and elevating the C/N ratio (Norby et al., 2001 and references therein). The microbial community will, therefore, emphasize groups (e.g. fungi Dorodnikov et al., 2009) specialized in decomposing poorly-available compounds. This may then lead to a higher production of enzymes that degrade previously stable SOM, thereby accelerating its turnover (Table 1).

4.4. Temperature increase

Increasing soil temperature accelerates most enzyme activities and, as a consequence, SOM decomposition. Noteworthy is that the decomposition of poorly-available SOM pools will be accelerated disproportionately compared to easily and moderately available SOM pools (Bol et al., 2003b; Leifeld and Fuhrer, 2005). Although the data on the preferable acceleration of poorly-available SOM pools at increasing temperatures are contradictory (von Lützow and Kögel-Knabner, 2009), most of them stem from incubation studies and neglect the additional input of freshly available organics that may induce PEs. The effect of priming on SOM decomposition is known to be higher than the effect of temperature (Hoosbeek et al., 2004). However, the reports on direct effects of temperature on PEs are scarce (Bader and Cheng, 2007; Kuzyakov et al., 2007) and cannot be generalized. One important research step in determining the sensitivity of PEs to temperature should involve 3-C-source partitioning (see above): C of the priming substance, and C from at least two SOM pools with different isotopic signature corresponding to contrasting decomposability.

Table 1
Future quantitative and qualitative changes of C input in soil and environmental conditions and their expected effects on priming of soil organic matter.

Expected changes of C input and environmental conditions	Changes of PE
C input by plants into soil at elevated CO_2	
– increase of root-C input	?↑
– increase of rhizodeposition	↑
– increase of C/N in roots and rhizodeposition	?↑
– increase of C/N in shoot litter	?↑
– decrease of N availability	?↑
Increase of temperature	?↓
– general increase of turnover rates	?↓
– decrease of available pools	?
– relative increase of recalcitrant pools	?↓
Decrease of soil moisture	?↓
Soil fertility and management	
– decrease of available C pools	?
– higher (optimized) fertilization	↓
– destruction of aggregates	↑
Involvement of subsoil	?

Increase (↑), expected increase (?↑), decrease (↓), expected decrease (?↓) of PE; (?) the effects are not clear.

4.5. Soil moisture decrease

Although any future changes in precipitation strongly depend on climatic zone and region, increasing heavy rains and longer drought conditions are expected (IPCC, 2007). Because the water from heavy rains cannot be completely absorbed by soil (especially soil whose structure has been degraded), because of higher temperatures that increase water losses by evapotranspiration, and longer drought periods are predicted, it is expected that the soil moisture will decrease. This will partly be counterbalanced by reduced evapotranspiration of plants under elevated CO_2 (Weigel et al., 2005). The few studies that investigated the effect of moisture on priming showed an increase of PE with increasing soil moisture (Niklaus and Falloon, 2006; Dijkstra and Cheng, 2007b).

4.6. Soil fertility changes

Intensive agriculture decreases soil fertility by decreasing C stocks and microbially-available C pools, destroying aggregates, increasing soil density, etc. This means that the contrast in the availability between annual C input (by rhizodeposition and litter) and SOM-C will increase, and the importance of available C for microorganisms will also increase. As the contrast between the hotspots of microbial activity and the bulk soil increases, the role of PEs may become greater.

4.7. Involvement of subsoil

Intensive agriculture (e.g. fertilization, ploughing, plough pan development, etc.) has led to a much higher allocation of roots within the Ap horizon (0–20 or 0–35 cm) compared to natural ecosystems. This has intensified the C turnover in the topsoil *versus* the subsoil. The decreasing input of available C by roots into the subsoil has lessened the importance of PEs in the subsoil. Recently, managements such as no-tillage practices, low fertilizer input and organic farming have attempted to increase rooting depth and to use water and nutrients from the subsoil. This may again accelerate C turnover in the subsoil, as it is controlled by fresh carbon supply (Fontaine et al., 2007). However, there are many uncertainties in these processes, and the mechanisms within the soil profile may be different compared to the topsoil (Jueschke et al., 2008; Salome et al., 2010).

4.8. Generalizations and the main question

As we stated in our 2000 paper PEs were observed in many soils after adding various substrates and following plant growth. We have reviewed previously recent progress since that paper (Blagodatskaya and Kuzyakov, 2008). One important question is whether PEs are unique to soils or whether other ecosystems having C sources of contrasting availability exhibit similar phenomena. Recently, in a mini-review Guenet et al. (2010) suggested that similar effects are common in aquatic ecosystems. This calls for more studies of PEs in other ecosystems and suggests that the ecological importance of the phenomena is much wider than that initially observed for soils.

There are many open questions with regard to the phenomena of PE and the interactions between living and dead organic matter in soil. Some of them – the hows (i.e. mechanisms), whats (microbial groups), wheres (hotspots), and whens (time periods) – are partly answered in the many original studies and the reviews. However, the most fascinating questions in science remain – these are the why. *Why* were PEs evolved and *why* are they necessary in soils, in the rhizosphere and for ecosystems? There are many hypotheses and speculations about the ecological significance of PEs (i.e. Kuzyakov et al., 2000; Kuzyakov, 2002; Frank and

Groffman, 2009; Lambers et al., 2009) but clear experimental confirmations are wanting.

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