cells it usually has a positive value as the entry of water causes the protoplast to push against the cell wall (see *Turgor Pressure*). In xylem cells there is a negative pressure potential, or tension, as a result of transpiration.

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PRIMING EFFECTS IN RELATION TO SOIL CONDITIONS – MECHANISMS

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Definitions and terms

Priming effect is defined as a short-term change in the turnover of soil organic matter caused by treatments, usually addition of organic C to the soil (Kuzyakov et al., 2000) (Figure 1). Usually since the soil organic matter (SOM) turnover is not directly measured, but it is determined by changes in CO_2 efflux rates or N mineralization rates, the origin of extra CO_2-C (*primed carbon*) or N cannot be directly evaluated. Therefore, the *real priming effect* (RPE) cannot be assessed based only on extra CO_2. Other processes, such as accelerated microbial turnover may contribute to the changes in the CO_2 efflux rates or N mineralization rates (Dalenberg and Jager, 1981; Wu et al., 1993; De Nobili et al., 2001). Accelerated CO_2 evolution in response to the activation of microbial metabolism and higher microbial biomass turnover is not related to the SOM turnover and is termed as *apparent priming effect* (APE). Usually, the microbial succession initiated by the input of fresh organic matter is accompanied by activation of various, previously dormant microorganisms that respond specifically to the added substrate. Accelerated activity of such microorganisms may enhance the degradation of soil organic matter as a result of co-metabolism and higher enzyme production, i.e., RPE. Thus, both apparent and real priming actions are governed by microbial activity. Few studies, however, have evaluated PE as a function of abiotic factors such as temperature, moisture, pH, etc.

Jenkinson et al. (1985) suggested that RPE is an increase in the decomposition of recalcitrant SOM, whereas APE is an increase of microbial C turnover, which is not linked with changes of SOM decomposition. Usually the term "apparent" has been used in relation to primed CO_2-C originated from soil microorganisms (De Nobili et al., 2001; Gioacchini et al., 2002; Bell et al., 2003; Fontaine et al., 2003; De Neve et al., 2004; Hamer and Marschner, 2005; Hopkins et al., 2006; Mondini et al., 2006). However, in a few cases, the term "apparent" priming has been also used to interpret extra CO_2 evolution derived from experimental errors due to the use of nonuniformly labeled substrate, incomplete trapping of evolved CO_2, addition of high amount of substrate to soil (Brookes et al., 1990; Conde et al., 2005), or enhanced decomposition of organic matter in response to improved soil moisture (Niklaus and Falloon, 2006). We suggest such PEs be termed as *artificial* to distinguish them from microbially originated apparent PE.

According to Jenkinson et al. (1985), most changes in N mineralization after addition of N to soil are to be considered as apparent effects caused by N displacement reactions (with fixed ammonium or with microbial N) or by pool substitution. They assumed that real acceleration of SOM mineralization requires an excess of fresh organic matter with a wide C/N ratio. We believe that this could be one cause, but not the sole one for real PE.

In recent years, new terms such as "signaling" and "triggering" (De Nobili et al., 2001; Mondini et al., 2006) have been proposed for some PEs but they were not clearly defined. Here we define the *triggering effect* as an acceleration of internal microbial metabolism with quick increase in the respiratory activity promoted by trace amounts of substrate. In many studies and under field conditions, the amount of C added to soil does not represent a significant source of energy but can promote changes whose energy demand can be much higher than the energy of the added substrate. This triggering effect can activate dormant soil microorganisms if promoted by the addition of available low molecular substrates such as glucose and amino acids to soil (De Nobili et al., 2001; Kuzyakov and Bol, 2006). The triggering effect induced by the input of external substrate should be distinguished from *quorum sensing,* which includes a wide range of signal exchanges *within* soil microbial community producing multiple cell–cell signaling molecules (Lazazzera, 2000; Burmolle et al., 2003; Wang and Leadbetter, 2005) and inducing gene expression, encoding a variety of both phenotypical and physiological responses upon reaching a critical threshold (Gray and Smith, 2005). Since the underlying molecular mechanisms of the triggering effect need to be investigated, we can hypothesize that permanent or occasional input of available low molecular weight substrates associated to plant residues, root exudates, excretes of soil animals etc., can act as *external inducer* and can *trigger* the mechanism of microbial communication similar to quorum sensing that can regulate the behavior of a group of organisms (Raffa et al., 2005). Thus, the triggering effect promoted by external compounds can represent the first step in a *signaling pathways cascade*, which alter the behavior on a population-wide scale by intra- and interspecies microbial interactions (Gray and Smith, 2005; Waters and Bassler, 2005; Little et al., 2008).

Introduction

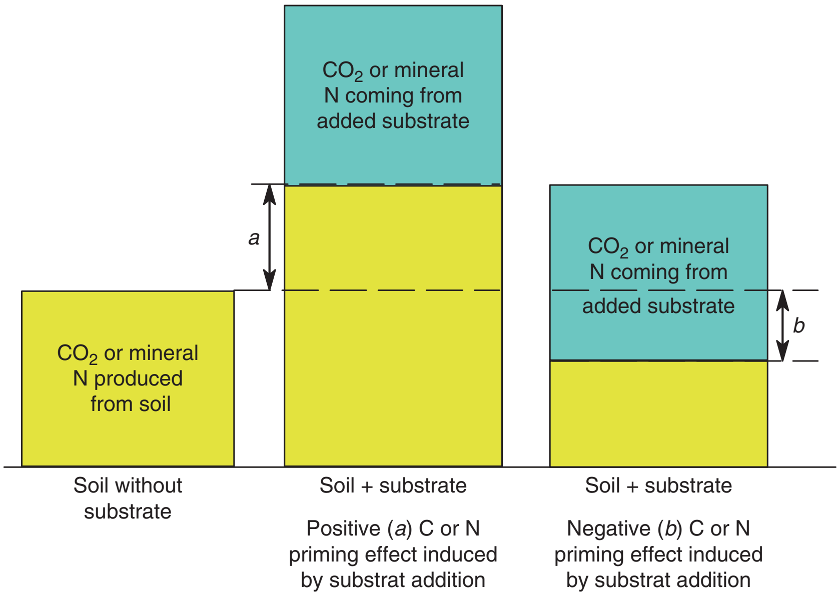
The term priming effect (PE) was introduced to describe changes in the SOM turnover affected by the addition of organic or mineral substances (Jenkinson et al., 1985; Kuzyakov et al., 2000) (Figure 1). Depending on soil conditions, such changes can result in acceleration or retardation of SOM decomposition (positive or negative PE, respectively). The intensity of both processes is governed by physicochemical factors such as temperature, soil moisture, and pH, which act indirectly – mainly by affecting microbial activity that drives the mineralization of SOM and plant residues. Beyond these abiotic factors, however, many biotic factors directly affect C mineralization in soil. These changes are due to changes in the microbial activity as a response to altered amounts and availability of C. The increase in the number of investigations on priming effects during the last decade (see Blagodatskaya and Kuzyakov, 2008 for details) reflects the interest in biotic mechanisms of carbon (C) turnover in soil (Chander et al., 1997; Carreiro et al., 2000; Bell et al., 2003; Falchini et al., 2003; Fontaine et al., 2003; Cheng and Kuzyakov, 2005; Conde et al., 2005; Perelo and Munch, 2005; Zyakun and Dilly, 2005; Brant et al., 2006; Fontaine et al., 2007) (Figure 2). The indirect effect of abiotic factors, which are the main drivers of C turnover in soil, is not considered in most of these studies.

There might be various mechanisms for the changes in microbial activity in soil after adding organic or mineral substances (Jenkinson et al., 1985; Kuzyakov et al., 2000; De Nobili et al., 2001; Fontaine et al., 2003; Schimel and Weintraub, 2003). However, most studies failed to prove the suggested mechanisms because the experiments were aimed at identifying priming effects (mainly by changes in CO_2 evolution) and not at identifying the mechanisms of these effects. This review will evaluate PE mechanisms based on CO_2 efflux data combined with other published data related to microbial biomass and activity. Therefore, we discuss the relationships linking the physicochemical soil conditions and the magnitude of priming effects observed in studies over the last decades. We distinguish real (SOM decomposition) and apparent (changes in microbial biomass turnover without effects on SOM decomposition) PE by considering the extra released C as affected by the amount of added C and microbial biomass C content (De Nobili et al., 2001; Luna-Guido et al., 2001; Hamer and Marschner, 2005; Mondini et al., 2006; Blagodatskaya et al., 2007). We also discuss the relationship between the phenomena of apparent or real priming effects and the role of soil properties, such as soil pH and aggregation, which were not considered earlier as affecting PE through their direct effect on biological activity.

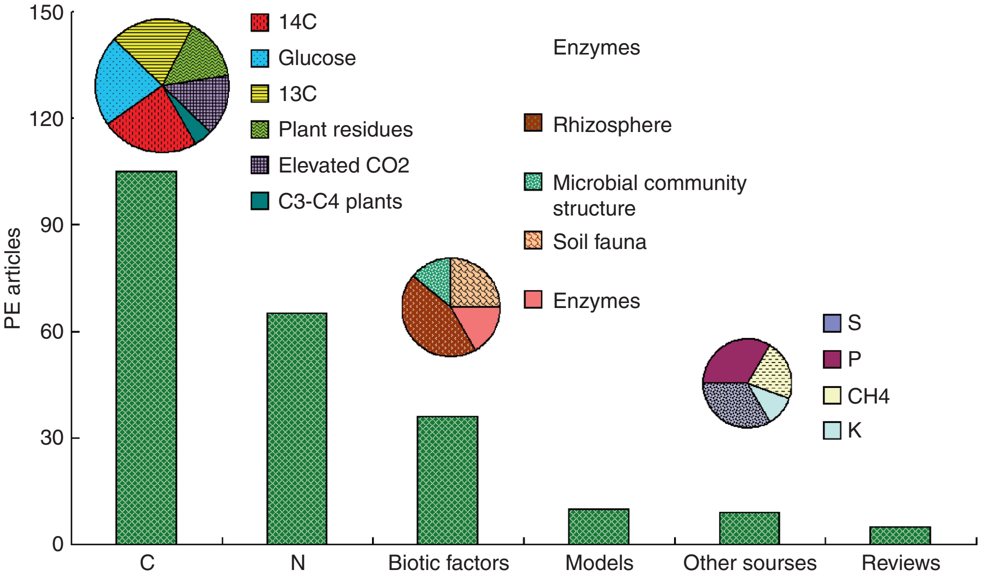
The amount of added substrate, the microbial biomass content, and priming effects

Adding easily available substances to soil provides C and energy sources to microorganisms. Depending on the amount of added C and energy, three types of changes can occur:

1. The amount of added substrate C is higher than the microbial biomass C content of soil and both microbial growth and changes in the community structure can occur.



Priming Effects in Relation to Soil Conditions – Mechanisms, Figure 1 Schema of the priming effect – nonadditive interactions between decomposition of the added substrate and of soil organic matter (*SOM*): (**a**) acceleration of SOM decomposition – positive priming effect, (**b**) retardation of SOM decomposition – negative priming effect.



Priming Effects in Relation to Soil Conditions – Mechanisms, Figure 2 Published papers to priming effects (*PE*) related to various questions: C and N mineralization, effect of biotic factors on PE, models simulating PE, release of S, P, CH_4, and K, and review articles from 1980 to late 2007. Web-of-Science citations with search options ("priming" AND "soil*") NOT "seed*" were evaluated.

2. The amount of added substrate C is similar or less than the microbial biomass C content of soil and changes in microbial activity and in turnover rate of the active microflora can occur, but the added substrate is not sufficient to induce microbial growth.
3. The amount of added C is much less than the microbial biomass C content of soil and the energy added is insufficient to directly accelerate microbial turnover. Either triggering or signaling effects can occur.

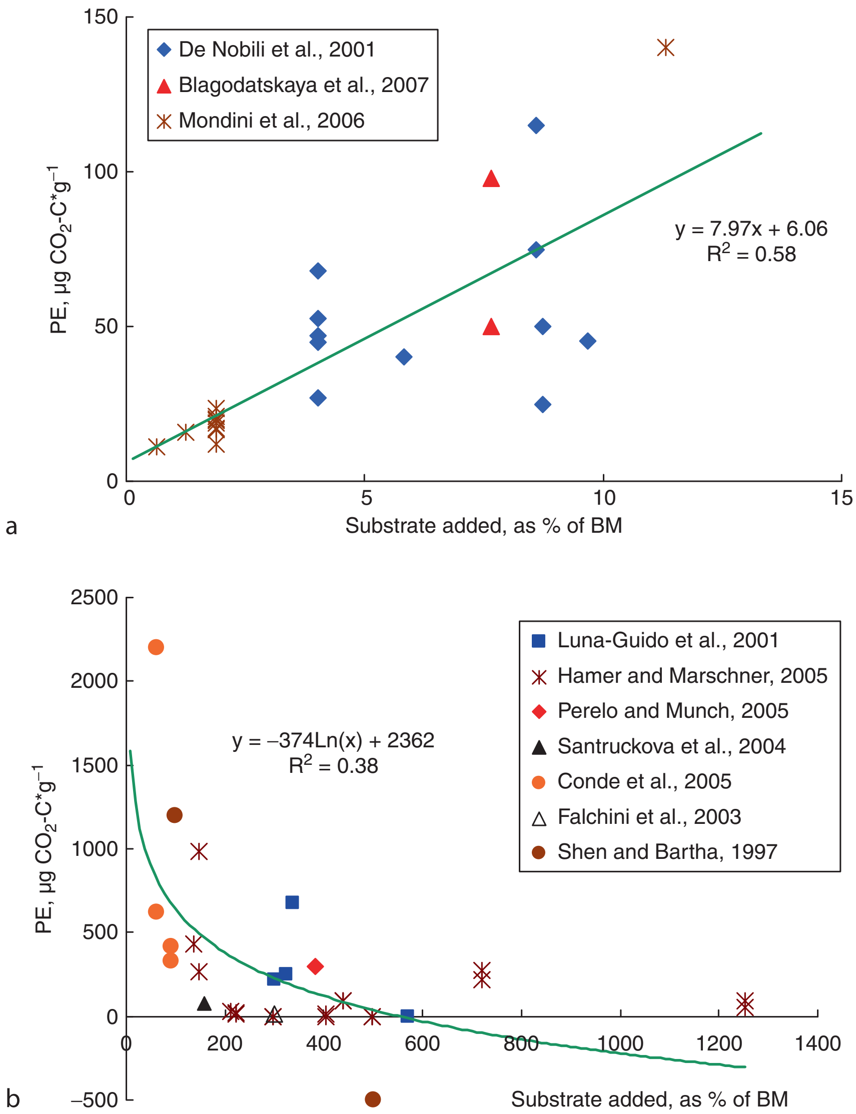
Here we discuss the threshold values for the three levels of substrate addition.

As the content of microbial biomass can differ in various soils, the amount of added substrate C should be expressed as the percentage of microbial biomass C (Figure 3). To find the threshold values for the three response possibilities mentioned above, we considered PE studies in which microbial biomass C was measured and a few studies (Shen and Bartha, 1997; Falchini et al., 2003; Fontaine et al., 2004; Conde et al., 2005), in which we calculated microbial biomass C considering that it represents 2% of the organic C content (Paul and Clark, 1989).

Surprisingly, two opposite relationships between the amount of added substrate and induced PE were found with different levels of added substrate C as related to microbial biomass C (Figure 3). When the amounts of added substrate C were lower than 15% of microbial biomass C, the magnitude of PE (here measured as extra CO_2) linearly increased with the amount of added C (Figure 3a). Therefore, for low levels of the added substrate, the PE is substrate limited and it confirms our hypothesis that priming effects are related to the energy input to the soil microorganisms by easily available substrates such as glucose and amino acids (Figure 3). This means that microorganisms were able to utilize these substrates within a few hours or less, and thus, these inputs probably represent a pulse of available energy promoting the shift from dormant to active state.

When the amount of added substrates C exceeded 50% of the microbial biomass C value, the amount of primed CO_2-C decreased exponentially by increasing the added C (Figure 3b). At the rates of substrate C exceeding 200–500% of microbial biomass C, the priming effect tended to be zero or even negative. Thus, the amount of added substrates switches the direction of PE. If easily available substrates were added in sufficient amounts, soil microorganisms start growing within 4–10 h (Blagodatskaya et al., 2007) and end within 1–3 days, depending on the used substrate and available nutrients. The 1–3 day period coincides with the maximal intensity of the observed priming effects. We suggest that such short-term priming effects induced at high levels of added substrates (comparable or higher than microbial biomass C) are mainly related with changes in microbial community structure and also involves their demand for other nutrients, such as N.

With a level of added substrate C being 2–5 times higher than microbial biomass C, priming effects tended to be close to zero or even negative. We assume that preferential microbial substrate utilization (Kuzyakov, 2002; Cheng and Kuzyakov, 2005) is the main process occurring at these levels of added substrates with the switch of substrate conditions for soil microflora from low available SOM to easily available and highly accessible added substrate. This can cause a lower SOM decomposition



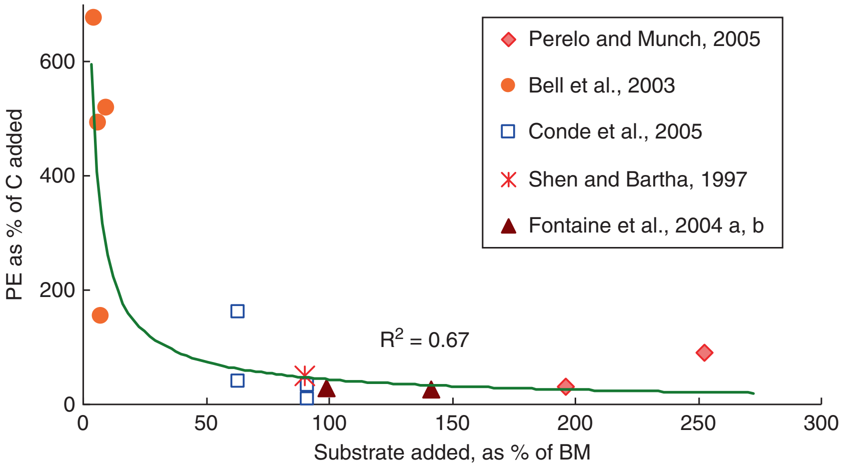
Priming Effects in Relation to Soil Conditions – Mechanisms, Figure 3 Primed CO_2–C efflux as affected by the amount of easily available substrate C added and expressed as percent of microbial biomass C; added C is $<$ 15% of microbial C (**a**); added C is $>$ 50% of microbial C (**b**).

with a negative PE. It is important to underline that the magnitude of PE by high levels of the added substrate is about one order higher than the PE induced at levels of added organic C lower than 15% of microbial biomass C.

When plant residues were added to soil, the relationship between PE and the amount of added substrate was similar to that occurring when easily available substrates were added to soil (Figure 4). The highest PE (expressed as percent of added substrate from study of Bell et al., 2003) was observed when the amount of plant residue-C accounted for 4–9% of microbial biomass C. By increasing the amount of plant residues an exponential decrease in PE was observed.

Therefore, studies comparing priming effects in different soils or in different horizons, should consider the microbial biomass content that can differ among different soils, and among different soil horizons. By considering that microbial biomass C varied in the range of 0.2–1% of total organic C in the study of Hamer and Marschner (2005), the amount of organic C added to soil as 1.3% of the SOM C was 1.4–12.5 times higher than microbial biomass C. This caused the absence of PE in some soil horizons when microorganisms were oversaturated by the added substrate. Regretfully, many reports on PE did consider neither organic C nor microbial biomass C content in soil.

In conclusion, when the added substrate C accounted for less than 15% of microbial C, a linear increase of extra



Priming Effects in Relation to Soil Conditions – Mechanisms, Figure 4 Relationship between the input of less available substrate (plant residues) to soil expressed as percent of microbial biomass C and CO_2–C primed expressed as percent of added C.

CO_2 occurred by increasing amounts of added substrate C. When the amount of added substrate C was between 50% and 200% of microbial biomass C, an exponential decrease in primed CO_2-C was observed. When the amount of added substrate C accounted for more than 200% of microbial C, no PE or negative PE occurred. When the added substrate C was lower than 15% of microbial biomass C, the magnitude of PE was one order lower than PE induced by substrate C amounting to 50–200% of microbial biomass C.

Apparent and real priming effects

Until now, no clear-cut approach has been suggested to distinguish apparent from real priming effects and it is not clear if the source of primed CO_2-C is SOM or the endogenous microbial metabolism (Bell et al., 2003). At least two different kinds of *apparent PE* can be caused by microbial activity when fresh available substrates are added to soil:

1. A triggering effect that is an acceleration of internal microbial metabolism by trace amounts of substrate with an immediate (several minutes to several hours) increase in the respiratory activity.
2. A pool substitution with acceleration of microbial turnover revealed by a long-term (several days or weeks) increase in respiratory activity (Jenkinson et al., 1985).

The *real PE* depends on the composition of added substrate used by microorganisms. If some nutrients, mainly N, are lacking, this shortage can be supplemented by an accelerated SOM decomposition resulting in a real PE. When complex organic substrates are added, soil microorganisms can use the energy of most available compounds to synthesize enzymes hydrolyzing the low available compounds. Therefore, SOM can be co-metabolized by microorganisms. Thus, *real PE* can be due to:

1. Mineralization of soil organic N to supply available N
2. Co-metabolism of SOM

The difficulties in distinguishing real and apparent PE also reflect the fact that both effects may occur simultaneously (Mondini et al., 2006).

We suggest relating the response time with PE magnitude for a better interpretation of PE. The following situations can occur:

1. *Short-term response: the amount of the primed carbon (C_{primed}) exceeds the rate of substrate additions (C_{added}) but it is lower than microbial biomass C (C_{BM}): $C_{added} < C_{primed} < C_{BM}$.* This type of PE is usually observed from hours to days after applying trace amounts (5–50 μg C g^{-1} soil) of substrate (De Nobili et al., 2001; Bell et al., 2003; Mondini et al., 2006; Blagodatskaya et al., 2007). It has been suggested that the quick short-term response with lower amount of primed CO_2-C versus microbial biomass C is a triggering effect that can be due to accelerated metabolism of soil microorganisms rather than to the decomposition of SOM. This hypothesis has been verified by adding unlabeled substrates to the ^{14}C-labeled microbial pool (Dalenberg and Jager, 1981; Bell et al., 2003). The flush of microbial primed $^{14}CO_2$-C detected immediately after adding ^{12}C derived from the increased turnover of microbial C. Therefore, if the amount of primed CO_2-C is much less than microbial biomass C, and if the additional CO_2 (or N_{min}) is released very shortly after substrate addition, then an apparent PE is probably observed.
2. *Long-term response: the amount of the primed carbon (C_{primed}) is higher than microbial biomass C: $C_{primed} > C_{BM}$.* This PE usually occurs during long-term incubation ranging from weeks to months (Shen and Bartha, 1997; Conde et al., 2005; Hamer and Marschner, 2005; Perelo and Munch, 2005) and can coincide

with a significant increase in microbial biomass. The presence of the apparent PE cannot be excluded even when the amount of extra CO_2 exceeds the initial microbial biomass C value since growing soil microorganisms can also contribute to the accelerated microbial turnover. Without applying isotopic labeled compounds, the real PE can only be evaluated if the amount of the primed carbon is higher than both microbial biomass C (C_{BM}) and the added C ($C_{added} < C_{primed} > C_{BM}$).

3. *Short and long-term responses*. Added substrate can accelerate both microbial turnover and decomposition of recalcitrant SOM. Thus, the observed PE may be the combination of both real and apparent PE. The triggering effect immediately after substrate addition is replaced by an apparent PE caused by pool substitution and occurring during the intensive substrate decomposition (Hamer and Marschner, 2005). Intensive mineralization results in a short-term increase in the active microbial biomass, which can also cause the real PE both during the intensive substrate mineralization and later at the beginning of microbial starvation. Thus, real PE can occur with apparent PE, as shown after the exhaustion of available ^{13}C-substrates added to soil (Perelo and Munch, 2005). It was shown that real PE occur as a significant increase in the incorporation of SOM-derived C in microbial biomass and this preceded the extra CO_2 evolution. Perelo and Munch (2005) suggested that substrate input increased the immobilization of soil organic C by soil microorganisms and then this microbial immobilized C was oxidized to CO_2 due to the accelerated microbial turnover.

To distinguish apparent from real PE in long-term incubation experiments, the amount of primed CO_2-C should be related to changes in microbial biomass during the studied period. We suggest that the contribution of real and apparent PEs to the total PE can be estimated by distinguishing substrate-originated and SOM-originated pools in the newly formed microbial biomass (Schneckenberger et al., 2008). Further studies with different labeling of the three most important pools (added substrate, microbial biomass, and recalcitrant soil organic matter) are required to distinguish apparent from real PE (Kuzyakov and Bol, 2006) and to precisely estimate the real PE.

Priming effects as related to substrate and soil properties

Substrate properties

As already mentioned, the availability, composition, and amount of substrate determine the magnitude and the type (real or apparent) of PE. The decomposition of easily available C sources (glucose, fructose, alanine) led to a greater PE than the addition of less available substrates, such as catechol, oxalic acid, plant residues, manure, or slurry to soil (Conde et al., 2005; Hamer and Marschner, 2005). Among the easily available substrates, glucose generally caused lower PE than L-glutamic acid (Mondini et al., 2006), a complex substrate mixture (root extract, rhizosphere soil extract; De Nobili et al., 2001), or an amino acid mixture (Mondini et al., 2006).

The amount of primed carbon is also dependent *on the amount of available N* in soil. Decrease in PE was observed when available N was applied to soil with organic C (Liljeroth et al., 1994; Cardon, 1996; van Ginkel et al., 1997; Martin-Olmedo et al., 2002; Blagodatskaya et al., 2007). This confirms the preferential substrate utilization (the added versus the SOM) if the main nutrients, such as N, are present. In the case of an input of C-rich substrates without N, soil microorganisms are activated to decompose SOM to acquire N with production of a real PE. However, it has been observed that N addition with glucose and plant residues can also produce a PE (Conde et al., 2005; Hamer and Marschner, 2005). Probably this depended on still high C-to-N ratio despite the N addition. The synthesis and the activity of various enzymes involved in C and N cycling are, respectively, controlled by N and C availability (Chander et al., 1997; Carreiro et al., 2000). Thus, N addition stimulated the activity of cellulases, while the activity of phenoloxidase, an important ligninolytic enzyme, was greatly reduced by the increased N availability (Carreiro et al., 2000). Similarly, the activity of amidohydrolases (Deng and Tabatabai, 1996) and other enzymes involved in N cycling (Skujins, 1976), was influenced by the organic C content of soils.

In conclusion, the addition of trace amounts of easily available substrates induces a short-term triggering effect, whereas the input of available substrate without nutrients in amounts sufficient for microbial growth leads to activation of SOM decomposition. If nutrients are present, no PE occurs or even preferential substrate utilization decreases SOM decomposition.

Soil physical properties

Since the effect of chemical (such as nutrient status and the C-to-N ratio of the active SOM pool) and physical soil properties on the PE were reviewed earlier (Kuzyakov et al., 2000; Kuzyakov, 2002), here we will focus on the effect of soil moisture, temperature, aggregation, and pH on PE as it is mediated by biological activity.

Soil moisture

Since soil moisture is the main driver of microbial activity, lower PE can be expected under limiting moisture conditions. The intensity of PE, however, can be also driven by the frequency and duration of drying–rewetting events. Rare rainfalls during long dry periods cause quick short-term activation of soil microorganisms metabolizing available substrates (microbial necromass, root exudates, plant residues. Quickly decreasing soil moisture is the main limiting factor of microbial activity under such conditions, so two types of PE can be expected before soil drying: (1) apparent PE caused by triggering microbial activity and by pool substitution mechanism or

(2) negative PE caused by preferential substrate utilization. Since SOM is not involved in such PE, carbon sequestration prevails under an arid climate. At high humidity the duration of decomposition processes can be relatively long, since microbial activity is not limited by soil moisture. So, other factors such as lack of nutrients become limiting at long-term wet periods. Microorganisms benefiting under such conditions can supply the lacking nutrients, degrading SOM and causing the real PE. Mineralization of SOM can occur under long-term high humidity resulting in accelerated SOM turnover. This mechanism can explain the relatively young age of humus in paleosoils formed during humid versus arid climatic periods (Alexandrovskiy and Chichagova, 1998). Thus, the alternation and duration of dry and wet periods are responsible for the type of PE prevailing in soil.

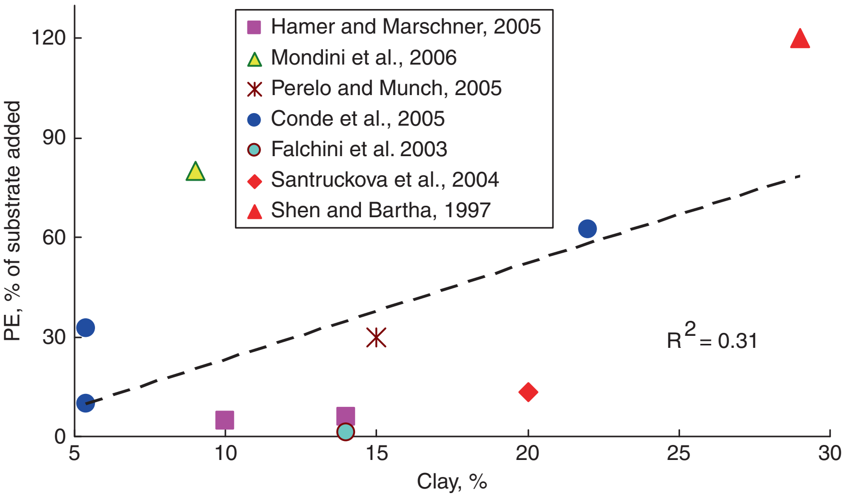
Soil temperature

It is still unclear, what type of PE can prevail at global climate warming. On the one hand, greater amount and availability of substrate (e.g., from enhanced rhizodeposition), accelerated microbial and enzymatic activity caused by increasing temperature, can result in greater PE intensity. On the other hand, psychrophylic microorganisms benefiting at low temperatures have the enzyme system with higher affinity to low available substrates such as soil humus. Both increase and decrease in PE were observed in different studies at low versus high temperature. Such discrepancy can be explained by the interactive effect of temperature and substrate availability, which should be considered in PE studies at low amounts of substrate (S) (Davidson and Jansesns, 2006). At high substrate amounts the decomposition rate does not depend on S and is only temperature dependent. Under substrate limitation, however, the rates of enzyme catalyzed reactions are mainly dependent on substrate affinity. Since psychrophylic microorganisms have greater affinity to low available substrates, no changes or even increase in decomposition rate can occur at low versus high temperature in the interval of very low substrate amounts (Kuzyakov et al., 2007).

Aggregate and particle-size fractions

The accumulation and physical protection of SOM as well as its mineralization depends on soil-aggregate size (Denef et al., 2001; Six and Jastrow, 2002) and the mean residence time of C in macroaggregates is shorter than that of C in microaggregates (Six and Jastrow, 2002). This indicates that the PE due to the response of microorganisms to substrate addition may vary in aggregates with different size. Indeed, Degens and Sparling (1996) observed that only the middle-sized fraction (1–2 mm) showed a significant and positive PE as a quick response to glucose addition and this PE was apparently related to microbial biomass. Both larger (>2 mm) and smaller (<0.25 mm) particles showed PE, long (21 days) after glucose application and probably both PEs were real because they were not due to microbial turnover (Degens and Sparling, 1996). The intermediate-aggregate size fractions (0.25–1 mm) showed a negative PE. Probably the differences in response in various aggregates size classes was due to the different localization of soil microorganisms; generally fungi predominate in macroaggregates, whereas bacteria predominate in microaggregates (Guggenberger et al., 1999).

Silt mainly contributes to the formation of microaggregates, while sand particles are mostly associated with macroaggregates. According to Kandeler et al. (1999), invertase activity mainly due to intracellular activity, was abundant in the silt fraction, whereas extracellular enzyme activities were distributed among particle-size fractions; thus xylanase activity was associated with sand, alkaline phosphatase activity with silt and clay, and protease activity with sand and clay. It is important to underline



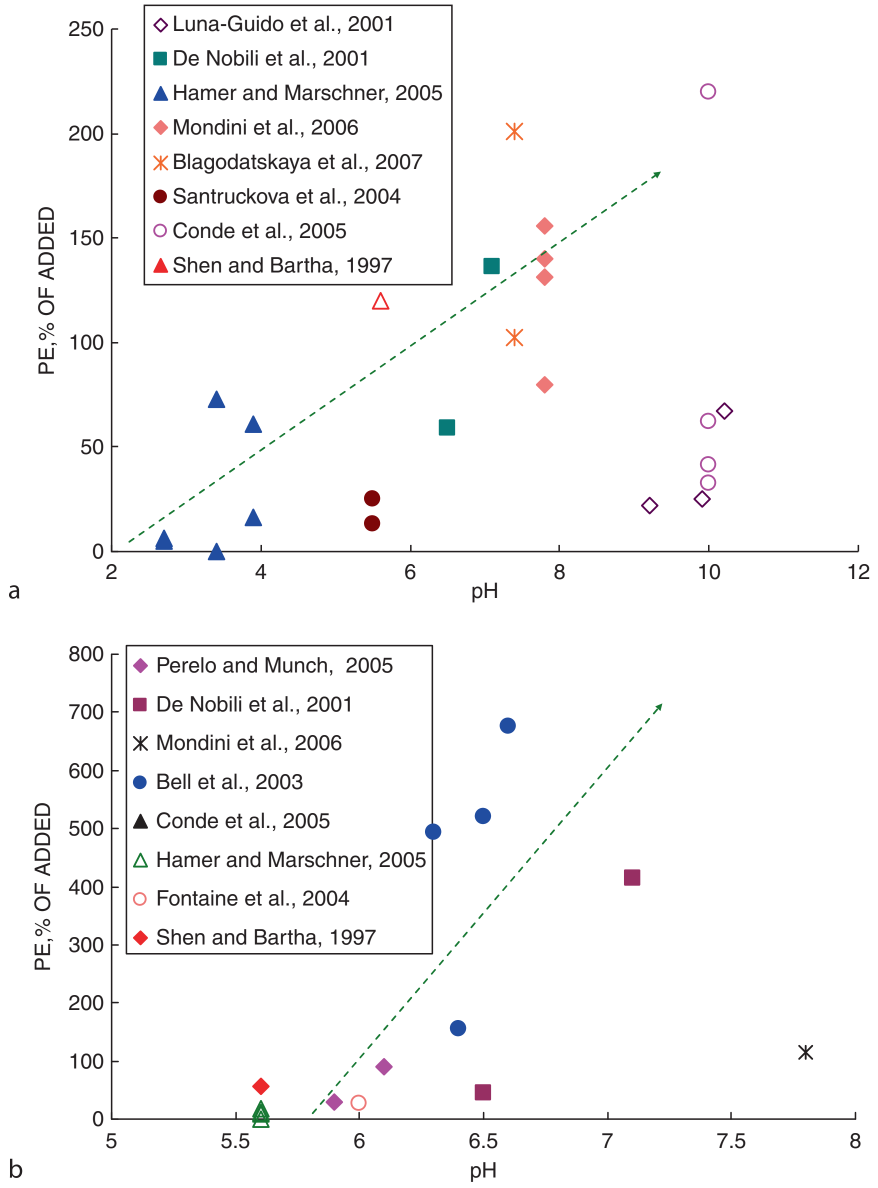
Priming Effects in Relation to Soil Conditions – Mechanisms, Figure 5 Relationship between primed CO_2-C efflux expressed as percent of added C and clay content in soil.

that since the present enzyme assays do not allow distinguishing the intracellular and extracellular enzyme activities, these are just hypotheses.

No differences in PE promoted by fructose and alanine were observed between soil fractions (sand, silt, and clay) obtained by mild sonication followed by wet sieving and sedimentation (Ohm et al., 2007). It is important to underline that available fractionation procedures can give artifacts. Sonication can promote not only disaggregation, but also desorption of microbial cells from soil particles and these desorbed microbial cells can redistribute during wet sieving to smaller size fractions. This can smooth the differences in microbial activity between fractions. The dry sieving method used by Degens and Sparling (1996) seems to yield a more realistic distribution of microbial activity among the soil particles (Figure 5).

Soil acidity (pH)

The higher intensity of PE occurs in neutral soils – in the pH range between 6 and 8 – when both easily decomposable substances and plant residues are added to soil (Figure 6). The changes of microbial activity and community structure as well as the enzyme synthesis are higher in



Priming Effects in Relation to Soil Conditions – Mechanisms, Figure 6 Relationship between primed CO_2-C efflux expressed as percent of added C and soil pH: easily available substrate (*top*) and plant residues (*bottom*).

soils with pH ranging from 5 to 8 than in acidic soils (Blagodatskaya and Anderson, 1998).

Most studies on priming effects are based on CO_2 measurements and artifacts can occur if the effect of soil pH on the solubility of CO_2 is neglected. Indeed, the equilibrium among H_2CO_3, CO_3^{2-}, and HCO_3^-, all derived from CO_2, in soil solution is pH dependent, and thus, the soil pH should be considered when interpreting results from CO_2 evolution. Possible misestimates of CO_2 evolution do not occur at pH values <5 because H_2CO_3 is the prevailing (about 98%) form that dissociates immediately into CO_2 and H_2O, and thus all CO_2 produced by soil microorganisms can be freely evolved as CO_2. At pH between 5 and 5.5, the contribution of H_2CO_3 decreases to 70% and some CO_2 can occur in soil solution as HCO_3^-, and this can give a small underestimation of the produced CO_2. As the total amount of soluble CO_2 species is less than 0.03 mM l^{-1} at pH 5–5.5, such underestimation does not exceed 0.1 μg CO_2-C g^{-1} however, this value can be neglected considering that the CO_2 production rate in most unamended mineral soils is 1–2 μg CO_2-C g^{-1} h^{-1}.

The prevailing forms of carbonate at pH values higher than 6.8 are HCO_3^- and CO_3^{2-}. Therefore, CO_2 produced by microbial respiration will initially dissolve in soil water until the saturation capacity of the solution is reached. In such a case, CO_2 evolution depends on the volume of soil solution. Assuming the soil water content to be 30% of dry weight with a CO_2 evolution rate of about 30–40 μg CO_2-C g^{-1} day^{-1}, the CO_2 evolution from soil can be underestimated by 10–100% at soil pH values of 8 and 9, respectively. This may explain the 1-day delay in the PE of alkaline soils (pH of 9.8–11.7) promoted by the addition of glucose or maize (Conde et al., 2005). Probably, CO_2 produced during the first day after treatment was accumulated as HCO_3^- and CO_3^{2-} in soil solution until the CO_2 saturation was reached; then the excess was evolved as CO_2. Therefore, the short-term PEs in soils at pH > 8, should be interpreted with caution. In soils with very high pH (9–11), the PE estimation is even more difficult because of carbonate recrystallization (Kuzyakov et al., 2006).

Summary

Priming effects are short-term changes in the turnover of soil organic matter caused by the addition of organic substances to the soil. Additions of easily available organic C up to 15% of microbial biomass C induce a linear increase of extra CO_2. When the added amount of easily available organic C is higher than 50% of the microbial biomass C, an exponential decrease of the PE or even a switch to negative values is often observed. PE increases with pH and clay content.

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Cross-references

Aeration of Soils and Plants
Agrophysical Properties and Processes
Carbon Losses Under Dryland Conditions, Tillage Effects
Organic Matter, Effects on Soil Physical Properties and Processes

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PROTON NUCLEAR MAGNETIC RESONANCE (NMR) RELAXOMETRY IN SOIL SCIENCE

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Proton NMR relaxometry is a very powerful tool for investigating porous media and their interaction with water with organic molecules in solution. It is commonly used in material science or earth science and is increasingly applied in soil science as detailed in the review (Bayer et al., 2010). NMR relaxometry is sensitive and promising to study pore size distribution in soils (Jaeger et al., 2009), wetting (Schaumann et al., 2005; Todoruk et al., 2003), swelling (Jaeger et al., 2010; Schaumann et al., 2004), biofilm formation (Jaeger et al., 2006), or metal-NOM binding (Jaeger et al., 2008; Melton et al., 2007). It further helps to study interactions between molecules in soil organic matter (Schaumann and Bertmer, 2008). Relaxation times determined by NMR relaxometry are sensitive to various factors that play a role in soil–water interaction which is both an advantage and shortcoming of the method: NMR relaxometry is a versatile method, which can be applied to numerous investigations in soil science, but at the same time interpretation of the results in such complex and heterogeneous systems like soils requires expertise from both soil science and NMR.

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PROXIMAL SOIL SENSING

See *Precision Agriculture: Proximal Soil Sensing*

PUDDLING: EFFECT ON SOIL PHYSICAL PROPERTIES AND CROPS

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Definition

Soil puddling for paddy rice production is the process of working saturated or near-saturated soil into soft structureless mud.

Tillage in lowland rice production systems (paddy rice) is synonymous with puddling. Puddling is achieved by cultivating the soil under saturated condition using animal drawn or tractor driven implements. Mechanical breaking and dispersing of soil aggregates destroys the soil structure and forms the puddled zone. Puddling softens the soil and assists manual transplantation of rice seedling, minimizes water use through reduced percolation losses and effective weed control. Over time, soil puddling also creates a compacted layer below the puddled zone which further reduces percolation losses. The least permeable zone is usually found just below the puddled layer where tillage implements created a thin smeared layer. The reduction in permeability is mainly caused by blocking of macropores with fine dispersed particles translocated during puddling process, and the smearing effect of the tillage implements.

Although lowland rice does not require saturated conditions to produce high yields, it is traditionally kept under submerged conditions to maximize water supply, mobilize