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Review

Review of mechanisms and quantification of priming effects

Y. Kuzyakov[a,*], J.K. Friedel[b], K. Stahr[a]

[a]Institute of Soil Science and Land Evaluation, University of Hohenheim, D-70593 Stuttgart, Germany
[b]Institute of Organic Farming, University of Agricultural Sciences, A-1180 Vienna, Austria

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Abstract

Priming effects are strong short-term changes in the turnover of soil organic matter caused by comparatively moderate treatments of the soil. In the course of priming effects large amounts of C, N and other nutrients can be released or immobilized in soil in a very short time. These effects have been measured in many field and laboratory experiments; however, only a few of the studies were aimed at an extended investigation of the mechanisms of such phenomena. The aim of this overview is to reveal possible causes and processes leading to priming actions using the references on agricultural ecosystems and model experiments. Multiple mechanisms and sources of released C and N are presented and summarized in Tables for positive and negative real and apparent priming effects induced after the addition of different organic and mineral substances to the soil. Soil microbial biomass plays the key role in the processes leading to the real priming effects. The most important mechanisms for the real priming effects are the acceleration or retardation of soil organic matter turnover due to increased activity or amount of microbial biomass. Isotopic exchange, pool substitution, and different uncontrolled losses of mineralized N from the soil are responsible for the apparent N priming effects. Other multiple mechanisms (predation, competition for nutrients between roots and microorganisms, preferred uptake, inhibition, etc.) in response to addition of different substances are also discussed. These mechanisms can be distinguished from each other by the simultaneous monitoring of C and N release dynamics; its comparison with the course of microbial activity; and by the labelling of different pools with ^{14}C or ^{13}C and ^{15}N. Quantitative methods for describing priming effects and their dynamics using ^{14}C and ^{15}N isotopes, as well as for non-isotopic studies are proposed. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Priming effect; Added nitrogen interaction; Microbial biomass; Soil organic matter; Carbon and nitrogen turnover; ^{13}C; ^{14}C; ^{15}N; Mineral fertilizers; CO_2

1. Introduction

In many studies on the transformation of substances added to soil, a side effect can be detected — an increased release of the soil-derived carbon as CO_2 or nitrogen as NH_4^- or as NO_3^+ compared to the mineralization in the soil without any additions. This is a result of the interactions between the transformation of the added substances and the natural soil cycles of both elements. A few extended studies concerned with these interactions have shown differing results strongly dependent on the experimental conditions, especially if C or N transformations were investigated and which kind of substances were added to the soil. These non-additive interactions, which cause an extra release of soil-derived C or N, were summarized under the generic term “priming effects”.

The priming effect was discovered by Löhnis (1926) by studying the decomposition of green manure of legume plants in soil. He found intensified mineralization of the humus N by the addition of fresh organic residues to soil. In the following 20 y the phenomenon was left out of consideration. It was not before the middle of the 1940s and in the 1950s that priming effects were studied again in experiments by Broadbent

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* Corresponding author. Tel.: +49-711-459-3669; fax: 49-711-459-4071.

E-mail address: kuzyakov@uni-hohenheim.de (Y. Kuzyakov).

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and colleagues (Broadbent, 1947, 1956; Broadbent and Bartholomew, 1948). Thus the experiments of Broadbent and Norman (1946) showed that CO_2 evolution from the soil can increase from 4- to 11-fold after addition of ^{13}C-labelled plant residues. This high "extra" CO_2 release gave rise to extended studies of this phenomenon. Priming effects were examined which are caused by the addition to soil of plant residues, dead microorganisms, high-molecular and low-molecular organic substances, or mineral N.

After the review and theoretical study of priming effects carried out by Jenkinson et al. (1985) many new publications have shown multiple mechanisms leading to an extra mineralization of C and N after the substance addition. Different fractions of soil organic matter or microbial biomass have been found as the main sources for the released C and N. Many hypotheses and mechanisms have been proposed to explain the processes leading to the priming effects. Nevertheless, the results of these studies have hitherto not been summarized. A classification of priming effects and new quantification methods are necessary to accelerate progress in this field.

The aim of this review is to reveal possible causes and processes leading to the priming actions using references on agricultural ecosystems and model experiments. We have tried to classify the mechanisms of changes in C and N mineralization after the addition of different substances to the soil, to suggest some methods for the quantification of priming effects, and to propose approaches for separation of those processes which cause the extra release of nutrients.

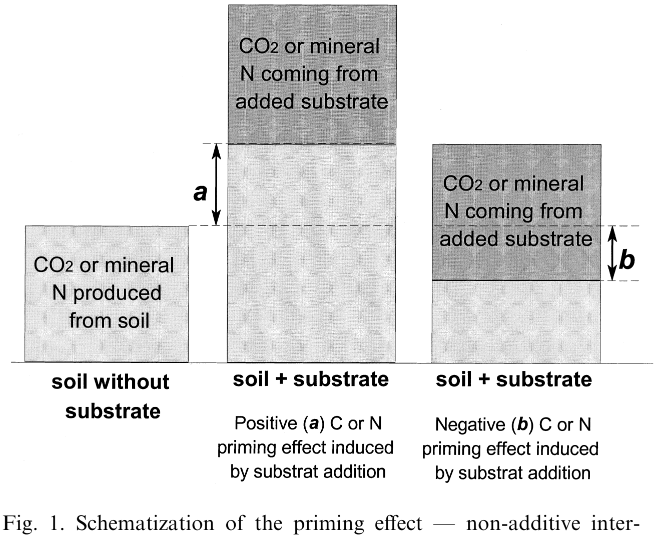

Fig. 1. Schematization of the priming effect — non-additive interactions between decomposition of the added substrate and of soil organic matter (SOM): (a) acceleration of SOM decomposition — positive priming effect; (b) retardation of SOM decomposition — negative priming effect.

2. Definition and description of terms

The term "*priming effect*" was introduced by Bingemann et al. (1953). In the meantime some synonyms are used also: priming action, added nitrogen interaction — ANI (introduced by Jenkinson et al., 1985), extra N and additional N (in the Russian literature). There are two different approaches to the definition of the term depending on whether the studies were made with special attention to N or to C. In studies of C turnover the definition is supported that the priming effect (Fig. 1a) is an extra decomposition of organic C after addition of easily-decomposable organic substances to the soil (Dalenberg and Jager, 1989).

In studies on N the following definition is supported in particular: the priming effect is extra soil N which is taken up by plants after addition of mineral N fertilizer, compared with non-N treated plants (Jenkinson et al., 1985; Leon et al., 1995). The latter definition only means N uptake by plants, and thus is production-oriented. Many studies, however, showed that the presence of plants is not essential for priming effects to occur. A definition for "added nitrogen interaction" frequently used, but also inexact, was suggested by Jenkinson et al. (1985): priming is every effect on N already in the soil by adding N to the soil.

The phenomenon, in fact, is much broader, and deals with a change (mostly an acceleration) in natural mineralization processes through a trigger: e.g. input of an easily decomposable energy source, respectively a limiting factor for microbial biomass. In addition, priming effects were found not only for C and N, but also for P (Fokin and Radzhabova, 1996), S (O'Donnell et al., 1994; Lefroy et al., 1994; Chapman, 1997), and some other nutrients too. The addition of different substances to the soil might cause not only an acceleration of mineralization (*positive* priming effect), but also its reduction, or an immobilization of the added C or N. In these cases one speaks of *negative* priming effects: e.g. temporal N unavailability due to immobilization (compare Fig. 1b).

Considering the above, the following definition is used in this review: *priming effects are strong short-term changes in the turnover of soil organic matter caused by comparatively moderate treatments of the soil.* Such interventions might be input of organic or mineral fertilizer to the soil, exudation of organic substances by roots, mere mechanical treatment of soil, or its drying and rewetting.

The need to study this phenomenon can be explained by our unsatisfactory knowledge of C and N transformation processes connected with priming effects. Disregarding the priming effect means that the extra mineralization may increase NO_3^- leaching (Barraclough et al., 1984; Kudeyarov et al., 1987; Kudeyarov, 1989), gaseous N losses (Wu et al., 1991) or decomposition of soil organic matter (Helal and Sauerbeck, 1986; Schmitt et al., 1991). An indirect but clear sign of this insufficient knowledge is the fact that none of the common models of C and N dynamics in the soil (overview over 23 models by Engel et al., 1993) takes the priming effects into consideration, although the additional nutrient release can be very large. Only a few models specialized for the turnover of the soil microbial biomass include the priming effect or are able to simulate it (Molina et al., 1990; Blagodatsky and Richter, 1998).

The following *undisputed facts* have been revealed so far:

- the priming effect arises either immediately or very shortly after the addition of a specific substance to the soil (Dalenberg and Jager, 1981, 1989; Kudeyarov, 1988; Pascual et al., 1998);
- priming effects in soils rich in C and N are larger than those in poor soils (Hart et al., 1986);
- real priming effects have never been observed under sterile conditions (Jansson, 1958);
- the size of the priming effects increases with the amount of the added organic substances (Dumontet et al., 1985; Kawaguchi et al., 1986; Mary et al., 1993; Asmar et al., 1994), or mineral fertilizers (Jenkinson et al., 1985; Kudeyarov, 1988; Laura and Parshad, 1992; Hamid and Ahmad, 1993; Azam et al., 1994a,b; Hejnak et al., 1996);
- in general, ammonia causes larger priming effects than NO_3^- (Rennie and Rennie, 1973; Kowalenko and Cameron, 1978; Steele et al., 1980; Stout, 1995).

In many studies on application of N fertilizers in which ^{15}N is used, if not in most of them, so-called *apparent priming effects* (Jenkinson et al., 1985) were observed. This shows how complex the phenomenon is. Apparent priming effects are connected with a release of soil-derived N. This release seems to be similar to the one observed in real priming effects. However, the triggering processes are not a change in the turnover rate of C and N. The exchange of added labelled mineral N with different unlabelled soil pools is responsible for apparent priming effects. The turnover rates of these pools remain constant. A simple example for an apparent priming effect is when ^{15}N fertilizer added to the soil leads to an isotopic equilibrium with an interchangeable soil-N-pool. In this case the plant with ^{15}N fertilization takes up more soil-derived N than the control plant without fertilization (Hart et al., 1986). Another example for apparent priming effects: an observed extra consumption of soil-derived N by fertilized plants compared with a control treatment without N fertilization. This additional consumption was due to an uncontrolled uptake of soil-derived N from unfertilized deep soil horizons, which could not be reached by the plants in the control due to shorter roots (Olson and Swallow, 1984; Gajri et al., 1989; Denobili et al., 1992). Other kinds of artifacts can arise in experiments with plant residues which are non-uniformly labelled with ^{14}C or ^{15}N. Some other causes of apparent priming effects are discussed by Jenkinson et al. (1985).

3. Most frequent mechanisms for priming effects

An extended search for mechanisms and sources of N priming effects (added nitrogen interactions — ANI) caused by adding ^{15}N fertilizer was initiated by Jenkinson et al. (1985). They carried out an extended theoretical study of the most important mechanisms of ANI and their dynamics, especially for the apparent ANI, caused by input of ^{15}N labelled fertilizer into the soil. Therefore, we will not reiterate the mechanisms for apparent priming effects. However, in the review of Jenkinson et al. (1985) the causes for C priming effects and those priming effects following an addition of organic substances to the soil are not examined. According to the definition used, C also plays an important role in these phenomena.

Tables 1–4 present a provisional summary of the literature on priming effects. We used the tables for differentiating the processes causing extra C or N release, and for a clear classification of priming effects. Priming effects for C and N are divided into four classes: positive real (Table 1), negative real (Table 2), positive apparent (Table 3), and negative apparent (Table 4). Then the dominant causes are listed, and references to the most likely cause are related, taking into consideration the particular experimental conditions and measured variables. In most of these references priming effects only are referred to, their causes, however, have not been intensively studied.

Analysis of the tables leads to the conclusion that for an effective study of the priming effects the simultaneous monitoring of the release of C and N is necessary. Labelling different pools with ^{14}C and ^{15}N gives the possibility to state clearly the source of released C and N. The dynamics of mobilization and immobilization of nutrients and its comparison with the course of microbial activities can aid significantly in the clarification of causes for priming effects.

Experiments dealing with causes for priming effects showed that artifacts can arise easily unless the particularities of an application of the labelled substance are not considered adequately. The most frequent causes for these artifacts are a non-uniformly ^{14}C labelling of plant residues added to the soil (Table 4), as well as an isotopic displacement in studies with ^{15}N (Table 3). An overview of the most frequent artifacts in studies with ^{15}N was presented by Jenkinson (1966) and Jenkinson et al. (1985). The dominant causes for these artifacts are summarized here under "positive apparent" (Table 3) and "negative apparent" (Table 4) priming effects. Apparent priming effects arise in most of the cases for N only. First of all, the existence of several N pools in the soil can lead to an isotopic displacement or pool substitution with the fertilizer ^{15}N. These two causes are frequently confused. Isotopic displacement is a physical process based on the diffusion of ions between the pools which are in isotopic equilibrium. Pool substitution is mostly a biological process, connected with the uptake of fertilizer N instead of soil-derived N by microbial biomass or by plants (Jenkinson et al., 1985). Therefore, soil sterilization can be used to distinguish the isotopic displacement and the pool substitution.

The apparent priming effects can easily be distinguished from the real ones by monitoring CO_2 efflux because C turnover is not affected in the apparent priming effects (Westcott and Mikkelsen, 1985). In contrast to the real priming effects the apparent priming effects are unusual for C but occur frequently after applying mineral-N fertilizers especially in NH_4^+ form. It is important that the apparent priming effects cannot be larger than the amount of mineral N applied, and are usually less than 50% of it (Stout, 1995). On the contrary, real priming effects change the CO_2 efflux from the soil after the addition of mineral N fertilizer (Semenov et al., 1992) (c.f. Table 1). Real positive priming effects for C and N can be much greater than the amount of C and N added to the soil.

Table 1
Mechanisms for and causes of positive real priming effects for carbon (C) and nitrogen (N), caused by addition of different substances (PE = priming effect; MO = microorganisms; SOM = soil organic matter)

PE for	Addition of	Possible causes	References
C and N	Mineral-N fertilizers	Acceleration of SOM mineralization through a lower C-to-N ratio	Lueken et al. (1962), Hart et al. (1986), Woods et al. (1987), Schmitt and Ahrens (1989), Semenov et al. (1992), Pascual et al. (1998), Raun et al. (1998), Sembiring et al. (1998)
	Easily available organic substances	Increase in MO activity and acceleration of SOM mineralization by means of co-metabolism	Broadbent (1947), Azam et al. (1989), Dumontet et al. (1985), Kawaguchi et al. (1986), Pascual et al. (1998), Breland and Hansen (1998)
	Plant rhizodeposition	Increase in MO activity and acceleration of SOM mineralization or microbial biomass turnover in the rhizosphere	Lavelle and Gilot (1994), Lavelle et al. (1995), Cheng and Coleman (1990), Bottner et al. (1988), Sallih and Bottner (1988), Kuzyakov et al. (2000), Helal and Sauerbeck (1984, 1986)
	Salts (also mineral fertilizers) or large amounts of soluble substances	Osmotic stress for MO, release of C and N through lysis and dying of MO	Wu et al. (1993)
	Mechanical treatment	Acceleration of SOM mineralization through improved aeration and destruction of aggregates	
	No addition; soil drying–rewetting	Dying of MO, flush of C and N from dead cells after rewetting	Birch and Friend (1956), Birch (1958), Vangestel et al. (1993), Magid et al. (1999), Pulleman and Tietema (1999)
C only	Mineral-N fertilizers	Acceleration of SOM mineralization as substrate and energy source	
	Easily decomposable organic substances and mineral-N fertilizers	Acceleration of SOM mineralization and N immobilization through increasing MO activity	Mary et al. (1993), Lavelle and Gilot (1994), Shen and Bartha (1997), Gerzabek et al. (1997), Bol et al. (1999), Van Lauwe et al. (1994), Blagodatsky et al. (1998)
	Easily decomposable organic substances	Acceleration of MO turnover, CO_2 flush from MO	Dalenberg and Jager (1981), Degens and Sparling (1996)
N only	Easily available organic substances or C-rich rhizodeposition	Activation of MO, acceleration of SOM mineralization in the rhizosphere, and release of NH_4^+ in case of predation	Asmar et al. (1994), Fiore et al. (1990), Clarholm (1985a,b), Kuikmann et al, (1991), Winding et al. (1997)
	Mineral-N fertilizers	Increase in atmospheric N_2-fixation	Sirota (1982), Umarov (1983)
	No addition; soil drying–rewetting	Mineralization of a part of a labile non-biomass soil organic matter N-pool	Cabrera (1993), Appel (1998)

Table 2
Mechanisms for and causes of negative real priming effects for carbon and nitrogen, caused by addition of different substances. Abbreviations as in Table 1

PE for	Addition of	Possible causes	References
C and N	Easily decomposable C and N sources	Switch of microbial biomass from SOM on the easily available C and N sources	Sparling et al. (1982), Reid and Gross (1983), Cheng (1996)
	Living plant roots	Competition between living roots and rhizosphere microorganisms for limited nutrients	Cheng (1996, 1999), Wang and Bakken (1997)
	Toxic substances	Direct inhibition of activity of microorganisms or their enzymes	
	Mineral-N fertilizers	Preferred uptake of C-rich substrates by MO	Sharkov (1986)
C only	Organic substances with C-to-N <16	Decrease in C-to-N ratio, C-immobilization in MO	Kuzyakov et al. (1997a, 1999)
	Mineral-N fertilizers	N-immobilization by MO due to sufficient easily available C-rich substrate in the soil	Cheng and Kurtz (1963), Stewart et al. (1963), Nielsen and Jensen (1986), Jawson and Elliot (1986), Jackson et al. (1989)
N only	Mineral-N fertilizers	Decrease in atmospheric N_2-fixation	Yin et al. (1997)
	Organic substances with C-to-N >16	N-immobilization by MO	Blagodatsky and Yevdokimov (1998), Blagodatsky et al. (1998)

It is striking that negative priming effects (Masayna et al., 1985; Nicolardot et al., 1986; Schmitt and Ahrens 1990; Schmitt et al., 1991; Kuzyakov et al., 1997a) are not described quite as often as positive priming effects. However, negative priming effects are probably of much greater significance to ecosystems than positive ones. In negative priming effects the nutrient losses of the soil organic matter are replaced. With reference to mobilization–immobilization of N Nicolardot et al. (1986) classified added substances according to their C-to-N ratio. Substances with a C-to-N ratio >10 cause negative N priming effects (N immobilization), and substances showing a C-to-N ratio <8 cause N release. Various C-to-N ratios of plant residues are recommended to predict whether immobilization or mineralization of N will prevail during decomposition. This C-to-N threshold value varies in different studies from 8 to 40 (Nicolardot et al., 1986; Vigil and Kissel, 1991; Hadas et al., 1992; Bloemhof and Berendse, 1995; Blagodatsky and Yevdokimov, 1998). An easy approach can be used for calculating this threshold value in short-term decomposition ex-

Table 3
Mechanisms for and causes of positive apparent priming effects for nitrogen[a], caused by addition of different substances[b]. Abbreviations as in Table 1

PE for	Addition of	Possible causes	References
N only	$^{15}\mathrm{N}_{\mathrm{min}}$ or salts specially $^{15}\mathrm{NH}_4^+$	Isotopic displacement of $^{15}\mathrm{NH}_4^+$ with unlabelled NH_4^+, or with some other cations (e.g. K^+) from different pools (e.g. MO, partly with fixed NH_4^+)	Barraclough et al. (1984), Feigenbaum et al. (1984), Shen et al. (1984), Masayna et al. (1985), Westcott and Mikkelsen (1985), Hart et al. (1986), Laura and Parshad (1992), Hejnak et al. (1996), Cadisch et al. (1998)
	$^{15}\mathrm{N}_{\mathrm{min}}$	Pool substitution through immobilization, N derived from MO or soil organic matter	Hamid and Ahmad (1993), Azam et al. (1994b), Stout (1995), Ehaliotis et al. (1998)
	$^{15}\mathrm{N}_{\mathrm{min}}$	Fast losses from $^{15}\mathrm{N}_{\mathrm{min}}$ pool through: (a) denitrification in case of a lack of O_2 (b) $^{15}\mathrm{NO}_3^-$-leaching (c) ^{15}N-plant uptake and the following $\mathrm{N}_{\mathrm{min}}$ release from SOM	Wu et al. (1991), Bernal and Kirchmann (1992), Kudeyarov (1989), Walther (1990)
	$^{15}\mathrm{N}_{\mathrm{min}}$ or H_2O	Tapping deeper soil layers through stronger and deeper root system[c]	Sapozhnikov et al. (1968), Hills et al. (1978), Olson and Swallow (1984), Feigenbaum et al. (1984), Gajri et al. (1989), Denobili et al. (1992)
	NO_3^- fertilizers	Stimulation of N uptake by roots	Leon et al. (1995)

[a] No positive priming effects were found for C alone, or for C and N together.

[b] Extended description, dynamics, and additional references for positive apparent PE are presented by Jenkinson et al. (1985).

[c] In contrast to Jenkinson et al. (1985) we classify this mechanism to apparent PE because the C or N turnover is unchanged.

periments; the first step of the transformation of plant residues in soil is their decomposition and use by microbial biomass. The efficiency of biosynthetic processes (Y) by incorporation of C into microbial biomass is about 0.4–0.5 (Payne, 1970; Hadas et al., 1992; Lettau and Kuzyakov, 1999) and cannot be higher than 0.62 (Payne, 1970). Assuming that an average C-to-N ratio of soil microbial biomass is about 8, the threshold value results in a C-to-N ratio of about 16, because only about 50% of C from the substrate will be incorporated into microbial cells. The other half will be used for energy and respired as CO_2. In contrast to C, microorganisms use the whole amount of N if the C source is not limited. The environmental conditions, especially the N_{min} content, the C-to-N ratio of easily available organic substances in soil, and the decomposition time may modify the calculated threshold C-to-N ratio of 16.

Dalenberg and Jager (1989) also divided the substances they studied into two classes. Substances belonging to the first class (amino acid, glutamate, aspartate) lead to positive C priming effects when decomposed. Substances of the second class (glucose, cellulose, wheat straw, sewage sludge) cause negative priming effects. The last substances and their metabolites contribute to the formation of soil organic matter or reduce its decomposition. However, in different studies the addition of glucose has led to negative priming effects (Dalenberg and Jager, 1989; Chapman, 1997), as well as to positive priming effects (Mary et al., 1993; Asmar et al., 1994; Shen and Bartha, 1996, 1997), or to its absence (Wu et al., 1993). The direction of these changes in the decomposition of SOM (acceleration or retardation) depends mostly on the nutrient status of the soil and the C-to-N ratio of the active SOM pool.

A promising approach to clarify the fluxes in priming actions is to quantify the rates of N gross-mineralization (Bjarnason, 1988; Murphy et al., 1998; Puri and Ashman 1998). Priming effects may be a temporary disturbance in the equilibrium between gross-mineralization and immobilization, leading to major fluctuations in net-N mineralization. Scheller (1993) suggested from time courses of mineral N in fallow soils and in unfertilized grassland that N mineralization in European soils follows a typical mineralization–immobilization rhythm. Depending on the latitude, he described one to three mineralization phases followed by immobilization phases over the year. During mineralization phases organic fertilization may exert positive priming effects for N, whereas fertilization may lead to greater binding of N during immobilization phases (Scheller, 1993).

4. Sources of nutrients released in priming effects

Published research on the sources of the additionally released C and N are contradictory. The following causes for an increased CO_2 efflux and an increased N mineralization have been discussed:

4.1. An increased decomposition of soil organic matter by stimulating the activities of microorganisms (Fiore et al., 1990; Asmar et al., 1994)

The most common idea is that substances released in additional mineralization are derived from soil *organic matter*, respectively, from its fractions. This release arises through the activity of microorganisms, as no real priming effects have been observed under sterile conditions (Jansson, 1958). Also, the dynamics of the growth and of the activity of microorganisms (particularly bacteria), and released nutrients indicate a close relationship between microbial biomass and real priming effects. Thus, after adding glucose to the soil Asmar et al. (1994) observed a high correlation between the N release from soil organic matter and the

Table 4
Mechanisms for and causes of negative apparent priming effects for carbon and nitrogen, caused by addition of different substances. Abbreviations as in Table 1

PE for	Addition of	Possible causes	Reference
C or N	Organic substances	Incomplete decomposition of C or N sources during the experiment	Kuzyakov et al. (1997a)
	^{14}C or ^{15}N labelled organic substances	Non-uniform ^{14}C or ^{15}N labelling	
	Sources of C or N	Sorption or physical–chemical protection and immobilization of the added substances	Saggar et al. (1999)
N only	NH_4^+ fertilizers	NH_4^+ fixation by clay minerals	Schmitt and Ahrens (1990), Johnson et al. (2000)

exocellular enzyme activities, especially the total and soluble protease. According to experiments of Schmitt et al. (1991), in soils well supplied with N, the dehydrogenase activity increased, the amount of ammonifying and protolytic bacteria increased, whereas the amount of total organic C (TOC) in the soil decreased. It is supposed that an increased availability of microbial substrate induces enzyme production or increases enzyme activity leading to a *co-metabolic decomposition of soil organic matter*. The statement about the decreased TOC solely by mineral N fertilization is not confirmed by long-term field experiments. These have shown that TOC content in soils increases by mineral N fertilization compared with an unfertilized treatment due to higher amount of root residues (Körschens and Müller, 1994). The discrepancies between these results on the effect of N fertilization on soil C content are explained by the short duration of the experiments studying priming effects in contrast to long-term field experiments. Thus, short-term experiments are representative only for a small part of the annual C turnover, mostly in the springtime, when root growth and the release of easily available organic substances are maximal. In summer and particularly in fall the humification of root remains and other plant residues prevails, so that the extra losses of C and N caused by priming effects are fulfilled.

Besides co-metabolism, low molecular organic acids released by roots or microorganisms contribute to chemical disruption of organic substances in the soil (Jones, 1998). Piccolo (1998) has shown the disruption of hydrophobic organic substances in soil by organic acids. This effect may also increase the microbial decomposability of soil organic matter when rhizodeposition or microbial activity is enhanced.

Specific experiments to identify single fractions of the soil organic matter as the source of C and N released by priming effects have not provided clear results (Schmitt and Ahrens, 1989; Molina et al., 1990; Asmar et al., 1994). In our opinion the identification problem has to do, among other things, with the fact that substances added to the soil were labelled, but not the humus fraction to be examined (Schmitt and Ahrens, 1989). The experiments with labelled SOM fractions have shown that the release of C occurs from labile (or active) humus fractions (Sparling et al., 1982; Asmar et al., 1994; Vanlauwe et al., 1994).

Despite this finding, studies on the effect of drying–rewetting of soil also indicate that soil organic matter is the dominant source of the N mineralization flush (Birch, 1958; Cabrera, 1993; Appel, 1998). A labile non-biomass soil organic N-pool was suspected to be the substrate for the extra N release. However, Magid et al. (1999) did not find any significant changes in the mineralization of SOM by the drying–rewetting regime.

4.2. A release of C and N from microorganisms

Dalenberg and Jager (1981, 1989) labelled different C pools (microbial biomass, components of the soil organic matter) to study the source of C released. In contrast to the above mentioned mechanism they have found that $^{14}CO_2$ released from the soil after the addition of plant residues and individual organic substances derives directly from the microbial biomass. Soil drying leads to the death of a part of the microbial biomass and to the additional release of CO_2 after rewetting (Vangestel et al., 1993; Pulleman and Tietema, 1999; Magid et al., 1999). However, this approach could only partly explain the scale of the priming effects.

4.3. An interaction of microorganisms, soil fauna and plants

An opinion expressed in the literature says that not only microorganisms alone contribute to priming effects (Clarholm, 1985a; Griffiths, 1994). *Interactions between soil microorganisms, soil fauna and plants* are regarded as one of the keys for understanding priming effects. Substances released by soil fauna can cause priming effects by stimulating microbial activity. Mucigels released by earthworms were found to produce a rapid priming response (Lavelle and Gilot, 1994; Lavelle et al., 1995). However, more prevalent in the literature are descriptions of the effects of faunal grazing on soil microflora (predation) (Alphei et al., 1996). The effects induced by predation were summarized by Ingham et al. (1985) as follows: increased CO_2 release, increased soil N and P mineralization, increased activity of bacteria, accelerated mineralization and release of nutrients immobilized in microorganisms, increased N uptake of plants, and intensified plant growth.

Both the release of C or N from soil microorganisms and from soil organic matter may be the cause for increased CO_2 flushes and N mineralization during predation (Clarholm, 1985a; Griffiths, 1994). Woods et al. (1982) point out that N mineralization may not be regarded as a mere microbial process. The contribution of soil fauna (particularly protozoa and nematoda) to N mineralization on arable sites or grassland is estimated to be about 10–40% (Elliott et al., 1988; Kuikmann et al., 1991; Griffiths, 1994; Alphei et al., 1996). Depending upon site conditions and cultivation the food chain on either a bacterial (most important predators: protozoa, nematoda) or a fungal basis (most important predators: nematoda, micro-arthropoda) prevails (Hendrix et al., 1986; Beare et al., 1992; Griffiths, 1994). Increased plant growth is said to be mostly the result of an increased release of nutrients through predation, particularly in the rhizosphere

(Clarholm, 1985a; Elliott et al., 1988; Zwart et al., 1994).

Plants increase the microbial activity in the rhizosphere through rhizodeposition and thus can enhance the N mineralization of the soil (Clarholm, 1985b; Haider et al., 1987; Kuikmann et al., 1991; Zagal, 1994; Kuzyakov et al., 2000). Therefore it is assumed that particularly the C supply of microorganisms is improved, and their activity is increased by rhizodeposition (Clarholm, 1985b). N additionally mobilized from the soil organic matter through this increased activity is released by predation (Elliott et al., 1979). The size of the extra N mineralization — due to trophical interactions — is dependent on the complexity of the food chains (Elliott et al., 1980; Woods et al., 1982; Griffiths, 1994) and the N availability (Clarholm, 1989). The released N is available for plants in mineral form (Clarholm, 1985a; Kuikmann et al., 1990) (Fig. 2).

Unless the mineralized N is removed (e.g. by the roots) a rapid N uptake by microorganisms under N limited conditions takes place — competition theory (Hunt et al., 1977; Griffiths, 1994; Cheng, 1999). Thus a further N release from the soil organic matter is retarded or halted (Clarholm, 1985b), and the soil microbial biomass may immobilize large amounts of nutrients (Smith and Paul, 1990). On the other hand, if N is taken up by plants, the turnover is increased and N-mobilization from the soil organic matter may continue. This hypothesis, developed in gnotobiotic systems, could explain priming effects after the addition of C-rich substrates (including rhizodeposition) under field conditions. The easily available exudates lead to higher priming effects compared to the root mucilage or root residues (Mary et al., 1993), probably due to a higher and more intensive activation of soil microorganisms. Helal and Sauerbeck (1986) observed a decrease of TOC content of 5–7% in two soils by young maize roots during one month. This acceleration of decomposition was explained by the priming effect. Root exudates of fully-grown *Lolium perenne* increased microbial activity and lead to an extra decomposition of soil organic matter amounting to approximately 60 kg C ha^{-1} d^{-1} (Kuzyakov, 1999; Kuzyakov et al., 2000). It corresponds to about 6 kg N ha^{-1} d^{-1}. Therefore, plants profit from the exudation of organic substances into the rhizosphere through an additional uptake of extra mineralized nutrients.

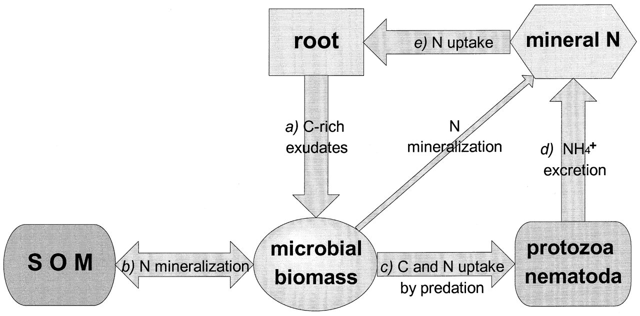

Fig. 2. Schematization of interactions in the rhizosphere caused by exudation of C-rich substrates, which trigger the additional N mineralization from soil organic matter (SOM): (a) release of C-rich substrates from the root, microflora (particularly bacteria) takes up C; (b) microflora starts to grow and increases the decomposition of soil organic matter to receive additional N, (c) protozoa (and other soil fauna) feed on the microbiota, and (d) release mineral N; (e) plants partly take up the mineral N (according to Clarholm, 1985b; Zwart et al., 1994, modified).

Other mechanisms may be responsible for real priming effects after the addition of N fertilizers. An increased salt concentration and microbial N availability may cause real priming effects. In this case, however, C-limited and N-limited conditions have to be distinguished. An increase in microbial activity or growth is not to be expected by improving N availability under C-limited conditions, as the necessary energy source is missing (compare model of Clarholm, 1985b). On the other hand, *improving N availability under N-limited (C-rich) conditions* (e.g. in the rhizosphere) allows increased microbial activity and growth (Wang and Bakken, 1997). This may again enhance predation, nutrient (and C) immobilization in microbial biomass, and co-metabolic decomposition of soil organic matter.

5. Quantification of priming effects

Jenkinson et al. (1985) recommended several methods for the quantification of *apparent* priming effects depending on their mechanisms and on the presence of plants. Although, only the A value (Fried and Dean, 1952; Jenkinson et al., 1985) is widely used. In addition, the A value can be applied for quantification of priming effects only by the presence of plants and only for N. A possible way for quantitative evaluation of the *real* priming effects in the studies with ^{14}C labelled substances was suggested by Shen and Bartha (1996, 1997) with the priming index (*PI*). We modified their equation so that a negative priming index corresponds to the immobilization or to the decreased decomposition of soil organic matter (Kuzyakov et al., 1997b). A positive priming index corresponds to an extra release of nutrients (Eq. 1).

$$PI(t) = {}^{14}\mathrm{CO}_2/net\mathrm{CO}_2 - 1 \qquad (1)$$

where: ^{14}CO$_2$ is the labelled CO$_2$ evolved from the soil (in % of total ^{14}C input), *net*CO$_2$ is the total CO$_2$ evolved from the soil (in % of total C input).

$$net\mathrm{CO}_2 = (SSR - BR)/C_\mathrm{S} \cdot 100\%$$

where: *SSR* is the total CO_2 evolved from the soil with substrate (soil with substrate respiration), *BR* is the basal respiration: total CO_2 evolved from the soil without substrate, C_S is the C amount in the substrate.

This priming index shows the release or immobilization of C or other nutrients from the soil organic matter per amount of added substance decomposed in soil for each time period. The disadvantage of the priming index is that it is very sensitive at the beginning of the decomposition, because very small amounts are released. In reverse order, it is very insensitive at the end of the decomposition because both variables, $^{14}CO_2$ evolution and $net CO_2$ evolution, shift during the decomposition towards 100% of the input.

The other possibility for the quantification of nutrient release dynamics (*NRD*) is to calculate the difference between the evolution of labelled and unlabelled C by decomposition:

$$NRD(t) = {}^{14}CO_2 - net CO_2 \tag{3}$$

The variables: $^{14}CO_2$ and $net CO_2$ are the same as described above. The second equation does not have the disadvantages of Eq. (1) for the priming index. The maximum and minimum of *NRD* correspond with maximal nutrient release and immobilization, respectively.

Eqs. (1) and (3) can be applied not only to C, but also to N, P, and other nutrients. Among other things, the advantage of this approach is that the dynamics of priming effects can be observed. It is important for the use of the Eqs. (1) and (3) that the substance added to the soil must be labelled (or the soil organic matter must be labelled). The labelling is necessary to distinguish the nutrient release from the added substance and from soil organic matter.

Real priming effects are also frequently observed in experiments without labelled substances. In order to describe them quantitatively, two possibilities can be distinguished:

1. The release of CO_2 or mineral N *without a lag phase* — in this case, the microbial community does not have to adapt to the added substance. This kind of release dynamics is common after addition of easily available organic substances (glucose and other sugars, amino acids, fresh green plant residues, etc.). In these cases exponential approaches (Eq. 4) are used for describing the release. Usually:

$$C(t) = C_S \cdot (1 - \exp(-k \cdot t)) \tag{4}$$

where: $C(t)$ is the release dynamics of CO_2 (or N_{min}), C_S is the maximum release possible, it corresponds to the total C amount in the added substrate, k is the decomposition rate of the substrate, t is time.

Because the priming effect is an extra decomposition, we modify Eq. (4) for consideration of the priming effect (PE) in addition to the C_S parameter (Kuzyakov et al., 1997a):

$$C(t) = (C_S + PE) \cdot (1 - \exp(-k \cdot t)) \tag{5}$$

2. The release of CO_2 or mineral N *with a lag phase* — in this case, the microbial community needs time to adapt to the new substrate. This kind of the release dynamics can be common after the addition of slowly decomposing organic substances to soil, like dry roots, wood, and other lignin containing compounds. In these cases several logistic functions can be applied for describing the release. For example:

$$C(t) = C_S/(1 + \exp(a - b \cdot t)) \tag{6}$$

where: a and b are the rates which are responsible for the duration of the lag phase and the increase of the function after the lag phase.

In the situation with a lag phase, an addition of the priming effect to the maximum amount of the added substrate can provide satisfactory quantitative statements about the size of the priming effect.

$$C(t) = (C_S + PE)/(1 + \exp(a - b \cdot t)) \tag{7}$$

It is remarkable that we have not found any references to priming effects induced by slowly decomposable organic substances.

Fitting of the parameters of Eqs. (5) and (7) to the experimental values of CO_2 or mineral N release by means of a non-linear regression also allows to quantify priming effects in experiments without labelled substances. Because the C_S is usually known, there is

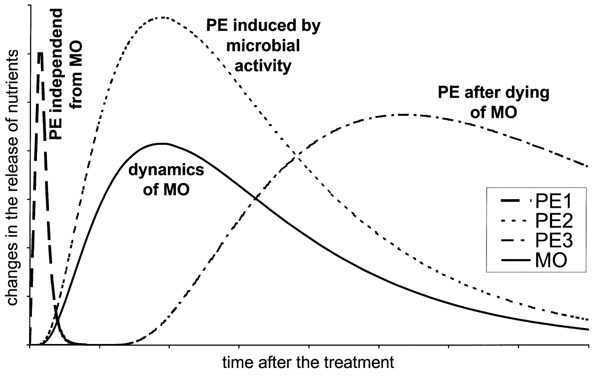

Fig. 3. Different relationships between the dynamics of priming effects and the dynamics of microorganisms after the soil treatment. (PE: priming effect; MO: activity or amount of microorganisms). Explanation in text.

no interaction between *PE* and C_S by the fitting of these parameters.

An advantage of the recommended Eqs. (5) and (7) for quantification of priming effects is that in these cases — with or without a lag-phase — the maximum intensity of the priming effect corresponds to the maximal decomposition of the added substrate, and thus to the maximum activity of microorganisms. An additional possibility to specify the results is to relate the intensity of the priming effect to both the amount of the added substrate and the basal respiration of untreated soil (Kuzyakov et al., 1997a).

A comparison of the dynamics of nutrient release or immobilization with the dynamics of biomass amount and activity can help interpret the mechanisms of the priming effect. We distinguish three cases of this comparison (Fig. 3):

1. The priming effect appears very shortly after the treatment of the soil, before the activity of microorganisms or its amount have changed (Fig. 3, PE1). This kind of priming effect is independent from the soil microbial biomass, and is most probably apparent. This kind of priming effect dynamics is typical after the addition of mineral fertilizers to the soil and the following isotopic displacement. If this very fast priming effect is negative (not shown here), then the fixation on clay minerals or the sorption on humic substances is responsible for the priming effect.
2. The maximum of the priming effect appears approximately at the same time as the maximum of the activity or amount of microorganisms (Fig. 3, PE2). These priming effects are real, and are caused by extra decomposition of soil organic matter due to increased microbial activity. If this priming effect is negative (not shown here), then the soil microorganisms immobilize the C or N, or both elements.
3. The maximum of the priming effect appears during the decrease of the amount of microbial biomass (Fig. 3, PE3). This priming effect can be caused by the release of nutrients from the death of microorganisms (or their predation), or the release of N after the consumption of C excess. If this priming effect is negative (not shown here), then the humification of microbial cells prevails (e.g. when the soil dries).

The reasons for increased microbial activity or the death of microorganisms can be multiple, and are described above. Here it is important that changes of the nutrient release as well as of microbial activity presented on Fig. 3 can also be below zero, when the negative priming effects occur. Comparison of the release dynamics of $^{14}CO_2$, $^{15}N_{min}$, total CO_2, total N_{min} with the activity and amount of microorganisms allows an explanation of most mechanisms of real priming effects described in Tables 1 and 2.

6. Conclusion and outlook

Finally one may draw the conclusion that there are no studies which are likely to explain causes, mechanisms, and sources of the extra C and N mobilization in priming effects in a satisfactory manner. The connection or the relationship between the C and N transformations has not been taken into consideration sufficiently. As shown in Tables 1 and 2, soil microorganisms are directly or indirectly responsible for most of the real priming effects. In contrast, the apparent priming effects are caused by multiple kinds of artifacts, and are not related to changes in the turnover of the microbial biomass or in the soil organic matter.

We hope that the classification of priming effects proposed in Tables 1–4 allows a specification of the types of research on this topic. New results and hypotheses of priming effects will fulfill the mechanisms described above, and extend the image of interactions between native C and N cycles in soil and the decomposition of added substances. Therefore, new approaches should be taken in the search for the triggers. In our opinion these are:

1. application of both ^{14}C and ^{15}N labelling (Nicolardot et al., 1986) of soil organic matter or soil microorganisms;
2. simultaneous monitoring of N gross-mineralization and of CO_2 efflux (Murphy et al., 1998);
3. the simultaneous observation of the dynamics of nutrient release and the microbial activity;
4. experiments concerning the simultaneous interaction of plants, micro-flora and soil fauna;
5. the necessity to quantify nutrients mobilized or immobilized in priming effects by means of the above mentioned approaches relative to the amount of the substrate added as well as relative to the unaffected natural mineralization, i.e. basal respiration (Kuzyakov et al., 1997a).

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