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Sources and mechanisms of priming effect induced in two grassland soils amended with slurry and sugar

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Abstract

The mechanisms and specific sources of priming effects, i.e. short term changes of soil organic matter (SOM) decomposition after substance addition, are still not fully understood. These uncertainties are partly method related, i.e. until now only two C sources in released CO_2 could be identified. We used a novel approach separating three carbon (C) sources in CO_2 efflux from soil. The approach is based on combination of different substances originated from C_3 or C_4 plants in different treatments and identical transformation of substances like C_3 sugar (from sugar beet) and C_4 sugar (from sugar cane). We investigated the influence of the addition of two substances having different microbial utilizability, i.e. slurry and sugar on the SOM or/and slurry decomposition in two grassland soils with different levels of C_{org} (2.3 vs. 5.1% C). Application of slurry to the soil slightly accelerated the SOM decomposition. Addition of sugar lead to changes of SOM and slurry decomposition clearly characterized by two phases: immediately after sugar addition, the microorganisms switched from the decomposition of hardly utilizable SOM to the decomposition of easily utilizable sugar. This first phase was very short (2–3 days), hence was frequently missed in other experiments. The second phase showed a slightly increased slurry and SOM decomposition (compared to the soil without sugar). The separation of three sources in CO_2 efflux from grassland soils allowed us to conclude that the C will be utilized according to its utilizability: sugar > slurry > SOM. Additionally, decomposition of more inert C (here SOM) during the period of intensive sugar decomposition was strongly reduced (negative priming effect). We conclude that, priming effects involve a chain of mechanisms: (i) preferential substrate utilization, (ii) activation of microbial biomass by easily utilizable substrate (iii) subsequent increased utilization of following substrates according to their utilizability, and (iv) decline to initial state.

Keywords: ^{13}C natural abundance; Grassland; Microbial activation; Separation methods; Partitioning CO_2 sources; Preferential substrate utilization; Priming effect; Slurry; Soil organic matter; Sugar

1. Introduction

Priming effects (PE) are strong, generally short-term changes in the turnover of native soil organic matter induced by comparatively moderate treatments of the soil (as defined in Kuzyakov et al., 2000). Such treatments might be, e.g. inputs of organic or mineral fertilizer to the soil (Bol et al., 1999; Bol et al., 2000; Bol et al., 2003; Olayinka, 2001; Leifeld et al., 2002; Clough et al., 2003), exudation of organic substances by roots (Mary et al., 1993; Fu and Cheng, 2002; reviewed by Kuzyakov, 2002; Paterson, 2003; Cheng and Kuzyakov, 2005) or remaining plant residues (Liang et al., 1999). In the course of priming large amounts of C, N and other nutrients can be released or immobilized in soil in a very short timescale, generally several days to weeks (Fu et al., 2000; Hamer and Marschner, 2002, 2005a; Bol et al., 2003; Fontaine et al., 2004). However, as such treatments may occur on a regular basis (e.g. fertiliser or manure applications) the overall influence of priming can become apparent in the long-term (annual or decadal) nutrient balance (Gerzabek et al., 1997).

Our proposed definition of the priming effect implies that the decomposition rates of soil organic matter (SOM) pools are not constant and depend not only on the environmental factors (i.e. temperature and soil moisture), but also on the state of microbial biomass. It also implies that

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the decomposition of C pools is interdependent and not additive. This contrasts with the concepts for SOM decomposition used in nearly all models of C and N dynamics in soil (reviewed by Engel et al., 1993; Smith et al., 1997, 1998). Some experimental studies showed that the degradation rates of carbon (C) substrates depends on composition of microbial community, size, and its physiology—the parameters which directly affect the enzyme activity in the soil (Schimel and Gulledge, 1998; Wall and Moore, 1999; Zogg et al., 1997). Therefore, more recently a few models have started to consider priming effects (Blagodatsky and Richter, 1998; Gignoux et al., 2001; Muller and Hoper, 2004).

The most important PEs are generally those of the acceleration or retardation of soil organic matter turnover due to increased or decreased activity, amount or composition of the microbial biomass, as discussed in the recent literature (Kuzyakov et al., 2000; Kuzyakov, 2002; Paterson, 2003; Fontaine et al., 2003; Waldrop and; Firestone, 2004; Subke et al., 2004). Some of the mechanisms for PEs have been partly proven (De Nobili et al., 2001; Fontaine et al., 2004; Hamer and Marschner, 2002, 2005a) and some new mechanisms were suggested (De Nobili et al., 2001; Stenström et al., 2001; Plante and McGill, 2002; Kuzyakov, 2002; Paterson, 2003; Bell et al., 2003; Fontaine et al., 2003; Dilly, 2004). However, the mechanisms of the priming phenomenon remain controversial and hypothetical, because the effects observed in earlier studies vary between different soils, substrates and timing of additions (Bremer and Kuikman, 1994; Shen and Bartha, 1996; Leifeld et al., 2002; Hamer and Marschner, 2002, 2005a).

The second relevant question regarding PE is the source of primed C (=extra CO_2) after addition of easily available substrate. It has been proposed and partly proven that additionally released CO_2 can originate from: (1) increased turnover of microbial biomass only (Dalenberg and Jager, 1989; Degens and Sparling, 1995; Chander and Joergensen, 2001; De Nobili et al., 2001), (2) pool substitution in the microbial biomass (Wu et al., 1993; Luna-Guido et al., 2001), (3) not from the microbial biomass, but without further specification (Chotte et al., 1998; Hamer and Marschner, 2005b), (4) from partly decomposed plant residues (Bell et al., 2003) and (5) from different pools of SOM (Asmar et al., 1994; Vanlauve et al., 1994; Bol et al., 1999; Fontaine et al., 2004). The question about the source of extra CO_2 (or mineralised N) remains unproven, until the specific pool of native SOM can be labelled and not the added substrate (as in all previous studies). There have been only a few studies, in which pools of SOM or partly humified plant residues were labelled (Bell et al., 2003).

However, two other reasons could help explain the reported differences and controversies in priming effects and mechanisms. Firstly, the calculation of PE is based on comparison of two methods of estimation of SOM-derived CO_2 efflux: (a) an isotopic (tracer) method allowing elucidation of CO_2 originated from the added substance and (b) a method based on difference in CO_2 efflux from soil with and without substrate addition. All unaccounted experimental errors as a result of one or both methods will be accounted in the PE.

Secondly, all previous results were based on methods which only allowed separation of two sources of CO_2 efflux: (1) of the substance added to the soil and/or (2) the sum of all others sources (different pools of SOM, microbial biomass, plant residues etc.). Hence, it was not possible to separate of any specific source within the sum of all other sources except the added substance. It was not possible to separate and evaluate the contribution of SOM pools having different utilizability (easily decomposable and inert SOM pools), from either the microbial biomass, or the remaining partly decomposed plant residues etc. It is our opinion that especially the last fact leads to many possible ('plausible') hypotheses and speculations.

We propose separation of more than two sources of total soil CO_2 efflux as the next step to examine the sources of C quantitatively contributing to PE. Recently, a new approach has been successfully used to quantify the contribution of three or more C sources to the total CO_2 efflux in grassland soil (Kuzyakov and Bol, 2004). The approach is based on combination of two (or more) different sets of C_3 and C_4 substrate additions (originated from C_3 or C_4 plants) applied to the soil and based on the assumption of identical transformation of C_3 and C_4 substances. Using this approach, we distinguished between three CO_2 sources having different microbial utilizability (see below): readily utilizable (sugar), medium utilizable (partly humified slurry) and hardly utilizable (SOM). We hypothesized that the substances having different microbial utilizability will (1) induce different effects on decomposition of SOM, and (2) will be decomposed corresponding to their utilizability.

Here we would like to introduce some terms useful for possible effects of the added substrates as well as of the C presented in the soil on microorganisms. Instead of commonly used 'availability' of substrates we used 'utilizability'. This is a result of the fact that many different C sources already present (=available) in the soil, such as SOM, cannot be readily utilized by soil microorganisms. The other frequently used term 'decomposable' reflects decomposition, but not the usage of the substrate by the microorganisms which is important in relation to the PE. Looking for an appropriate term describing the effect of the substrate on the activity of soil microorganisms and possible changes of their composition, we decide on 'utilizability'. In this study, we regard sugar as a 'readily utilizable substrate', slurry as a 'medium utilizable substrate', and native SOM as a 'hardly utilizable substrate'.

The present study examined if the direction and magnitude of the PEs depends on: (1) utilizability of the added substrate, (2) utilizability of the substrates already presented in the soil, and (3) on the soil properties, specifically the organic carbon (C_{org}) content (as reviewed

in Kuzyakov et al., 2000; Kuzyakov, 2002). The CO_2 efflux dynamics were measured for two grassland soils with and without added partly humified slurry in response to freshly added sugar. Furthermore, using the new method described previously the absolute and relative contribution three of its sources (native soil C, slurry C and sugar C) to total CO_2 efflux and PE were quantified.

2. Material and methods

2.1. Field site, soil sampling and preparation

Soil material was collected from two grassland sites with differences in soil type, total C, total N contents and soil texture, but similar in management history (Table 1). The two sites, De Bathe (DB) and Rowden Moor (RM), were both located near North Wyke, Devon, Southwest England (50°45′ N, 4°53′ W; grid reference SS675012).

At each field site, three subsites where randomly selected for soil sampling, which took place on January 19, 2001. For sampling we isolated intact soil cores (20×25 cm^2) from the topsoil (0–10 cm) and stored them at 5 °C. The upper 0–4 cm contained too many roots and was therefore not used in the experiment. The remaining soil (4–10 cm depth) was then wet sieved (<7 mm) after the removal of vegetation and bigger roots. We weighed 118 g of the RM soil (C_{org} = 5.09%) and 257 g of the DB (C_{org} = 2.33%) into Kilner jars to give a 6.0 g C of soil C. This was required for a true comparison of C respiration dynamics between the two soils in response to slurry and sugar additions.

2.2. Experiment design, slurry and sugar application

A 3×2 factorial experiment was established for each soil. The first factor was C_{org} content of the soil (see above). The second factor was slurry application. No slurry, C_3 slurry or C_4 slurry was applied to each of both soils on 26 January 2001 (Table 2). C_3 slurry contained 37.4% C, 2.5% N and has C–to–N ratio of 15.0. C_4 slurry contained 46.3% C, 2.16% N and has C–to–N ratio of 21.5. The detailed description of C_3 and C_4 slurry preparation was presented earlier (Bol et al., 2003). After the slurry application the soil was incubated for 40 days at 27 °C and 70% of field capacity (FC). The results of the CO_2 fluxes, their partitioning and observed priming have been published (Bol et al., 2003) and will not be described here. After this incubation leading to partly humification of added slurry, the soil was let to dry and stored for one year. On April 4, 2003 the soil was mixed, and 15 g soil was put into 150 ml jars. The soil was moistened to 70% of FC and pre-incubated for 2 weeks at 20 °C.

Table 1
Type and chemical properties of the soils (4–10 cm) used in the experiment

	De Bathe	Rowden Moor
British classification	Typical brown earth (Crediton series)	Pelo-stagnogley (Hallsworth series)
FAO classification	Eutric Cambisol	Dystric Gleysol
USDA classification	Dystric Eutrocrept	Typic Haplaquept
C (%)	2.33±0.1	5.09±0.08
N (%)	0.30±0.01	0.63±0.07
C/N	7.7	8.0
Original soil δ^{13}C (‰)	−26.9±0.1	−28.6±0.1
pH ($CaCl_2$)	4.6	4.8
Field capacity	39	58
Soil texture		
% fine sand	41	2
% coarse sand	30	10
% silt	20	50
% clay	9	38

The third factor was sugar application (added on 23th April 2003). No sugar, C_3 sugar or C_4 sugar was applied to each soil-slurry treatment (factor 1). Two commercially produced sugars were used. The C_3 sugar from sugar beet had δ^{13}C of −27.2±0.1‰, and C_4 sugar from sugar cane had δ^{13}C of −11.0±0.1‰. The amount of sugar C applied to each pot corresponds to 1% of previously applied slurry C or to 0.3% of C_{org} amount; equivalent to 2.544 mg C (6.36 mg sugar) and 1.167 mg C (2.92 mg sugar) applied per pot for RM and DB soils (Table 2). Because slurry and sugar were applied at different dates, the direct comparison between the PE induced by slurry and sugar was not possible. The control soils did not receive any slurry or sugar, but equivalent volume of double distilled water was added instead of glucose solution. The detailed description of sugar application was presented by Kuzyakov and Bol (2004). The final experiment design included nine treatments, different in slurry or sugar application, for each of the two soils. The summary of the amount of the C and δ^{13}C values in different sources before sugar addition are presented in Table 2.

2.3. Incubation, CO_2 measurements and δ^{13}C analyses

Periodically (on 17, 42, 68, 96, 139, 169, 233, and 258 h after sugar addition) the CO_2 evolved from soil/slurry/sugar mixture was sampled. The 150 ml jars were flushed with CO_2 free air and sealed with a greased rubber ring and a lid with a septum for the needle. After the time between 2 (at the beginning) and 4 (at the end of incubation) h after sealing the jar, the air samples (12 ml) were taken from the headspace using evacuated exetainers and then analysed for their CO_2 concentration and δ^{13}C value using a GC-IRMS (Europa, Crewe, UK). The jars were left open between the CO_2 samplings.

The moisture content of both soils and slurries were determined by weighing before and after drying in an oven at 85 °C. Soil, sugar, and slurry samples were then ground in a pestle and mortar to pass through a 600 μm sieve. Total C and N content of soil, sugar, and slurry samples was determined using a CHN auto-analyser (Carlo Erba NA2000, Milan, Italy). The determination of δ^{13}C values

Table 2
Amount of C in different pools at the start of sugar addition, their $\delta^{13}C$ values and mean mineralisation rate of C from SOM, slurry and sugar

C pool	$\delta^{13}C$ (‰)		Amount at the start				Mineralisation rate (d^{-1})	
	DB	RM	DB		RM		DB	RM
			mg C g^{-1}	%[a]	mg C g^{-1}	%[a]		
SOM	−27.9	−28.5	23.33	100	50.88	100	4.0×10^{-4}	5.7×10^{-4}
C_4 slurry	−21.3		8.68	37.3	13.37	26.3	1.4×10^{-3}	1.6×10^{-3}
C_3 slurry	−30.7						1.4×10^{-3}	1.6×10^{-3}
C_4 sugar	−11.0		0.0778	0.33	0.1696	0.33	>1.3[b]	≫0.4[b]
C_3 sugar	−27.2							

[a] SOM content at the start of the experiment was taken for 100%.
[b] Because of very fast decomposition of sugars, their decomposition rates could not be exactly estimated on the used time scale.

of soil, sugar, and slurry samples were analysed at IGER North Wyke using a continuous flow ANCA 20/20 SL system (Europa, Crewe, UK). Natural abundances of ^{13}C were expressed as $\delta^{13}C$ (‰) which represents the ratios of ^{13}C:^{12}C relative to the standard (VPDB). The $\delta^{13}C$ values are defined as $[(R_{sample}-R_{standard})/R_{standard}]\times1000$. The analytical precision of the $\delta^{13}C$ measurements was 0.1‰.

2.4. Calculations and statistical analysis

To calculate the contribution of C_4–C (slurry or sugar derived) to the CO_2 efflux for the treatments with two C sources the following equation was used:

$$C_4^* = \frac{C_t(\delta_t-\delta_3)}{(\delta_4-\delta_3)} \quad (1)$$

where $C_t = C_3^* + C_4^*$, was the C from total CO_2, C_3^* was the amount of C–CO_2 derived from the C_3 soil, C_4^* was the amount of C–CO_2 derived from C_4 slurry or sugar, δ_t was the $\delta^{13}C$ value of the C_t, δ_4 was the $\delta^{13}C$ value of the C_4 slurry (= −21.3‰) or C_4 sugar (= −11.0‰), and δ_3 was the $\delta^{13}C$ value of the C_3 soil ($\delta^{13}C$ of RM soil was −28.6‰, $\delta^{13}C$ of DB soil was −26.9‰). The contribution of SOM (C_3) carbon from the cases with two C sources was calculated as the difference.

In the treatments with three CO_2 sources, in which slurry or sugar were originated from C_4 vegetation, the contribution of the C_4 source was calculated according to Eq. (1), and the contribution of the sum of two C_3 sources was calculated as difference.

In the treatments with three CO_2 sources, in which slurry and sugar both originated from C_4 vegetation, it was not possible to calculate the contribution of the sum of both C_4 sources to total CO_2 efflux according to Eq. (1) because C_4 sugar and C_4 slurry had different $\delta^{13}C$ values. We used the calculation method based on identical decomposition of C_3 and C_4 sugars, i.e. the decomposition C_3 sugar was equal to the C_4 sugar. Hence, the rate of C_4 sugar decomposition instead of C_3 sugar decomposition was used in the soil treatment with C_4 slurry and C_3 sugar decomposition, i.e. assuming that the slurry origin (C_3 or C_4) had no effect on the sugar decomposition. The intensity of C_4 sugar decomposition in the treatment C_4 slurry $+C_4$ sugar was therefore evaluated according to the decomposition of C_4 sugar in the treatment C_3 slurry $+C_4$ sugar. The detailed background to calculations and their possible inaccuracies have been described in Kuzyakov and Bol (2004). The specific experiment design allows the calculation of different kinds of priming effects:

(i) changes of SOM decomposition induced by slurry application (PE_{SOM}^{Slurry}) were calculated as

$$PE_{SOM}^{Slurry} = C_{C_3SOM}^{Soil+C_4Slurry} - C_{C_3SOM}^{Soil} \quad (2)$$

(ii) changes of SOM decomposition induced by sugar application (PE_{SOM}^{Sugar}):

$$PE_{SOM}^{Sugar} = C_{C_3SOM}^{Soil+C_4Sugar} - C_{C_3SOM}^{Soil} \quad (3)$$

(iii) changes of SOM and slurry decomposition induced by sugar application:

$$PE_{SOM+Slurry}^{Sugar} = C_{C_3SOM+C_3Slurry}^{Soil+C_3Slurry+C_4Sugar} - C_{C_3SOM+C_3Slurry}^{Soil+C_3Slurry} \quad (4)$$

and

$$PE_{SOM+Slurry}^{Sugar} = C_{C_3SOM+C_4Slurry}^{Soil+C_4Slurry+C_4Sugar} - C_{C_3SOM+C_4Slurry}^{Soil+C_4Slurry} \quad (5)$$

where PE are priming effects, C is Carbon contributing to CO_2 efflux originated from sources named as subscript in the treatment with C sources named as superscript.

This approach based on ^{13}C natural abundance and different complexity of C sources in the various treatments enables: (a) the differentiation of three C sources contributing to CO_2 efflux and (b) the calculation of primed C induced by two different substrates (slurry or sugar) from two C pools in soil (native SOM and partly humified slurry). To evaluate the dynamics of primed C, the rates (% of C_{org} d^{-1}) of released primed CO_2 were presented, with the extend of PE given as percentage of the C available in soil before the sugar addition (Table 2). This allows direct comparison of the extend of PEs in soils with different C_{org} content, as well as soils amended or not amended with slurry. We refer (SOM + slurry)-C or (SOM + slurry)-derived CO_2 if we present the sum of C (or CO_2) released

from both SOM and slurry. In other cases SOM-derived CO_2 or slurry-derived CO_2 are mentioned.

To calculate the dependence of the intensity of PE from the intensity of sugar or slurry decomposition, the linear regression between CO_2 primed from the target C pool (SOM or partly humified slurry) and CO_2 originated from sugar were calculated. The significance level of regression parameters is presented with *, **, and *** correspondingly to $P<0.05$, 0.01 and 0.001 level, respectively.

3. Results

3.1. Microbial utilizability of C derived from SOM, slurry and sugar

Microbial utilizability of C is a crucial factor influencing the soil CO_2 efflux and activity of microorganisms (Stenström et al., 2001; Dilly, 2003, 2004). Hence, we suggest that the microbial utilizability of C is also critical for PEs: for substances inducing PE, as well as for SOM pools involved in changing decomposition. The three C sources examined in the present study: (1) native SOM, (2) partly humified slurry, and (3) added sugar, strongly differ in both their availability in the soil and microbial utilizability. Table 2 presents these differences in the context of mineralisation rates, which were calculated according to CO_2 efflux from each pool. The mineralisation rates of glucose (>0.38–$>1.3\ d^{-1}$) were about 3 orders of magnitude higher than that of slurry (1.4–$1.6\times10^{-3}\ d^{-1}$) or SOM (4.0–$5.7\times10^{-4}\ d^{-1}$) (Table 2). Theses differences in the mineralisation rates led to comparable amounts of CO_2 respired from each pool at the start of the experiment, despite the fact that the amounts of C in the pools differed by about 2.5 orders of magnitude (Table 2). Here it is important to note, that the mineralization rates of slurry and SOM were calculated as for bulk pools without their separation into sub-pools with different turnover. Therefore, the calculated turnover rates are only an estimation and are only suitable for relative comparison within the experiment. The mineralisation rates at least of SOM and slurry were higher in the soil with higher C_{org} content and higher microbial biomass. We also expected that the sugar mineralisation rate was higher in the RM soil, but its exact calculation was not possible, because CO_2 and its $\delta^{13}C$ value were not continuously monitored.

3.2. SOM-derived CO_2 efflux from soil amended and not amended with C_4 sugar or with C_4 slurry

The total CO_2 efflux after sugar addition increased (4–8 fold) for 2–4 days in both soils (Fig. 1). However, in the first two samplings after the sugar addition, the SOM decomposition decreased in both soils when compared to control treatment (soil only). Therefore, the addition of the easily utilisable C such as sugar induced a negative PE

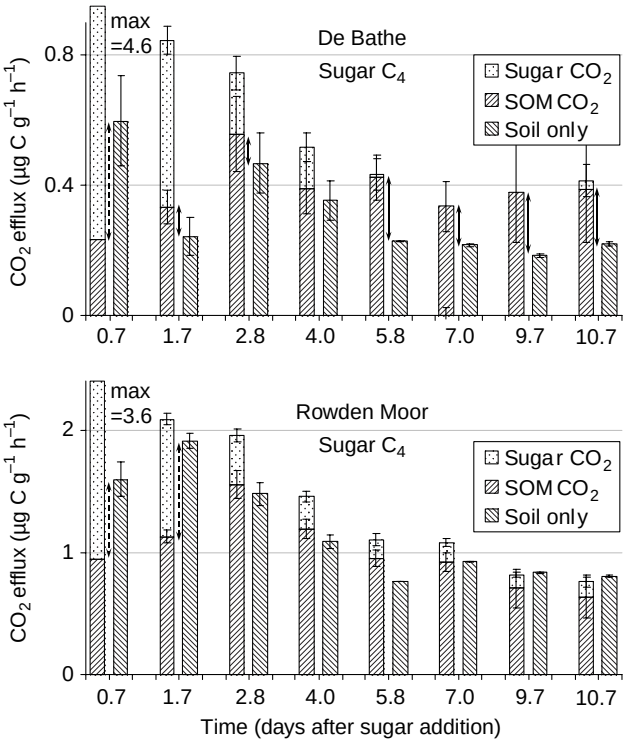

Fig. 1. Sugar-derived CO_2 (Sugar CO_2) and SOM-derived CO_2 (SOM CO_2) efflux rate (µg C g^{-1} h^{-1}, ±SE) from the De Bathe (top) and Rowden Moor (bottom) soils after C_4 sugar addition. 'Soil only' presents the total CO_2 efflux from the respective soil without sugar addition and includes only SOM-derived CO_2. Positive and negative priming effects are shown with continuous and dashed arrows, respectively.

(suppression of SOM decomposition) for a very short period that was over after 2 days for DB soil and after 3 days for RM soil. After the initial suppression, the SOM decomposition in the two soils with added sugar (especially in DB soil) was slightly increased compared to the control (Fig. 2; Table 3, significant values are in bold). Although most individual points of PE measured 4 days after sugar addition were not significantly different from zero ($P>0.05$), practically all points for DB soil and the most points for RM soil were positive. Separate estimation of mean changes of SOM decomposition for the first 2 days and the period after 4 days (Table 3) showed that the first phase was significantly ($P<0.05$) negative for both soils and the second phase was positive for DB soil. This showed the presence of the second phase for DB soil, in which the SOM decomposition was enhanced compared to the control without treatments. The decrease of CO_2 efflux in the first phase caused by sugar addition was stronger in the RM than in the DB soil (Table 3). In contrast, the increase of SOM decomposition in the second phase was strongly pronounced in the DB soil. These quantitative differences between the two soils were a result of different C_{org} content, however the directions of the PE effect for the first and second phase after sugar addition were the same.

The dependence between primed SOM-derived CO_2 and CO_2 evolved by sugar decomposition showed that

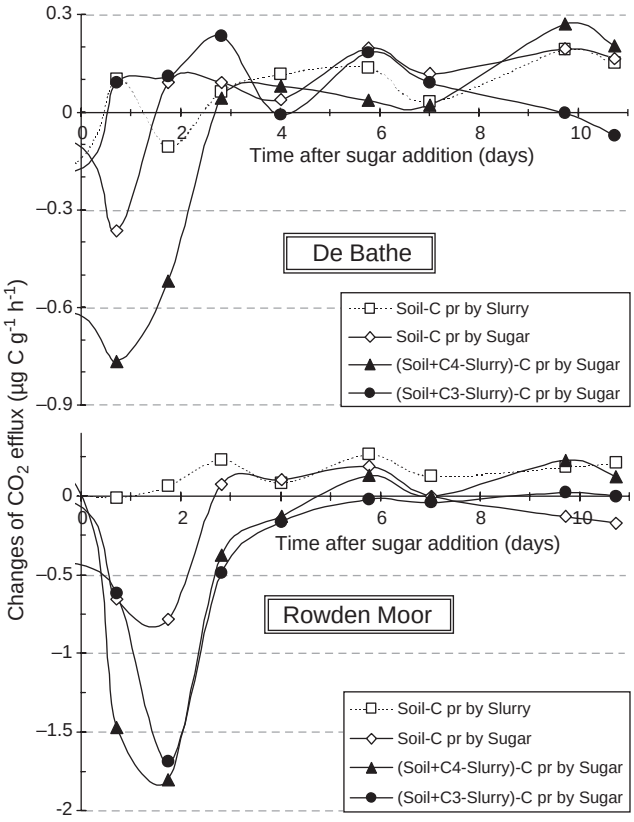

Fig. 2. Dynamics of changes of SOM or the sum of SOM + slurry mineralization (measured as changes of CO_2 efflux) induced by addition of C_4 sugar or C_4 slurry in the De Bathe (top) and Rowden Moor (bottom) soils previously amended (closed symbols) and not amended (open symbols) with slurry.

the suppression corresponds to about 10% of sugar-derived CO_2 for DB soil and to 30% for RM soil (Table 4). Clearly, the response of the soil with higher C_{org} content was stronger. However, it is necessary to mention that these regression lines were mainly affected by one or two points at the maximal intensity of sugar-derived CO_2 emission (clustered data). Therefore, the parameters are not suitable to predict PE based on sugar-derived CO_2.

The presence of partly humified slurry also changed the decomposition of native SOM (Table 4, significant intercept for both soils), however no significant relationship was observed between slurry-derived and SOM derived CO_2 (Table 4, not significant slope for both soils).

Table 3
Two phases of priming effects and average changes of SOM or SOM + Slurry decomposition induced by slurry or sugar (in µg C–CO_2 g^{-1} h^{-1}) evolved from different C sources

		Phase 1: 0–2 d		Phase 2: 4–11 d	
Soil	Treatment	Mean	±SE	mean	±SE
DB	SOM by slurry	−0.003	±0.104	**+0.125**	**±0.027**
	SOM by sugar	−0.136	±0.227	**+0.142**	**±0.030**
	(SOM+C_4-slurry) by sugar	**−0.643**	**±0.124**	**+0.122**	**±0.049**
	(SOM+C_3-slurry) by sugar	**0.100**	**±0.009**	+0.038	±0.045
RM	SOM by slurry	0.026	±0.038	**+0.177**	**±0.032**
	SOM by sugar	**−0.720**	**±0.063**	−0.002	±0.068
	(SOM+C_4-slurry) by sugar	**−1.639**	**±0.167**	+0.070	±0.062
	(SOM+C_3-slurry) by sugar	**−1.153**	**±0.535**	−0.040	±0.033

The values significantly different from zero are in bold (calculated as SE × 1.96).

3.3. SOM- and slurry derived C primed by sugar addition

The CO_2 efflux strongly increased after addition of sugar to soils previously amended with slurry, mainly as a result of the sugar decomposition (the data not shown). However, the effect of sugar on the decomposition of the sum of SOM and slurry C ((SOM + slurry)-C) was different between both soils (Fig. 2). Sugar did not significantly change the (SOM + slurry)-derived CO_2 efflux from DB soil compared to the treatment (soil + slurry) without sugar. The regression of the primed CO_2 from DB soil depending on sugar-derived CO_2 was also not significant (Table 4). In contrast, a pronounced effect of sugar addition on RM soil + slurry was observed and this was similar to the effect of the treatment without slurry, sugar induced microbial switch from (SOM + slurry)-C to sugar C. This decrease of (SOM + slurry)-C decomposition was completely over after day 4. It implied, that after 4 days, the decomposition of (SOM + slurry)-C from soil amended with and without sugar were identical.

The application of the C_3 slurry to the C_3 soil did not allowed us to differentiate whether the CO_2 coming after sugar addition originated from native SOM or from partly humified slurry C. However, this problem can be overcome by using the soil pre-treated with C_4 slurry (see below) assuming that the slurry decomposition does not affect sugar derived CO_2 (see Ref. Kuzyakov and Bol, 2004).

3.4. SOM- or slurry-derived C primed by sugar addition

The comparison of CO_2 efflux originated from treatments with different slurry origin showed that addition of sugars had very similar effect on CO_2 originated from C_4 or C_3 slurries. All regression lines of primed (SOM + slurry)-C depending on sugar CO_2 show slightly increased retardation of (SOM + slurry)-C decomposition by increasing sugar-derived CO_2 in the first days after sugar addition.

The full separation of the three sources of CO_2 is presented on Fig. 3 (left). The respective control treatments with C_4 slurry, but without sugar addition are also presented there. This 3-C-sources separation showed that the sugar addition had different effects on the two other C sources examined, i.e. increasing slurry-derived C decomposition, but strongly decreasing native SOM-C decomposition. The decrease of SOM decomposition was nearly 2-fold larger than the increase of slurry decomposition (Fig. 4, right).

Table 4
Parameters of linear regression of changes of SOM and slurry decomposition (primed C, measured as additional CO_2 efflux from respective source) depending on decomposition of slurry or sugar (measured as CO_2 derived from slurry or sugar)

	Addition		De Bathe, C_{org} = 2.3%			Rowden Moor, C_{org} = 5.1%		
Treatments	Slurry	Sugar	Slope	IC	R^2	Slope	IC	R^2
SOM-C primed by slurry	C_4	–	-0.27^{ns}	$+0.19$*	0.34	-0.14^{ns}	$+0.26$**	0.47
SOM-C primed by sugar	–	C_4	-0.12***	$+0.14$***	0.93	-0.29**	$+0.01^{ns}$	0.53
(SOM + slurry)-C primed by sugar	C_3	C_4	$+0.01^{ns}$	$+0.07^{ns}$	0.01	-0.39^{ns}	-0.15^{ns}	0.23
(SOM + slurry)-C primed by sugar			-0.19***	$+0.03^{ns}$	0.95	-0.45^{ns}	$+0.15^{ns}$	0.36
Slurry-C primed by sugar	C_4	C_4	$+0.28$***	$+0.05^{ns}$	0.68	$+0.91$***	$+0.63$***	0.95
SOM-C primed by sugar			-0.48***	$+0.07$*	0.99	-1.46***	-0.57*	0.88
(SOM + slurry)-C primed by sugar			-0.25**	$+0.07^{ns}$	0.72	-0.86*	$+0.08^{ns}$	0.62
Slurry-C primed by sugar	C_4	C_3	$+0.28$***	$+0.05^{ns}$	0.95	$+0.91$***	$+0.63$***	0.95
SOM-C primed by sugar			-0.53***	$+0.02^{ns}$	0.94	-1.76***	-0.54*	0.90

IC: intercept. ^{ns}: not significant; *, **, ***: significant at 0.05, 0.01 or 0.001 error probability level, respectively. Only the regressions having significant slope are significant.

These effects were very similar in the soils amended with C_4 slurry after addition of C_3 sugar (Fig. 5, right).

There were differences of the dynamics of the PEs between both soils (Figs. 4 left and 5 left). For RM soil (higher C_{org} content) after a fast initial increase, a very prolonged decline of the priming for both SOM-C and slurry-C mineralisation was observed. It is noticeable, that the lines for changes of SOM-C and slurry-C mineralisation in RM soil were nearly mirrored (Figs. 4 bottom and 5 bottom). For the DB soil (with lower C_{org} content), the processes were mainly over within 3 days. However, in both soils the decline phase of the PE for both SOM and slurry was very short—2–3 days and the relative changes of SOM and slurry mineralisation after sugar addition were very similar. So, in both soils, the maximal decrease of SOM decomposition was ca. 0.15% C_{org} d^{-1}, and the maximal

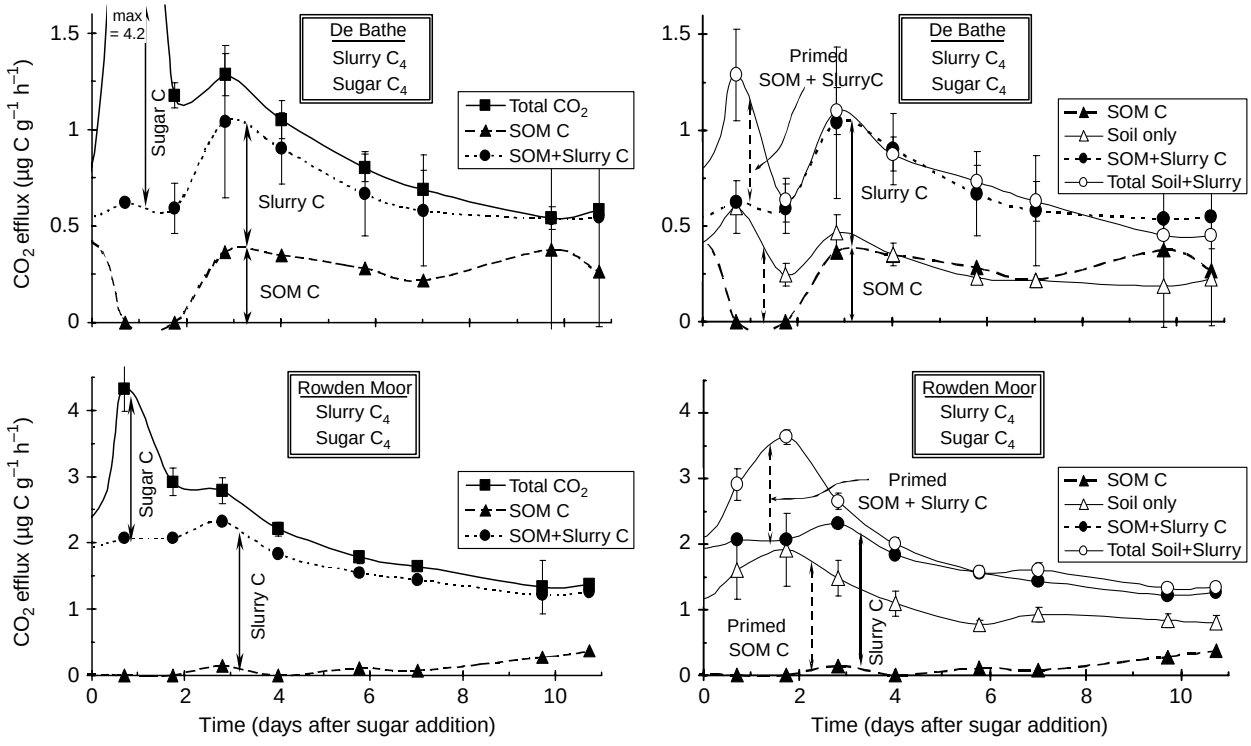

Fig. 3. Left: Absolute contribution (±SE) of three C sources (SOM, C_4 slurry and C_4 sugar) to the total CO_2 efflux from the De Bathe (top) and Rowden Moor (bottom) soils calculated indirectly by $\delta^{13}C$ values of CO_2 and the acceptance of identical decomposition of C_3 and C_4 sugars. Right: Priming effects of slurry or SOM decomposition presented as changes of slurry-C or SOM-C mineralization induced by sugar addition as compared to the respective treatment without sugar. The total CO_2 efflux from the soil pre-treatments with C_4 slurry without sugar is presented as a control. Vertical arrows show different C sources. ■, ▲, ●, respectively, total CO_2 efflux, SOM-derived CO_2 efflux and (SOM + slurry)-derived CO_2 efflux from the soils amended with C_4 slurry and C_4 sugar, △ represents total CO_2 efflux from the soil without any additions (SOM-derived CO_2 only), ○ represents CO_2 efflux from the and amended only with slurry ((SOM + slurry)-deriveds CO_2). Negative priming effects for SOM-C or slurry-C are shown on the right with dashed arrows.

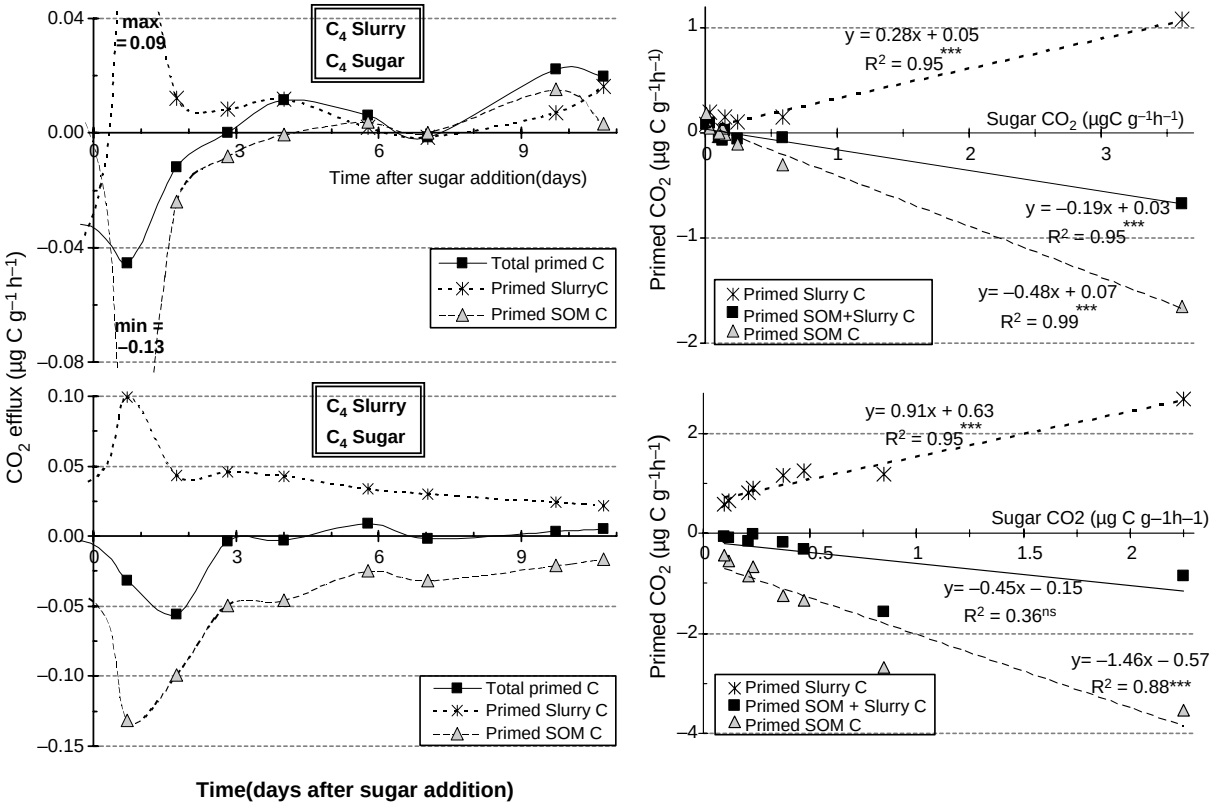

Fig. 4. Relative changes of SOM-C and slurry-C mineralization (in % of C_{org}) induced by C_4 sugar addition in the De Bathe (top) and Rowden Moor (bottom) soils pre-treated with C_4 slurry (left) and the absolute dependence of changes of SOM-C and slurry-C mineralization on the intensity of sugar decomposition measured as sugar-derived CO_2 efflux (right).

increase of slurry-C mineralisation was ca. 0.1% $C_{org}\ d^{-1}$) (Figs. 4 and 5).

The regression parameters of the dependence of the PE (extra CO_2 from SOM and/or slurry) depending on the CO_2 originated from sugar as well as the significance of the parameters were summarized in Table 4. The regression parameters showed clear differences between PEs induced by slurry and by sugar as well as the importance of the distinguishing between the sources of C released in the extent of priming. The addition of slurry as medium utilizable substrate showed small but significant increase of SOM decomposition (significant 'Intercept' values), which was not dependent on the intensity of the slurry decomposition itself (not significant 'Slope' values). This means that the average intensity of the SOM decomposition was increased by slurry addition, but was independent of the intensity of slurry decomposition. In contrast, the addition of sugar as easily utilizable substrate showed strong changes (increase and decrease) of SOM and/or slurry decomposition, which were strongly dependent on the intensity of sugar decomposition (significant 'Slope' in Table 4).

The regression parameters (Table 4) clearly show the importance of the separation of the sources of CO_2 primed. The effect of sugar on the changes of (SOM + slurry)-C mineralization was much less or absent compared to the effect of sugar on the SOM or slurry decomposition. In all treatments with three C sources, the CO_2 efflux from sugar was positively correlated with CO_2 produced by slurry decomposition and negatively correlated with CO_2 produced by SOM decomposition. The response of CO_2 primed from SOM and from slurry was always nearly three times higher in the RM soil compared to the DB soil ('Slope' values, Table 4). The ratio between the C_{org} in RM to DB soil was about 2.2. This means that the PE was strongly pronounced in the soils with high C_{org} not only in absolute terms, but also relative to the total C_{org} content.

4. Discussion

We examined three specific factors which may affect priming effects: (1) microbial utilizability of added substances: readily utilizable for sugar and medium utilizable for slurry, (2) microbial utilizability of C pools present in soil: partly humified slurry and native SOM, and (3) level of C_{org} in the soil: 2.3% for De Bathe and 5.1% Rowden Moor. Concerning these three factors we will discuss (1) the dynamics of changes in SOM or/and slurry decomposition, (2) sources of CO_2 evolved by priming, and (3) possible mechanisms for the observed priming.

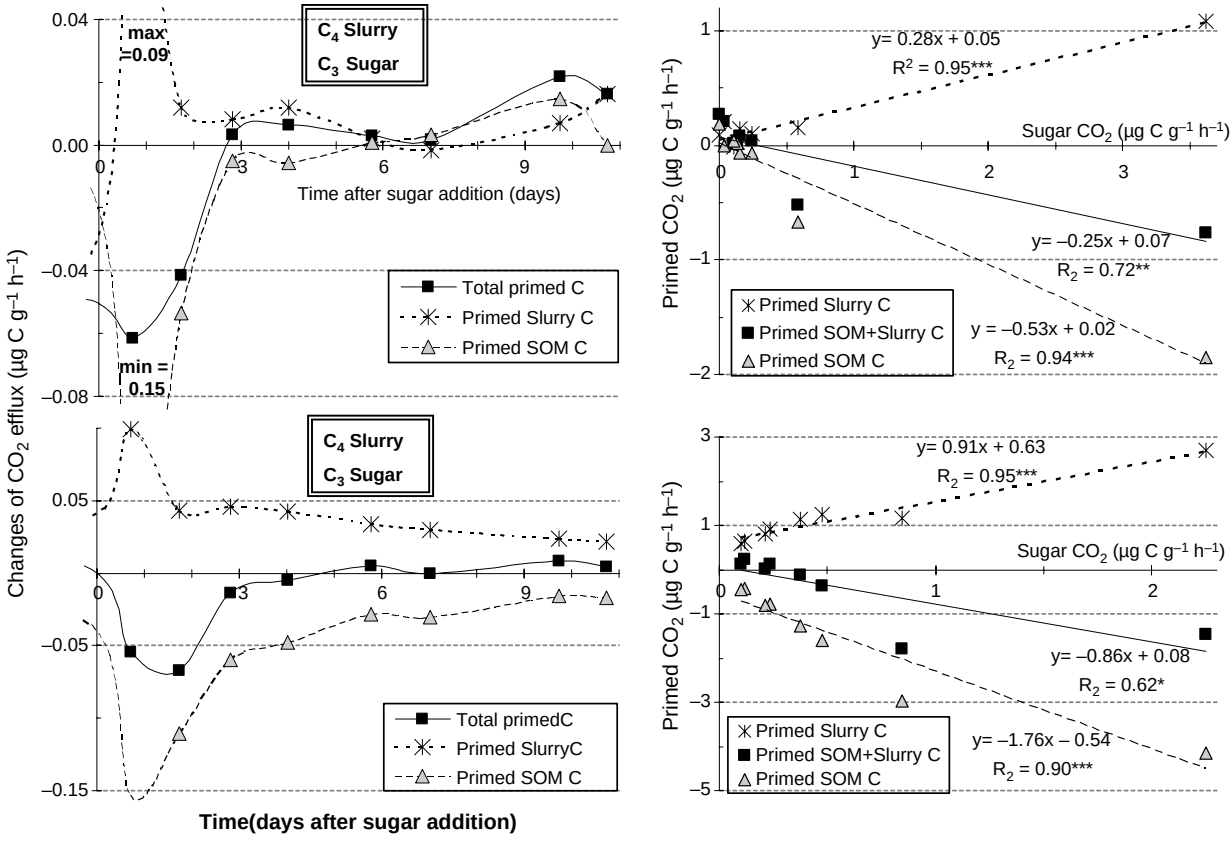

Fig. 5. Relative changes of SOM-C and slurry-C (in % of C_{org}) mineralization induced by C_3 sugar addition in the De Bathe (top) and Rowden Moor (bottom) soils pre-treated with C_4 slurry (left) and the absolute dependence of changes of SOM-C and slurry-C mineralization on the intensity of sugar decomposition measured as sugar-derived CO_2 efflux (right).

4.1. Dynamics of changes of SOM or/and slurry decomposition

The temporal change of SOM-derived CO_2 or/and slurry-derived CO_2 efflux, and hence their decomposition, as was induced by addition of slurry or sugar, provides the first clues about the mechanisms behind the changes. Typically, on the first CO_2 sampling (17 h) after sugar addition, a strong decrease of CO_2 efflux from SOM occured. This could be observed in SOM-derived CO_2 efflux of the treatment with sugar only or for the sum of SOM + slurry-derived CO_2 efflux. This decrease was completely over after 2–3 days for both soils. So, we conclude that the first phase was directly connected with addition of easily utilizable C source resulting in the switch of microorganisms from the decomposition of the hardly utilizable substrate like SOM to the easily utilizable C source like sugar. In the second phase, a slight increase of SOM (in the treatment with sugar only) or of the sum of SOM and slurry-derived CO_2 was observed. At first glance, such PE dynamics (switch between negative and positive effects) seems to be unusual because in the most previous experiments one directional changes: decrease (Hamer and; Marschner, 2002) or increase (Hamer and; Marschner, 2002; De Nobili et al., 2001) of SOM decomposition were observed. However, most previous studies analysed total CO_2 (De Nobili et al., 2001) or labelled $^{14}CO_2$ from added substrates (Hamer and; Marschner, 2002) with longer sampling intervals. This means that a switch from decreased to increased decomposition (or *vice versa*) could have been missed. A short-time sampling scale is probably especially important for low molecular substances, such as sugars, amino acids, carboxylic acids etc., which will be completely decomposed within few hours (Jones et al., 2005). It is to note here that in the most PE studies mainly simple low molecular substrates with very fast decomposition rates were used.

The response of microbial biomass to the addition of easily utilisable substrate is very fast and persists less than few hours (Stenström et al., 2001). This feature is used in substrate induced respiration (SIR) method for measuring microbial biomass (Anderson and Domsch, 1985). Therefore, short sampling time or continuous monitoring of concentration and isotopic signature (e.g. ^{14}C, ^{13}C or $\delta^{13}C$) of CO_2 is necessary to obtain the dynamics of PEs induced by low molecular organic substances. Our first CO_2 sampling was conducted 17 h after sugar addition. Therefore, we also might have already missed the maximal rate of CO_2 efflux from both soils, or the maximum of changes of

SOM and/or slurry decomposition after sugar addition. However, the main dynamics of the changes and the switch of priming were caught.

For both soils and both slurries (C_4 and C_3), strong decrease of SOM decomposition and simultaneous increase of slurry decomposition after sugar exhaustion was observed. It suggests that microorganisms, mainly responsible for decomposition of more utilizable organics were stimulated by sugar addition. In our opinion, these observations support the view of Hamer and Marschner (2005b) that microorganisms having *r* strategy were mainly responsible for the observed PE.

4.2. Sources of primed CO_2

Application of slurry to both soils increased SOM decomposition as additional SOM-derived CO_2 was evolved (Fig. 2). This additional CO_2 might have been released from the microbial biomass and not from SOM (Degens and Sparling, 1995; Chander and Joergensen, 2001; De Nobili et al., 2001). However, since added slurry was incubated in the soil for ca. 2 months before the actual experiment, the increased C_3–CO_2 cannot simply be explained by the CO_2 release from microbial biomass only. If so, the C in microbial biomass would be strongly depleted. For the full comparison of primed CO_2 with the amount of C in the microbial biomass, cumulative CO_2 efflux must be taken into account. The cumulative amount of CO_2 released from SOM or slurry cannot be calculated in this study, as CO_2 was sampled at some discrete periods. Hamer and Marschner (2005b) conducted such direct comparison and showed that not more than for 35% of PE could be explained by the accelerated turnover of microbial biomass. Also Vanlauwe et al. (1994) clearly showed that primed CO_2 was released from native SOM.

If two C sources with different utilizability were present in soil before sugar addition, the cumulative effect of both C sources on CO_2 efflux was similar to the soil without slurry pre-treatment, i.e. a decrease of (SOM + slurry)-derived CO_2 was observed. However, the effect of added sugar was strongly dependent on the utilizability of C sources present in the soil. Specifically, when there was a very large decrease in SOM decomposition then this was partly compensated by a large increase of slurry-C mineralisation (Figs. 4 and 5, left). This supports the general hypothesis that *r*-strategists were activated by addition of easily utilizable substrate, and subsequently preferentially used substrates according to their utilizability. This results in the decreased decomposition rates of the substrate with the lowest availability, in our experiment-the native soil organic matter.

The dependence of changes of SOM and slurry mineralization on the intensity of sugar decomposition (Figs. 4 and 5, right) showed that the response was related to the soil C_{org} content. The priming in RM soil having twice the C_{org} content compared to the DB soil was also about two times greater. This corroborates the hypothesis that the PE intensity depends, not only on the intensity of utilization of the added substrate, but also on the SOM content (higher amount of C sources for priming as well as higher microbial biomass). Similar PE intensities presented as relative values (% of C_{org}) (Figs. 4 and 5, right) confirmed that in the investigated range of C_{org} content, the PE depends nearly linear on the C_{org}. This result is similar to that obtained by Mary et al. (1993), but is in contradiction with the observation of Hamer and Marschner (2005a,b) investigated different horizons of Cambisol, Podzol and Phaeozem, who found that soils with lowest C content or C with low biodegradability have strongest PEs. However, the genesis and the management of the soils used in these studies were very different compared from ours. We used grassland soils. As concluded by Waldrop and; Firestone (2004), the PE in grassland soils was much higher than in the forest soil.

4.3. Mechanisms of priming effect

The explanation of mechanisms of priming effects should include their dynamics (which include size, length and timing), the sources of primed or conserved C and the groups of microorganisms induced the effect. The dynamics and sources were directly investigated in the present experiment. However the conclusions concerning the groups of microorganisms are mainly based on the CO_2 efflux dynamics and availability of C sources.

The dynamics of priming effects can be explained by the following chain of mechanisms:

(1) After addition of a substrate, which utilizability is much higher than of the substrates already present in the soil, the most active part of microbial community (*r* strategists) switch onto the utilization of the freshly added substrate. This switch frequently termed 'preferential substrate utilization' (Sparling et al., 1982; Billes et al., 1988; Cheng, 1999) leads to a temporary decrease of the decomposition of the most inert substrates.
(2) The most active part of microbial community benefits first from the added substrate: their activity and, if the substrate amount is sufficient, the total number strongly increase. This mechanism has frequently been called 'microbial activation' (Helal and Sauerbeck, 1984; Sallih and Bottner, 1988; Cheng and Coleman, 1990; De Nobili et al., 2001).
(3) When the most easily utilizable substrate was completely consumed, the activated microorganisms will target remaining substrates with the highest utilizability and use these until there is no substrate, which is more utilisable than those normally present in the soil. In our experiment, this phase was connected with increased slurry and partly increased SOM decomposition.
(4) Subsequently, the initial balance between differently available pools of SOM and the microorganisms groups

responsible for their utilization will be restored (Stenström et al., 2001). Depending on the C_{org} content of the soil and probably its utilizability, this phase of reaching the initial state can be continued after a few days (DB soil, Figs. 4 top and 5 top) or few weeks (RM soil, Figs. 4 bottom and 5 bottom). This phase can be described as decline of microbial activity and biomass and return to the initial state.

5. Conclusions and outlook

Separation of three CO_2 sources allowed to estimate the contribution of C pools with different utilizability to the PE as induced by sugar addition. The PE dynamics depended on the utilizability of the added substrate, as well as on the composition of SOM pools. The chain of PE mechanisms can be summarized as: (1) preferential substrate utilization (negative PE), (2) microbial activation (positive PE), and (3) decomposition of the other available substrates according to their utilizability, (4) decline and return to the initial state (levelling out). Large changes of the SOM decomposition occurred at the first phase, when the added easily utilizable substrate was used by microorganisms. The microorganisms preferably utilize pools with the highest utilizability and decomposition of the less utilizable C pools was retarded compared to the initial state. Our results clearly showed that the separation of more than two sources of CO_2 efflux after substrate addition, as well as short-term sampling of released CO_2 is crucial for the evaluation of the PE mechanisms. Concerning the brevity of the induced changes, this supports are stated definition that priming is a short-term effect.

The situation with C pools having different utilizability occurs very frequently in soils. Seeking for nutrients, roots grow into fertile patches originated from decomposing plant or animal residues, manure or slurry. Root exudates have very similar utilizability as sugar in our experiment and the organic substances of the patches can be well compared with partly decomposed slurry. The third source having the lowest utilizability remains SOM. Therefore, this experiment reflects the situation in the rhizosphere of roots growing into fertile patches and leading to mobilization of nutrients from C sources according to their utilizability.

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References

Anderson, T.-H., Domsch, K.H., 1985. Determination of ecophysiological maintenance carbon requirements of soil microorganisms in a dormant state. Biology and Fertility of Soils 13, 81–89.

Asmar, F., Eiland, F., Nielsen, N.E., 1994. Effect of extracellular-enzyme activities on solubilization rate of soil organic nitrogen. Biology and Fertility of Soils 17, 32–38.

Bell, J.M., Smith, J.L., Bailey, V.L., Bolton, H., 2003. Priming effect and C storage in semi-arid no-till spring crop rotations. Biology and Fertility of Soils 37, 237–244.

Billes, G., Bottner, P., Gandais-Riollet, N., 1988. Effet des raciness de graminees sur la mineralization nette de l'azote du sol. Reviews Ecology, Biology du Sol 25, 261–277.

Blagodatsky, S.A., Richter, O., 1998. Microbial growth in soil and nitrogen turnover: a theoretical model considering the activity state of microorganisms. Soil Biology & Biochemistry 30, 1743–1755.

Bol, R., Ostle, N.J., Friedrich, C., Amelung, W., Sanders, I., 1999. The influence of dung amendments on dissolved organic matter in grassland soil leachates—preliminary results from a lysimeter study. Isotopes in Environmental and Health Studies 35, 97–109.

Bol, R., Amelung, W., Friedrich, C.F., Ostle, N.J., 2000. Natural ^{13}C abundance as a tool to assess the carbon release from dung patches. Soil Biology & Biochemistry 32, 1337–1344.

Bol, R., Moering, J., Kuzyakov, Y., Amelung, W., 2003. Quantification of priming and CO_2 respiration sources following slurry C incorporation in two grassland soils with different C content. Rapid Communication in Mass Spectrometry 17, 2585–2590.

Bremer, E., Kuikman, P., 1994. Microbial utilization of C-14[U]glucose in soil is affected by the amoung and timing of glucose additions. Soil Biology & Biochemistry 26, 511–517.

Chander, K., Joergensen, R.G., 2001. Decomposition of ^{14}C glucose in two soils with different amounts of heavy metal contamination. Soil Biology & Biochemistry 33, 1811–1816.

Cheng, W., 1999. Rhizosphere feedbacks in elevated CO_2. Tree Physiology 19, 313–320.

Cheng, W., Coleman, D.C., 1990. Effect of living roots on soil organic matter decomposition. Soil Biology & Biochemistry 22, 781–787.

Cheng, W., Kuzyakov, Y., 2005. Root effects on decomposition of organic matter. In: Wright, S. (Ed.), Roots and Soil Management: interactions Between Roots and Soil Soil Science Society of America Book Series. Soil Science Society of America, Inc., Madison, Wisconsin, USA (in press).

Chotte, J.L., Ladd, J.N., Amato, M., 1998. Sites of microbial assimilation and turnover of soluble and particulate ^{14}C-labelled substrates decomposing in a clay soil. Soil Biology & Biochemistry 30, 205–218.

Clough, T.J., Sherlock, R.R., Kelliher, F.M., 2003. Can liming mitigate N_2O fluxes from a urine-amended soil? Australian Journal of Soil Research 41, 439–457.

Dalenberg, J.W., Jager, G., 1989. Priming effect of some organic additions to ^{14}C-labeled soil. Soil Biology & Biochemistry 21, 443–448.

Degens, B., Sparling, G., 1995. Repeated wet–dry cycles do not accelerate the mineralization of organic C involved in the macro-aggegation of a sandy loam soil. Plant and Soil 175, 197–203.

De Nobili, M., Contin, M., Mondini, C., Brookes, P.C., 2001. Soil microbial biomass is triggered into activity by trace amounts of substrate. Soil Biology & Biochemistry 33, 1163–1170.

Dilly, O., 2003. Regulation of the respiratory quotient of soil microbiota by availability of nutrients. FEMS Microbiology Ecology 43, 375–381.

Dilly, O., 2004. Effects of glucose, cellulose, and humic acids on soil microbial eco-physiology. Journal of Plant Nutrition and Soil Science 167, 261–266.

Engel, T., Klöcking, B., Priesack, E., Schaaf, T. 1993. Simulationsmodelle zur Stickstoffdynamik. Agrarinformatik 25. Ulmer, Stuttgart.

Fontaine, S., Mariotti, A., Abbadie, L., 2003. The priming effect of organic matter: a question of microbial competition? Soil Biology & Biochemistry 35, 837–843.

Fontaine, S., Bardoux, G., Benest, D., Verdier, B., Mariotti, A., Abbadie, L., 2004. Mechanisms of the priming effect in a savannah soil amended with cellulose. Soil Science Society of America Journal 68, 125–131.

Fu, S.L., Cheng, W.X., 2002. Rhizosphere priming effects on the decomposition of soil organic matter in C-4 and C-3 grassland soils. Plant and Soil 238, 289–294.

Fu, S.L., Coleman, D.C., Schartz, R., Potter, R., Hendrix, P.F., Crossley, D.A., 2000. C-14 distribution in soil organisms and respiration after the decomposition of crop residue in conventional tillage and no-till agroecosystems at Georgia Piedimont. Soil & Tillage Research. 57, 31–41.

Gerzabek, M.H., Pichlmayer, F., Kirchmann, H., Haberhauer, G., 1997. The response of soil organic matter to manure amendments in a long-term experiment at Ultuna Sweden. European Journal of Soil Science 48, 273–282.

Gignoux, J., House, J., Hall, D., Masse, D., Nacro, H.B., Abbadie, L., 2001. Design and test of a generic cohort model of soil organic matter decomposition: the SOMKO model. Global Ecology and Biogeography 10, 639–660.

Jones, D.L., Kemmitt, S.J.., Wright, D., Cuttle, S., Bol, R., Edwards, A.C., 2005. Rapid intrinsic rates of amino acid biodegradation in soils are unaffected by agricultural management strategy. Soil Biology & Biochemistry (on line).

Hamer, U., Marschner, B., 2002. Priming effects of sugars, amino acids, organic acids and catechol on the mineralization of lignin and peat. Journal of Plant Nutrition and Soil Science 165, 261–268.

Hamer, U., Marschner, B., 2005a. Priming effects in different soil types induced by fructose, alanine, oxalic acid and catechol additions. Soil Biology & Biochemistry 37, 445–454.

Hamer, U., Marschner, B., 2005b. Priming effects in soils after combined and repeated substrate additions. Geoderma 128, 38–57.

Helal, H.M., Sauerbeck, D.R., 1984. Influence of plant root on C and P metabolism in soil. Plant and Soil 76, 175–182.

Kuzyakov, Y., 2002. Review: factors affecting rhizosphere priming effects. Journal of Plant Nutrition and Soil Science 165, 382–396.

Kuzyakov, Y., Bol, R., 2004. Using natural ^{13}C abundances to differentiate between three CO_2 sources during incubation of a grassland soil amended with slurry and sugar. Journal of Plant Nutrition and Soil Science 167, 669–677.

Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biology & Biochemistry 32, 1485–1498.

Leifeld, J., Siebert, S., Kogel-Knabner, I., 2002. Biological activity and organic matter mineralization of soils amended with biowaste composts. Journal of Plant Nutrition and Soil Science 165, 151–159.

Liang, B.C., Gregorich, E.G., MacKenzie, A.F., 1999. Short-term mineralization of maize residues in soils as determined by carbon-13 natural abundance. Plant and Soil 208, 227–232.

Luna-Guido, M.L., Beltran-Hernandez, R.I., Dendooven, L., 2001. Dynamics of C-14-labelled glucose in alkaline saline soil. Soil Biology & Biochemistry 33, 707–719.

Mary, B., Fresneau, C., Morel, J.L., Mariotti, A., 1993. C-cycling and N-cycling during decomposition of root mucilage, roots and glucose in soil. Soil Biology & Biochemistry 25, 1005–1014.

Muller, T., Hoper, H., 2004. Soil organic matter turnover as a function of the soil clay content: consequences for model applications. Soil Biology & Biochemistry 36, 877–888.

Olayinka, A., 2001. Effect of co-applied cowdung and inorganic nitrogen on microbial respiration in soil under laboratory conditions. Communications in Soil Science and Plant Analysis 32, 3229–3242.

Paterson, E., 2003. Importance of rhizodeposition in the coupling of plant and microbial productivity. European Journal of Soil Science 54, 741–750.

Plante, A.F., McGill, W.B., 2002. Soil aggregate dynamics and the retention of organic matter in laboratory-incubated soil with differing simulated tillage frequencies. Soil & Tillage Research 66, 79–92.

Sallih, Z., Bottner, P., 1988. Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. Biology and Fertility of Soils 7, 67–70.

Schimel, J.P., Gulledge, J., 1998. Microbial community structure and global trace gases. Global Change Biology 4, 745–758.

Shen, J., Bartha, R., 1996. Priming effect of substrate addition in soil-based biodegradation tests. Applied and Environmental Microbiology 62, 1428–1430.

Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma 81, 153–225.

Smith, P., Andren, O., Brussaard, L., Dangerfield, M., Ekschmitt, K., Lavelle, P., Tate, K., 1998. Soil biota and global change at the ecosystem level: describing soil biota in mathematical models. Global Change Biology 4, 773–784.

Sparling, G.S., Cheshire, M.V., Mundie, C.M., 1982. Effect of barley plants on the decomposition of 14C-labelled soil organic matter. Journal of Soil Science 33, 89–100.

Stenström, J., Svensson, K., Johansson, M., 2001. Reversible transition between active and dormant microbial states in soil. FEMS Microbiology Ecology 36, 93–104.

Subke, J.A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., Cotrufo, M.F., 2004. Feedback interactions between needle litter decomposition and rhizosphere activity. Oecologia 139, 551–559.

Vanlauwe, B., Dendooven, L., Merckx, R., 1994. Residue fractionation and decomposition— the significance of the active fraction. Plant and Soil 158, 263–274.

Waldrop, M.P., Firestone, M.K., 2004. Microbial community utilization of recalcitrant and simple carbon compounds: impact of oak-woodland plant communities. Oecologia 138, 275–284.

Wall, D.H., Moore, J.C., 1999. Interactions underground: soil biodiversity, mutualism, and ecosystem processes. Bioscience 49, 109–117.

Wu, J., Brookes, P.C., Jenkinson, D.S., 1993. Formation and destruction of microbial biomass during the decomposition of glucose and ryegrass in soil. Soil Biology & Biochemistry 25, 1435–1441.

Zogg, G.P., Zak, D.R., Ringelberg, D.B., MacDonald, N.W., Pregitzer, K.S., White, D.C., 1997. Compositional and functional shifts in microbial communities due to soil warming. Soil Science Society of America Journal 61, 475–481.