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Letter to the Editor

Comments on the paper by Kemmitt et al. (2008) 'Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass – A new perspective' [Soil Biology & Biochemistry 40, 61–73]: The biology of the Regulatory Gate

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ABSTRACT

Kemmitt et al. (Kemmitt, S.J., Lanyon, C.V., Waite, I.S., Wen, Q., Addiscott, T.M., Bird, N.R.A., O'Donnell, A.G., Brookes, P.C., 2008. Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass – a new perspective. Soil Biology & Biochemistry 40, 61–73) recently proposed the "Regulatory Gate" hypothesis, which states that decomposition of soil organic matter (SOM) is regulated solely by abiotic factors. Without studying the mechanisms of such regulation, Kemmitt with coauthors challenged the classical Winogradsky theory of soil microbiology and questioned the concept of autochtonous and zymogenous microbial populations. In this letter, we revive the significance of microbial activity for SOM decomposition especially for the short-term (hours to weeks) processes and show that the "Regulatory Gate" is (micro)biologically driven.

We explain the results of the three experiments in Kemmitt et al. (2008) from a microbiological point of view and suggest that SOM decomposition is mainly regulated by exoenzymes. We criticize the abiotic Regulatory Gate hypothesis based on bottleneck processes and pools limiting the SOM decomposition rate, comparison of constant and changing environmental conditions, as well as the connection between community structure and functions. We explain the results of Kemmitt et al. (2008) according to the properties of soil microbial community: functional redundancy and inconsistency between the excessive (but largely inactive) pool of total microbial biomass and the real mineralization activity. Finally, we suggest that to gain new perspectives on SOM decomposition and many other biochemical processes, future studies should focus on hot spots of (micro)biological activity (i.e., the rhizosphere, drillosphere, detritosphere, biopores, etc.) rather than on the bulk soil.

1. Introduction

In a recent paper, Kemmitt et al. (2008) measured CO_2 efflux from soil after fumigation with chloroform ($CHCl_3$) to partially kill the microorganisms. They found no effect of $CHCl_3$ on cumulative CO_2 efflux during 20–60 days after the fumigation when the flush caused by mineralization of $CHCl_3$-killed microorganisms was finished. They found no connection between the SOM mineralization (measured as CO_2 efflux) and the size, PLFA profile, and specific respiration of the microbial biomass. Based on the absence of a direct link between CO_2 efflux and these microbial properties, Kemmitt et al. (2008) hypothesized that SOM decomposition is regulated solely by abiotic processes and termed this regulation as the "Regulatory Gate". Rather than proving the mechanisms of the regulation, they challenged the classical theory of soil microbiology (Winogradsky, 1924) and of general ecology (Odum, 1953) that various (micro)organisms are characterized by various niches (Gause, 1934) and challenged the existence of autochtonous and zymogenous microbial populations.

We agree with Kemmitt et al. (2008) that abiotic factors are important for the decomposition of SOM and partly regulate the SOM level over long periods. However, these abiotic factors act indirectly – mainly by affecting the microbial activity that drives SOM mineralization. In these comments, we will revive the importance of microbial activity that greatly affects SOM turnover, especially in the short-term processes, and will show that the "Regulatory Gate" is (micro)biologically driven.

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2. Experimental evidence

2.1. Were the "experiments designed to determine if the Regulatory Gate operates"?

Kemmitt et al. (2008) suggested the abiotic "Regulatory Gate" hypothesis based on three experiments. None of these experiments, however, tested the underlying mechanisms of regulation of SOM decomposition. Therefore, biotic regulation was not found. The authors at first hypothesized abiotic mechanisms of regulation (p. 62) and than stated it as a theory (p. 68) without experimental confirmation. Because the experiments did not investigate the mechanisms of the limiting step but instead investigated the properties of microbial biomass (which is not limiting, see below), we disagree that the "experiments were designed to determine if the Regulatory Gate operates" (p. 61).

2.2. Cumulative CO_2 production in fumigated and nonfumigated soils (notes on experiment 1)

Investigation of the mechanisms of microbial processes is possible only in short time steps that are comparable with the turnover rates of active microbial biomass. Therefore, the cumulative curves (as in Fig. 2a and b in Kemmitt et al., 2008) are not very informative. When the sampling periods are longer than the turnover rates, the data reflect the result of many (frequently compensatory or multidirectional) processes, but cannot distinguish the individual processes and their mechanisms. So, the similar slopes of CO_2 accumulation curves for fumigated and unfumigated soil observed over long periods in Kemmitt et al. (p. 61) are not convincing support for abiotic regulation.

2.3. Release of organic C into the soil solution during chloroform perfusion (notes on experiment 3)

Kemmitt et al. (2008) stated that the small amount of C (less than 5 $\mu g\,C\ g^{-1}$ soil d^{-1}) released 20–60 days after fumigation in experiment 3 (Fig. 6 of their paper) was due to an "unknown" abiotic mechanism that controls the size of the Regulatory Gate. However, this small C amount may originate from (1) the activity of microorganisms that survived the fumigation and (2) the solubilization of SOM by $CHCl_3$. Let us consider both possibilities. Regarding the activity of surviving microorganisms, it is well known that a remarkable part of the microorganisms survives $CHCl_3$ fumigation: from 1 to 10% as measured by plate counts for bacteria (Toyota et al., 1996; Hu and van Bruggen, 1998) and up to 37% as measured by direct counts for active fungi (Ingham and Horton, 1987). Kemmitt et al. (2008) did not check the sterility of the soil after fumigation and only stated that "near sterility" was maintained (p. 64). From a microbiological point of view, it is clear that any "negligible" amount of microorganisms that survived fumigation would then proliferate (and mineralize SOM).

Regarding solubilization of SOM by $CHCl_3$, Kemmitt et al. referred to Jenkinson (1976) concluding that $CHCl_3$ solubilization of non-biological SOM is insignificant (pp. 71–72). However, how "insignificant" is it? Could this small C amount account for the C eluted in experiment 3 of Kemmitt et al.? A very low estimate (0.2% of total C content; Badalucco et al., 1990) for chloroform-susceptible non-biomass C will yield 65 $\mu g\,C\ g^{-1}$ for soil No. 4 used in leaching experiment. This amount exceeds the amount of C leached due to $CHCl_3$ perfusion during days 20–50 of the experiment. This means that when the initial 20 days C-flush from killed microbial biomass is over, C found in leachate can be produced by $CHCl_3$ solubilization of non-biomass SOM and so, is an experimental artifact.

3. Basics of soil microbial ecology

Rather than requiring a new hypothesis (that the rate limiting step in SOM decomposition is abiotic), the results of Kemmitt et al. can be explained by biological processes and two principles of soil microbial ecology:

(1) Excessive pool principle (or "storage effect", Morris and Blackwood, 2007): soils have excessive pool of total microbial biomass. Whereas only a small portion of the microbial biomass is active, a very large pool of dormant microorganisms with a broad spectrum of potential metabolic activities provides a quick growth response in case of input of any easy available substrate.
(2) Redundancy principle: many similar functions can be carried out by different microbial taxonomic groups (Stres and Tiedje, 2006).

These two principles of microbial ecology ensure the sustainability of the soil microbial community and processes in spite of environmental perturbations, such as drying/rewetting, freezing/thawing, or here $CHCl_3$ fumigation. So, there is nothing unusual in the absence of a direct relationship between the total microbial biomass (estimated by fumigation) and the SOM mineralization when nonfumigated and fumigated soils are compared.

3.1. The limiting pool

We agree that total microbial biomass in the bulk, nonrhizosphere soil is limited by the availability of C (Vance and Chapin, 2001; Kemmitt et al., 2008, p. 62). Therefore, it does not make sense to look for the regulation of SOM decomposition by the total amount of microbial biomass, as it is not limiting. So, the absence of differences in microbial biomass in the fumigated–inoculated compared to fumigated–not inoculated soils (experiment 1) confirms that sufficient microorganisms survived fumigation to mineralize the necromass released by fumigation and to slowly decompose SOM. The absence of limitation by the microbial biomass clearly explains why, in Kemmitt et al. (2008), the microorganisms that survived $CHCl_3$ fumigation decomposed SOM at the same rate as in the nonfumigated soil. Because microbial biomass was not limiting, its decrease did not change the process rate. From this point of view, fumigation has similar effects on the CO_2 release as other impacts leading to the death of part of the microorganisms, including freezing/thawing (Matzner and Borken, 2008) and drying/rewetting (Van Gestel et al., 1993).

3.2. CO_2 production under constant environmental conditions

If we accept that solely abiotic impacts (freezing/thawing, drying/rewetting, mechanical disturbance, etc.) regulate SOM decomposition, then at constant environmental conditions (i.e., constant temperature and moisture, absence of mixing or tillage, etc.) we should expect a strong decrease and then cessation of SOM mineralization over periods longer than those required for the mineralization of fresh and available substrates. This is because in Kemmitt et al., the SOM is accepted as "non-biologically available" (Fig. 7 in Kemmitt et al., 2008). Obviously CO_2 production during incubations at constant conditions was lasted for over 260 days (Fig. 5 in Kemmitt et al., 2008) showing that SOM continued to decompose under constant environmental conditions. Constant CO_2 production (Fig. 5 in Kemmitt et al., 2008) in the absence of environmental changes clearly shows that biotic rather than abiotic processes regulate SOM decomposition.

3.3. The limiting step

We fully agree with Kemmitt et al. (2008) that the limiting step in SOM decomposition is the conversion of organic substrates with low availability to those with high availability. However, the identification of the bottleneck does not necessarily mean the identification of mechanisms of the limiting processes. Because chemically complex plant residues and SOM are decomposed by exoenzymes produced by microorganisms, this limiting step is biologically driven (Fig. 1, from Schimel and Weintraub, 2003). These enzymes (mainly hydrolases) are fully functional after $CHCl_3$ fumigation (Tiwari et al., 1988; Renella et al., 2002). The level of enzymatic activity definitely depends on the microbial biomass pool in nonfumigated soils, so that arable and grassland soils with differing microbial biomass amount (Fig. 2 in Kemmitt et al., 2008) differed in basal respiration after fumigation. However, there was no direct relationship between the microbial biomass recovered after fumigation and the SOM mineralization rate because extracellular enzyme activity persists after fumigation and maintains the previous "nonfumigated" activity level.

3.4. The biology of possible conversion mechanisms

We agree with "possible mechanisms involved in the conversion of non-biologically available to biologically available SOM" (Kemmitt et al., 2008, p. 62): (1) chemical oxidation or hydrolysis; (2) diffusion from inaccessible soil pores or aggregates; (3) desorption from the solid phase; and (4) action of extracellular stabilized enzymes. Chemical (or abiotic) oxidation or hydrolysis (mechanism 1), however, is of very limited importance for high molecular weight organic substances, because the complementary process, the action of exoenzymes (which is biologically driven and listed as mechanism 4) is of much greater significance (Ringe and Petsko, 2008). The relevance of diffusion of available soluble organics (mechanism 2) is important, but such diffusion occurs over small distances (μm up to mm) and usually takes hours to days before the substances will be decomposed (Kuzyakov et al., 2003). So, the second mechanism listed above is of minor importance over weeks and months, for which the SOM decomposition was measured. Diffusion of insoluble organics cannot be accepted as a significant contribution. The release of available organics from the solid phase (mechanism 3) occurs mainly by exoenzymes (biologically) (Nannipieri, 2006). Because the concentration of available C in solution is controlled by microbial uptake, the third mechanism is also biologically driven. The fourth mechanism is obviously biological. So, of the mentioned four "possible mechanisms" of Regulatory Gate, the first two are of very minor importance and the last two are biologically controlled.

In fact, the concept suggested by Kemmitt et al. (2008) and drawn in their Fig. 7 is oversimplified and lacks a very important detail, which is accepted by the majority of soil microbiologists (see Fig. 1, from Schimel and Weintraub, 2003): the conversion of SOM to soluble organics is mediated by exoenzymes (Gianfreda and Ruggiero, 2006). The quantity, activity, and properties of exoenzymes largely depend on the size, activity, and properties of the microbial community.

3.5. Community structure and functions

Kemmitt et al. (2008) (Fig. 3) analyzed the community structure by PLFA before and after fumigation. Because the PLFA profiles of the two soils examined changed after fumigation but the cumulative CO_2 efflux remained the same, the authors concluded that the SOM decomposition is independent of community structure. PLFA profiles, however, only roughly reflect community structure and are useless for describing the functions. This is because many soil microorganisms are functionally redundant (Setälä and McLean, 2004). In other words, many microorganisms with different PLFA profiles have the same or similar functions, especially with respect to the decomposition of SOM and plant residues. It follows that a change in PLFA profile after fumigation does not mean that some function has been reduced, lost, or altered at all. In addition, soil microorganisms of different groups have a great potential for adapting their growth traits depending on the decomposability of the substrate.

The relevant approach to link the PLFA profile with functions would be the application of ^{13}C labeled substrates and evaluation of ^{13}C incorporation in individual PLFA (Glaser, 2005; Kramer and Gleixner, 2006). Because the experiments of Kemmitt et al. were done without ^{13}C (or ^{14}C) and the investigated soils were more or less in *steady state*, the community structure measured by PLFA (and by any other descriptive approaches) is not informative about functions.

3.6. Autochtonous and zymogenous microbial populations

Because $CHCl_3$ fumigation does not remarkably alter SOM mineralization (Jenkinson and Powlson, 1976 – cited by Kemmitt et al., p. 62), most CO_2 evolved after fumigation originates from the decomposition of killed microorganisms rather than from the decomposition of SOM – this is the principle underlying the fumigation–incubation approach (Jenkinson, 1976). Therefore, experiment 1 of Kemmitt et al. is an excellent illustration of two population-based theories: (1) theory distinguishing zymogenous and autochtonous soil microorganisms (Winogradsky, 1924), and (2) general ecology theory distinguishing slow-growing K-strategists and fast-growing r-strategists (Odum, 1953). When soil is fumigated, available substrates released from the killed microorganisms are used by the surviving, fast-growing microorganisms (zymogenous, r-strategists) within two weeks. After the easily available substrate is exhausted (between day 15 and 20 in experiment 1 of Kemmitt et al.), the zymogenous microorganisms become dormant, and the slope of the respiration curve for fumigated soil becomes less steep, reaching the level of nonfumigated soil. Starting from this time, slowly growing microorganisms that slowly use substrates of low availability become dominant. In experiment 1 of Kemmitt et al., the similar slopes for cumulative CO_2 release in fumigated and nonfumigated soil after two weeks (when the killed microorganisms were decomposed) only indicate similar levels of available substrate before fumigation and after the fumigation flush. It is well known that only a small part of the total microbial biomass is active in soil without fresh substrate amendments (Blagodatsky et al., 2000; Werth et al., 2006). The data from experiment 1 confirm that *total* biomass (rather than active biomass) cannot explain cumulative CO_2 release. The small portion of active, slow-growing microorganisms was responsible for long-term SOM mineralization in both soils, but this portion was not measured (Kemmitt et al., 2008; Section 4.3). Kemmitt et al. (2008) argued that Winogradsky's theory (1924) cannot explain the results of experiment 1, but they did not consider the two distinct stages of decomposition (fast and slow) that follow fumigation and changes in microbial physiology (Dilly, 2001, 2006). The results from experiment 1 exactly fit microbial population theories.

Certainly, the simple partitioning of the whole microbial community into autochtonous and zymogenous populations or r- and K-strategists does not cover all functional diversity. Since Winogradsky (1924), the microbial system theory has been further developed. Illustrative comparison of different classifications of functional microbial groups was done by Panikov (1995).

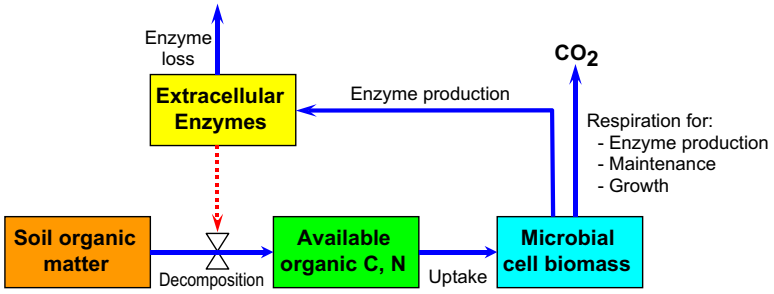

Fig. 1. Conceptual scheme of C turnover in soil (from Schimel and Weintraub, 2003, changed). Solid lines indicate flows of material, dashed line connected to the 'valve' indicates regulation point. Decomposition is a function of extracellular enzyme activity rather than of SOM concentration alone.

3.7. Is the "abiotic" step really proven?

Regarding experiment 2 of Kemmitt et al., we agree (p. 70, Section 4.4) that microbial activity was a sink that maintained a concentration gradient, resulting in further conversion of non-available SOM to available substrates. So, the authors themselves suppose that first "abiotic" step of the 'Regulatory Gate' is mainly biologically mediated. Numerous attempts to reduce SOM decomposition to simple dependency on temperature, moisture, physico-chemical properties of soil, and constant decomposition rate were unsuccessful. The data in Kemmitt et al. (2008) are consistent with biological regulation of the first decomposition step by exoenzymes (Fig. 1). Kemmitt et al. (2008) have neglected the role of microbial biomass in production of the exoenzymes that degrade insoluble SOM. They also ignore another phenomenon of biological origin – the priming effect, whereby SOM decomposition is accelerated by addition of labile substrates (Dalenberg and Jager, 1981; Bell et al., 2003). They state (p. 68) that "mineralization of SOM is little, if at all altered, even if the microbial population size, diversity and activity have all been greatly altered by fumigation or *previous substrate addition*" [words not emboldened in the original]. The significance of the priming effect, however, has been documented in many studies (Hamer and Marschner, 2005; Blagodatskaya et al., 2007). We also note that the priming effect has never been observed in sterilized soil and therefore cannot be abiotic.

4. Perspectives

4.1. Is the Regulatory Gate hypothesis a new perspective?

The title of the paper by Kemmitt et al. claims that abiotic regulation of SOM decomposition is a new perspective. Is it really new? Let us consider the models of SOM dynamics developed in the last century (reviewed by Molina and Smith, 1997). Most of these models do not consider the activity or composition of microbial biomass. Because the approaches used in these models were usually supported by many previous studies, and because most of these models were elaborated 5–15 years before the review of Molina and Smith (1997), we cannot agree that the "idea" of abiotic regulation is new.

In the last decade new kinds of models of SOM dynamics explicitly include the activity and composition of the microbial community as the main factors driving SOM dynamics (Blagodatsky and Richter, 1998; Schimel and Weintraub, 2003; Fontaine and Barot, 2005; Neill and Gignoux, 2006). Such models are especially helpful for understanding short-term dynamics, because they reflect mechanisms underlying the processes and not simply the cumulative results.

4.2. A new perspective: priming effects and hot spots

To evaluate the effect of microbial activity on SOM mineralization, microbial activity should be directly tested as a factor, and should be varied independently of temperature, moisture, and other abiotic factors. Additionally, the source of CO_2 released during the incubation should be identified by ^{14}C or ^{13}C. These conditions have been met by many studies that were unfortunately ignored by Kemmitt et al. (2008). These studies have shown that addition of easily available substrates enhances SOM mineralization and that the enhancement depends on microbial activity (Dalenberg and Jager, 1981; Bell et al., 2003; Perelo and Munch, 2005; Hamer and Marschner, 2005; Blagodatskaya et al., 2007; and many others). Such "priming effects" were reviewed by Kuzyakov et al. (2000) and by Cheng and Kuzyakov (2005).

It may be claimed that addition of easily available substrates is an artificial treatment. However, similar input of available organics occurs frequently in nature and is one of the most important factors controlling high microbial activity in hot spots in the soil. Such hot spots include the rhizosphere, drillosphere, detritosphere, biopores, etc. In our view, these hot spots are the main drivers of the cycles of most elements, especially of C and N. So, to investigate SOM decomposition (and many other processes), not the bulk soil but the hot spots of (micro)biological activity will give a new perspective.

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