



Priming of soil organic matter: Chemical structure of added compounds is more important than the energy content



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ABSTRACT

The addition of easily degradable compounds to soil (e.g. root exudates, plant residues) can result in priming effects (PE), a short-term change in the turnover of soil organic matter (SOM). Although PE are recognized to be large enough to be taken into account into the ecosystem carbon balance, the exact mechanisms are still unknown. Here, we examined the effect of two characteristics of added compounds on PE, namely metabolic usable energy for microbes and resemblance to recalcitrant fractions of soil organic matter (SOM). For this purpose, glucose, cellobiose (energy rich compounds, low resemblance with recalcitrant SOM) and vanillic acid (energy-poor compound, higher resemblance with recalcitrant SOM) were selected. In addition the effect of mineral nitrogen (N) on PE was tested. ¹³C labelled compounds were mixed with sandy soil from an ex-arable site. To separate the effect of energy content from that of resemblance to SOM, the amount of carbon and the amount of energy content of added compounds was kept constant in treatments, respectively. The community structure of microbes that were able to use added compounds was evaluated using stable isotope probing (DNA-SIP) combined with qPCR and Illumina sequencing.

When corrected for energy content, vanillic acid induced the highest CO₂ respiration and PE. DNA-SIP revealed that bacterial classes like β - and γ -Proteobacteria, that are known to harbour many opportunistic bacteria, responded quickly (5 h) with incorporation of ¹³C from added substrates, whereas classes like Acidobacteria and Actinobacteria responded over a longer incubation time. In treatments where the energy-level of added compounds was kept constant, vanillic acid caused an increase in DNA copy numbers of bacteria and fungi using native SOM after prolonged incubation. The contribution of fungi to PE was minor, reflecting the low F:B ratio of the soil used for the experiment. Different substrates resulted in different PE but appeared to stimulate the growth of similar bacterial groups. This suggests that the added compounds stimulate different enzyme systems within similar bacterial taxa. Although combined addition of mineral nitrogen (ammonium nitrate) and organic compounds caused a slightly extra increase in PE in most treatments, this might be an artefact as addition of mineral N only decreased respiration. Overall our results indicate that the effect of chemical structure of added compounds on PE is much larger than the effect of energy-content.

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1. Introduction

The addition of easily degradable compounds (e.g. root exudates, plant residues) to soil can result in priming effects (PE), defined as a short-term change in turnover of soil organic matter

(SOM) (Blagodatskaya et al., 2007; Hamer and Marschner, 2002; Kuzyakov et al., 2007; Wu et al., 1993). PE can be positive (acceleration of SOM decomposition) but also negative (retardation of SOM decomposition) (Kuzyakov et al., 2000). PE can be classified as real or apparent, and the distinction is based on the origin of the extra CO₂ released from the soil. In apparent PE the increased CO₂ originates from the turnover of microbial compounds such as reserve materials, whereas in real PE it is due to the decomposition of SOM (Kuzyakov et al., 2000). This process is considered large

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enough to influence ecosystem carbon balance as PE generated by living roots can suppress or stimulate up to 50% and 400% of SOM decomposition, respectively (Wieder et al., 2013; Zhu et al., 2014).

The amount and quality of added substrates can influence the direction and magnitude of PE. It has been suggested that the added compounds can trigger the microbial production of extracellular enzymes which decompose fractions of SOM, especially when the added substrate resembles compounds present in SOM (Fontaine and Barot, 2005). It has also been suggested that a limited inorganic nitrogen (N) availability can influence PE by stimulating microbes to mine for N in SOM (Dijkstra et al., 2013). According to the latter theory, addition of substrates with high C:N ratio will stimulate positive PE. Furthermore, both microbial biomass and microbial community structure appear to affect the intensity and direction of PE (Blagodatskaya and Kuzyakov, 2008). Differences in capabilities of microbial species to decompose different fractions of SOM are suggested as possible explanation for this effect (Fontaine et al., 2011, 2003).

Recently it was suggested how two competing hypotheses on organic matter decomposition, namely “microbial stoichiometric theory” (Craine et al., 2007; Hessen et al., 2004) and “nitrogen mining theory” (Craine et al., 2007; Moorhead and Sinsabaugh, 2006), can coexist in the same system and influence the strength and size of PE (Chen et al., 2014). Chen et al. (2014) propose that the contribution of microorganisms to SOM decomposition is controlled by mineral N availability and their growth strategies: under low-N availability K-strategists were predominant (nutrient mining theory), whereas r-strategists played a more important role with high-N availability (stoichiometry theory).

SOM is a mixture of partially decayed plant residues, soil microorganisms and soil fauna, by-products of decomposition and humic substances (Schmidt et al., 2011). Three major factors of SOM stabilization have been proposed: 1) physical stabilization, 2) chemical stabilization and 3) structural inherent recalcitrance of specific organic molecules (Mikutta et al., 2006). In addition, a fourth mechanism was proposed, namely the scarcity of “fresh C” which prevents microbial decomposition of the stable organic carbon pool, representing PE (Fontaine et al., 2007). Recently it has also been shown that decomposition of recalcitrant, lignin-rich plant residues only occurs when easily decomposable carbon sources are available (Klotzbücher et al., 2011). Taken together, it is clear that decomposition of SOM is highly controlled by the availability of “fresh C”.

During the biological breakdown (oxidation) of SOM, small water-soluble compounds are released and these are energy sources for the growth of microorganisms. Compounds differ with respect to the amount of energy that can be used for growth. For instance, the increase of soil microbial biomass has been found to be much higher for glucose than for equimolar amounts of oxalate and phenol (Brant et al., 2006). Hence, the quality of the added substrate can also be expressed in terms of the energy that can be used for microbial growth and growth-supporting functions. Limitation in energy for growth-supporting functions (e.g. production of extracellular enzymes) may be constraining microbial

decomposers to break down more complex components of SOM (Wild et al., 2014). Therefore, it can be expected that more energy-rich added compounds would result in higher positive priming effects.

Several studies have shown that different microbial groups (e.g. fungi, Gram-positive and Gram-negative bacteria) take part in PE (Blagodatskaya et al., 2014; Creamer et al., 2015; Perveen et al., 2014; Xiao et al., 2014). Bacteria show a wide metabolic diversity and often an opportunistic strategy that allow them to rapidly absorb soluble substrates. Fungi, on the other hand, are able to connect sources of easily-available carbon with stable SOM via transport through their hyphae (Boberg et al., 2011). They can also produce a wide range of enzymes (e.g. lignin-degrading peroxidases) allowing the degradation of recalcitrant compounds such as those present in SOM. Because of these properties fungi are thought to be more important in PE than bacteria (Fontaine et al., 2011).

In the present study we will address the following hypotheses: 1) a positive PE increases when the availability of energy for microbial growth increases 2) positive PE will also increase with increasing availability of the added compounds that resemble fractions of recalcitrant SOM, 3) fungi are more important than bacteria in causing PE and 4) addition of mineral N will negatively affect PE. To test these hypotheses, three ¹³C-labelled substrates, namely glucose, cellobiose and vanillic acid, were added to natural grassland soil in a mesocosm approach. Glucose and cellobiose represent energy rich compounds with low resemblance to recalcitrant SOM, whereas vanillic acid represents an energy-poor compound with higher resemblance to recalcitrant SOM. We measured soil respiration and changes in the microbial community to provide a better understanding of the underlying mechanisms of PE and the role played by the microbes.

2. Materials and methods

2.1. Soil sampling and processing

In March 2014 soil (0–10 cm) was collected in Dennenkamp, a former arable site that has developed into a natural grassland (van der Wal et al., 2006). The site is located in the central part of the Netherlands (N 52°01'43", E 005°48'2"). The soil is a sandy soil with a disturbed profile due to former agricultural activities and can be classified as a Typic Haploorthod (US soil taxonomy) (van der Wal et al., 2007). The fungal: bacterial ratio is 0.06 (based on PLFA analysis) and C:N ratio of 19.90 (Table 1). In the laboratory, fresh soil was sieved (4 mm) and homogenized, removing fine roots and other plant debris. Field-moist soil was then stored at 4 °C until further use.

2.2. Estimation of microbial usable energy released by the priming substrates

For the purpose of our study it is important to know how much of the available energy in substrates is actually converted into microbial biomass. This means that also loss of energy, such as due to

Table 1
Edaphic and biological properties of the soil (0–10 cm). Edaphic properties are from van der Wal et al. (2006), while biological data are from two different sampling times 2003 (van der Wal et al., 2006) and 2012 (Morriën et al., 2017). Values from the different years are separated by a slash. Bacterial biomass was calculated using the average of the PLFA data converted in mg C/g soil according to the conversion factors reported.

Abandoned from agriculture	Former crop	pH	C [g/kg]	C:N ratio	% Sand >53 µm	Soil texture	Bacterial PLFA [nmol/g soil]	Fungal PLFA [nmol/g soil]	Fungal/bacterial	Ergosterol content [mg/kg]	Microbial biomass [mg C/g soil]
1982	Rye, potatoes, asparagus	5.60	34.30	19.90	86.2	Sand/coarse sand	39.84/42.09	2.56/2.38	0.064/0.057	1.36/1.03	0.235

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