

Soil carbon controlled by plant, microorganism and mineralogy interactions

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Abstract

Rhizosphere, a thin area of soil surrounding roots receiving carbon (C) exudation from plants, represents a site of intense competition for available C and nutrient between surface-reactive particles and soil microorganisms. This competition can reduce the amount of available C to a critical level, it becomes limiting for microbial growth and soil organic matter decomposition. On the other hand, acceleration or retardation of decomposition of soil organic C caused by root activity is termed rhizosphere priming effect (RPE). This effect has been increasingly recognized to play a crucial role on native C destabilization as is influenced by fresh C availability, microbial activity and soil mineralogy such as crystallinity of clay minerals and Al-, Fe-oxides. Combining microbial ecology and soil mineral interactions, we can understand how soil characteristics and climate change can influence below ground competition and finally RPE. In this review, we focus on the competition for available C in soil, limiting our analyses to the interaction at rhizospheric space, where most processes between microorganisms and mineral phase occurs.

Keywords: Rhizosphere-priming effect, DOC, mineral interaction, carbon exudates

1. Introduction

Carbon input from plant to soil through root exudation is one of the major sources of available carbon (C) for microorganisms (Luo *et al.*, 2014). Exudates from living roots stimulate a quick response of soil microbes with acceleration of native soil organic C mineralization, the so-called rhizosphere priming effect (RPE). Soil microbial activities are driven primarily by readily available

or labile C provided by root turnover and root-exudates influxes (Dijkstra *et al.*, 2013). Rhizosphere priming can also be affected by nutrient availability and substrate quality (Murphy *et al.*, 2015). These interactive effects may be of particular relevance in understanding microbial growth and nutrient supply in response to increased atmospheric CO₂ concentration and temperature. It is well established that increase

in atmospheric CO₂ increases photosynthesis, hence root exudation (Drigo *et al.*, 2008). Competition between microorganisms and soil reactive particles for nutrient and dissolved organic C (DOC) is often neglected in the rhizosphere. Traditionally, it has been assumed that microorganisms can access quickly to labile C released into soil, although a number of biotic and abiotic processes can regulate the relative C in soil solution. In addition to microbial uptake, available C can decrease in the rhizosphere due to diffusion and convection process (Raynaud, 2010), and adsorption by soil particles with formation of soil aggregates (Albalasmeh and Ghezzehei, 2014). Weathered Al and Fe can complex DOC quickly in periods of time ranging from seconds to hours (Sparks, 2002). Microbial uptake of low molecular weight organic substances (LMWOS) (e.g., organic acids, amino acids and polysaccharides) from the soil solution takes place within minutes (Jones *et al.*, 2004). In contrast, the half-life time of the same processes for C from LMWOS adsorbed onto mineral clay is longer – from several hours to months or even decades (van Hees *et al.*, 2005).

We often assumed that microorganisms are better competitors than plant roots for nutrients (Kuzyakov and Xu, 2013), because: i) they are involved in the mineralization process, ii) they present a great surface area: volume ratio and iii) they have rapid growth rates (Peng *et al.*, 2008). Microorganisms have numerous strategies to increase their resource acquisition and competition for available C using biotic (e.g. extracellular enzymes release) and abiotic (e.g. redox and metal complexation) mechanisms (Hibbing *et al.*, 2010). It is difficult to assess direct competition between microorganisms and minerals for soil C because of the multiple loops and pathways, through which C circulates amongst different C pools. Furthermore, abiotic factors such as soil pH, amorphous Fe and Al oxides and hydroxides

concentration (Kaiser and Guggenberger, 2000), and/or clay types (McDowell and Sharpley, 2003) contribute to protection of soil organic matter (SOM) from microbial decay (Jastrow *et al.*, 2007). Consequently, the effects of available C on microbial activity in mineral soils at rhizosphere scale are poorly understood.

Here we discuss the impact of fast growing microorganisms competing for soluble C from root-exudates substrate in the rhizosphere on priming intensity. Root exudates can be released shortly after C fixation (15 minutes to hours) (Matus *et al.*, 2014a) and soil mineralogy regulates labile C gradient concentration in the soil solution by adsorption processes and indirectly by pore size distribution.

The aim of this study is to discuss the biotic and abiotic factors controlling RPE and availability of C for soil microorganism assimilation. We have reviewed recent literature concerning RPE and chemical composition of SOM related to soil mineralogy operating mainly in temperate mineral soils. As a result, this review has three sections. First, we focus on available C and rhizosphere priming and its dependence on labile organic C compound in open interaction with soil surface minerals. In the second section, we discuss the interactions between mineralogy, plant and microorganism control on available C and the implications of these interactions on RPE. Finally, in the third section, RPE as an important mechanism of soil C transport into the subsoil is discussed.

2. Available carbon and rhizosphere priming

Carbon input by plants into the soil is the primary source of SOM (Kuzyakov, 2002). This input and the availability of C induce fast turnover near the roots, because rhizosphere space is not limited by available C (Kuzyakov, 2002), but C is available in hot spots (Kuzyakov and Blagodatskaya, 2015).

The RPE intensity is generally short lived changed by the transformation of C following the addition of moderate levels of carbonaceous and nitrogenous materials, including C rhizodeposition from roots (Kuzyakov, 2002). It is increasingly accepted that RPE intensity depends on the availability of fresh C energy and succession of soil microbial community (Fontaine *et al.*, 2004). Root exudates consist of a complex mixture of C rich substrates, such as sugars (50–70%), carboxylic acids (20–30%) and amino acids (10–20%) (de Graaff *et al.*, 2010). Plant roots exert significant control over the flow rate of C (Lal, 2004). Plants spend a large part of their photosynthetic C in the development and maintenance of the rhizosphere (de León-González *et al.*, 2006). The fate of C exudates released into the soil solution depends on root fluxes, soil mineral adsorption, diffusion across soil pores, and microbial utilization (Kuzyakov *et al.*, 2003). For example, and as previously mentioned, LMWOS are rapidly metabolized, whereas high molecular-weight compounds have to be hydrolysed to low molecular-weight products before they can be taken up by microbial cells (Weintraub *et al.*, 2007). Neutral sugars can be quickly assimilated by microorganisms, because they are not electrically charged, with a half-life of only 20 to 40 minutes in soil (Fischer *et al.*, 2010). While neutral sugars are fast metabolized, carboxylic acids (e.g. citric and malic acids) bearing charge, can rapidly be adsorbed by soil minerals (Dakora and Phillips, 2002). Half-life of organic acids and amino acids in the soil have been measured between 2 h and 12 h (Jones and Darrah, 1994; Jones, 1999). Organic acids, such as citrate, may be strongly sorbed into soil components (clay minerals) with the reduction of the relative mineralization rates (Bruun *et al.*, 2010). Within 10 minutes, 99% and 83% of the added citrate was adsorbed by Fe oxides and kaolinite,

respectively. Citrate decomposition was reduced for about 99% and 75% in the presence of Fe oxides and kaolinite, respectively (Jones and Edwards, 1998). Therefore, the organo-mineral complex formation is of a critical importance of controlling organic C availability to soil microorganisms (Lopez-Sangil and Rovira, 2013). Mineralization does not depend on the C input rate only, but also on the substrate quality, the initial N: C: P, and the chemical composition of the substrate. Microorganisms controls the available C by quickly uptake of free sugars from the soil, but represents a small proportion being immediately available in hot spots (Kuzyakov and Blagodatskaya, 2015). Most SOM is present in forms that are unavailable to microorganisms (Fontaine *et al.* 2003). The short-lived RPE in the rhizosphere related to the fast consumption of C during initial stage of mineralization is poorly understood.

In summary, it is important, therefore, to consider microorganisms and soil mineralogy competing for fresh organic C for microorganism assimilation. The interactions of these factors can accelerate (positive) or reduce (negative) the RPE by the decomposition of native soil organic matter (Dijkstra *et al.*, 2009). The magnitude and direction of RPE are determined by the amount and type of C exudates released from the root, as well as intrinsic soil mineralogy. At the most basic level, understanding the general characteristics of C fluxes within the soils is difficult because of the diversity of microbial communities, the complexity of mineral soil interactions and the inherent environmental heterogeneity of soil ecosystems.

3. Mineralogy, plant and microorganisms control the available carbon

Very little is known about adsorption or desorption of different pools of organic components related to RPE

in different soil types due to different mineralogy (Fischer *et al.*, 2010). Rasmussen *et al.* (2006; 2007) studied the importance of the mineralogical composition on C mineralization in temperate rain forests. They found soil with amorphous clay (volcanic soils) showed a negative priming (Xue *et al.*, 2005; Rasmussen *et al.*, 2006) attributed to the strong adsorption of organic compounds, probably by ligand exchange reaction (Matus *et al.*, 2014b).

Soil mineralogy controls the available C in the soil solution not only by adsorption processes, but indirectly limiting diffusion of oxygen and water due to the importance of soil minerals in the formation of soil aggregates (Six *et al.*, 2004). This makes available C in soil less vulnerable to microbial degradation (Kalbitz and Kaiser, 2008). There is a physical occlusion of C in the interstitial space mesopores (2-50 μm) in mineral soils (Zimmermann *et al.*, 2009). The interactions between mineral phase and organic matter can lead to a stabilization of available C trapped or physically protected in soil micropores (< 2 μm) (Baldock and Skjemstad, 2000). Apart from physical protection, as it was already mentioned, the intermolecular interactions between C and surface of clay particles and oxides of Fe and Al play an important role too (Matus *et al.*, 2008). Amorphous Al and Fe oxides are the most reactive components of acidic and neutral soils (Matus *et al.*, 2014b) and have a key function in chemical speciation, bioavailability of nutrients and detoxification (Olaniran *et al.*, 2013). The role of Al and its effects on water extractable organic matter was evaluated in two old growth temperate rain forests (Merino *et al.*, personal communication). Mineralization of soluble C was not affected by increasing Al addition rate and potential toxicity by Al^{3+} was not observed after 15 days of incubation experiment. This study suggests that Al^{3+} is toxic when Al:C ratio < 0.12 (Scheel *et al.*, 2008). However, the effects of Al on natural DOC degradation in mineral soils of forests are poorly understood and

it is necessary to study Al-humus formation and Al^{3+} detoxification for their effect on C availability.

Indeed, the quantitative information on the degradation of available C has been obtained by studying the decomposition of LMWOS differing for the position of labelled C (Apostel *et al.*, 2015). Alanine ^{14}C labelled in C-1, C-2 and C-3 position was adsorbed by iron oxides, clay minerals (2:1 and 1:1) and activated charcoal. The highest sorption capacity resulted in the low C utilization by soil microbes. Mineralization of alanine peaked within the first 5 h and it was always the highest for C-1 position (-COOH group), whereas C-2 and C-3 mineralization exceeded the mineralization rate of C-1 after 10–50 h. The metabolic pathways, i.e. glycolysis depended on C oxidation and the Krebs cycle of sorbed Alanine at initial stage of decomposition (Dippold *et al.*, 2014). This raises the question whether these low molecular weight compounds are used by the overall soil microflora or by different microbial groups. On the other hand, plants may alter the dynamics of microbial C fluxes and C use efficiency by balancing the catabolic and anabolic metabolism in the rhizosphere. Carbon utilization efficiency by soil microbes was 1.5 times higher in root-free soil than in the rhizosphere soil (Blagodatskaya *et al.*, 2014).

Extracellular soil enzyme activities play a key role in RPE by breaking down native organic matter (depolymerization, e.g., peroxidase) producing soluble simple compounds for microbial assimilation (Sinsabaugh *et al.*, 2009; Sinsabaugh *et al.*, 2010; Nannipieri *et al.*, 2012). Once organic C is inside the microbial cell, it can be mineralized to CO_2 with the production of ATP (Meir *et al.*, 2013). Under aerobic conditions, the oxidative metabolism of organic compound produces more energy, ATP and CO_2 than the anaerobic metabolism (Zhu *et al.*, 2014). The literature on soil enzymology is extensive (Nannipieri *et al.*, 2012) as well as the enzyme-organo-mineral interaction such as the enzyme adsorption to minerals (Nannipieri

et al., 1996) and enzyme–clay interaction (Gianfreda and Bollag, 1994), but the role of enzymes-organomineral on RPE is poorly understood. Some priming studies have looked directly at enzyme activities, but the results have been contradictory (Table 1).

If biotic processes are modified by soil mineralogy, the latter also plays a control on C turnover with an important catalytic role in accelerating abiotic polymerization of phenolic compounds and amino acids to the formation of humic substances. Silicates and Fe oxides can catalyze redox reactions and promote SOM oxidation (Derry *et al.*, 2005). Besides, enzyme-like reactions can affect C turnover in soil (Ruggiero *et al.*, 1996). For instance, humid tropical forests have the fastest rates of organic matter decomposition, which often coincides with fluctuating oxygen (O₂) availability in surface soils. Alike tropical soils, humid temperate rain forest soils are typically rich in short-range ordered iron oxide Fe³⁺ minerals. Those soils show fluctuating oxygen availability over scales of hours to weeks where Fe³⁺ is reduced to ferrous Fe²⁺ and subsequently re-oxidized via biotic or abiotic reactions (Dubinsky *et al.*, 2010; Hall *et al.*, 2012). This mechanism stimulates organic matter decomposition via: organic matter oxidation, likely driven by reactive oxygen species; and acidification (Hall and Silver, 2013). Dissimilatory Fe reducing bacteria are well known to oxidize soil organic matter and can account for the majority of C oxidation under anaerobic conditions (Dubinsky *et al.*, 2010). Abiotic processes have been underestimated across soil profile and should be addressed in future research.

4. Rhizosphere priming effect and molecular transport to the subsoil

Complexation of labile compounds with metal such as Al and Fe Oxides provides a direct mechanism

for translocation of organic C within the soil profile (Kaiser and Kalbitz, 2012).

Sorption by mineral surfaces can protect simple molecules from microbial degradation to some extent (van Hees *et al.*, 2002; Jones and Edwards (1998) compared degradation and sorption of citrate and glucose, and similar studies by Jones and Hodge (1999) were carried out for glutamate, glycine and lysine. Results from both investigations indicated that the reduction of the availability of C for microbial assimilation depended on the type of root exudates and the mineral type. Adsorption of simple molecules onto clay surfaces is almost irreversible, that means short term mineralization of these organic acids while they are available (Boudot, 1992).

The studies of Jones (1999); Jones and Hodge (1999); and Owen and Jones (2001) have shown a rapid mineralization of free amino acids (glycine, glutamate and lysine) by microflora from soil solution.

Preferential C uses by soil microorganisms of these compounds can lead to a change in the SOM turnover induced by fresh C input (Sparling *et al.*, 1982) from not exudate. We have already mentioned that Rasmussen *et al.* (2007; 2006) studies in which mineralogical composition of surface forest soil induced a negative priming because of amorphous minerals. Besides, the chemical interaction of SOM, Al- and Fe-oxides can protect SOM against microbial degradation, since it promotes SOM-humus complexes and stable soil aggregation thereby providing physical protection of SOM aggregation (Panichini *et al.*, 2012).

It has been long hypothesised that non-crystalline minerals like allophane as been formed *in situ*, rather than by translocation (Dahlgren *et al.*, 2004). However recently, the transport of mineral-SOM complexes to deeper soil has been reported by conversion of tropical forest into grassland (Osher *et al.*, 2003). In high precipitation regions, C losses from the soil appear to occur via downward transport, either as colloids or in

solution. There are almost no studies that address the organic translocation in the subsoil. Kaiser and Kalbitz (2012) indicate that sorbed organic compounds can be desorbed because of protective site saturation. This effect is due to complex reactions of Al with soil organic C from the soil solution and the subsequent

precipitation of insoluble complexes of Al-SOM (Rasmussen *et al.*, 2006). It is needed empirical evidence showing the importance of labile compounds available for microorganism and transport. This is important for determining the type of organic matter that is sorbed under specific conditions.

Table 1. Organic compounds and enzymes identified in root exudates used in studies of priming effect.

Organic compounds	C-input g C kg ⁻¹ soil	Enzyme activity	References
Citric acid	0.3–0.6	Phosphomonoesterase ^a , Urease, phosphodiesterase	Lundström <i>et al.</i> (2000); Clemens <i>et al.</i> (2002); Renella <i>et al.</i> (2007); Luo <i>et al.</i> (2014)
Oxalic acid	0.6	Phosphomonoesterase	Lundström <i>et al.</i> (2000); Zheng <i>et al.</i> (1998); Yang <i>et al.</i> (2000); Luo <i>et al.</i> (2014)
Acetate	8	β-glucosidase, phosphomonoesterase	Allison <i>et al.</i> (2005);
Malic acid	6–41		Clemens <i>et al.</i> (2002); Chowdhury <i>et al.</i> (2014); Rukshana <i>et al.</i> (2012)
Glucose	0.6–25	Phosphomonoesterase, urease, casein-hydrolyzing enzymes	Luo <i>et al.</i> (2014); Strickland <i>et al.</i> (2012); Nannipieri <i>et al.</i> (1983)

^aWe have replaced the term acid or alkaline phosphatase by “phosphomonoesterase”, since the term phosphatase includes several enzymes in biochemistry e.g. phosphomonoesterases, phosphodiesterases, etc (Nannipieri *et al.*, 2011).

5. Concluding remarks

. Root exudates into the soil solution can be: 1) consumed by soil microorganism and degraded, 2) mineralized abiotically by mineral catalytic effect or, 3) leached from the soil profile, 4) sorbed to the solid phase or even taken up by plants.

. The low molecular weight of organic substances assimilated directly from soil solution might affect the intensity of RPE, but this process depends on spatial heterogeneity of the rhizosphere.

. Available C for microflora consumption depends on the mineral composition and the type of exudates, and their relative concentrations.

. The microbial interactions with the mineral phase can affect reactions and the process of soil C. Organic C derived from microbial activity and root exudates is probably the most mobile and bioavailable fraction of C in the rhizosphere. The retention and mobility of organic compounds depend on soil properties and can affect the availability of soluble C for soil microbes.

. The effects of root exudates and DOC on RPE across the soil profile need to be further investigated, because the primed compounds may occur in hotspots at root scale.

. Aluminium humus-complex formation needs further attention because Al may be toxic for soil microorganisms, but also it can detoxify the soil solution and enhance C assimilation.

. The saturation of the C-storage capacity of soil, mainly due to organo-mineral interactions, can affect the transport of DOC to deeper soil horizons.

. Rhizosphere priming effects may occur, but it is unknown whether it affects SOM mineralization across the soil profile. There is evidence that RPE on the topsoil SOM of Volcanic soils under forest cover may account for approximately 1/5 of the annual CO₂ evolution from the soil.

6. Future directions

. The hypothesis that RPE is driven by low molecular weight organic substances from root exudates requires further research. Based on current knowledge, research regarding SOM competition between soil microflora and mineral phase over time also needs to be addressed in future studies.

. The hypothesis that DOC is the most susceptible to stabilize through different organo-mineral interactions through the soil profile requires further studies.

. We have hypothesised that SOM mineralization due to RPE may be important across the soil profile. This is supported by new conceptual models explaining colloidal transports in soil with different mineralogy.

. The composition of microbial communities during RPE needs to be monitored in soil with different mineralogy. In high reactive soil e.g. allophanic, RPE will be less intense than soils with crystalline clays.

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