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The priming effect generated by stoichiometric decomposition and nutrient mining in cultivated tropical soils: Actors and drivers

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ABSTRACT

The priming effect (PE) in soil, when induced by a fresh carbon supply, is believed to result from two different mechanisms, "stoichiometric decomposition" and "nutrient mining", and contributes to either long-term SOM stabilization or depletion. Understanding how to affect the balance between both mechanisms can provide valuable insight into agroecology, especially in Southern countries where organic matter management is the primary method of fertilizing cultivated plots. Therefore, the objective of this study was to investigate the bacterial actors in each mechanism and the influence of three drivers in Malagasy Ferralitic soils: the quality of the inducing substrate, the quality of the SOM, and the soil nutrient status. Three different agricultural Ferralitic soils, characterized by different levels of NH_4 and PO_4 availability, different SOM size fractionation profiles, and different bacterial communities, were amended with three types of ^{13}C-labeled organic substrate (glucose, wheat residue, and rice residue) and the PE was measured at two incubation times (7 and 42 days). The results showed that a PE generated by stoichiometric decomposition was mainly induced by the polymerized fraction of crop residues, especially in soil enriched by decaying plant tissues, mineral N, and its associated decomposers guild such as Verrucomicrobia, α- and δ-Proteobacteria and Actinomycetes. Conversely, when this young SOM pool was reduced, the PE was mainly generated by N mining, especially when induced by soluble compounds and when N was limiting but P was available.

1. Introduction

Fresh organic matter (FOM) entering the soil is decomposed by a succession of heterotrophic microbial populations that have specific and complementary catabolic activities. Each organic molecule loses between 40 and 60% of its carbon content through respiration (Brookes et al., 2008). Consequently, as the decomposition process proceeds, soil organic matter (SOM) becomes richer in the nutrients N and P, as well as increasingly recalcitrant, increasing its stability and residence time. In the SOM decomposition process, microorganisms involved at each step have a life strategy adapted to their preferred substrates. Some of them feed on low molecular weight compounds (LMWC) and are very efficient at scavenging inorganic nutrients from the soil solution. Those populations, sometimes called r-strategists, copiotrophs or opportunists depending on the chosen terminology, alternate rapid growth and resting phases, depending on the availability of labile substrates (Fierer et al., 2007; Panikov, 2010). In contrast, some populations are adapted to low availability of easily assimilable compounds (oligotrophic), have slow growth rates (K-strategists), or share specific catabolic enzymes that break down the old SOM to release nutrients (SOM miners). Finally, in between those two extremes, many populations share different catabolic capabilities and an intermediate or versatile growth rate and are therefore classified as decomposers (Moorhead and Sinsabaugh, 2006).

Initially, FOM input to soil may stimulate the mineralization of SOM through a phenomenon called the priming effect (PE). Some authors have proposed that the PE could be generated by two different mechanisms based on the interactions between populations feeding on FOM and/or SOM (Fontaine et al., 2003). The PE could (1) be the result of an increase in extracellular enzymes released by FOM decomposers, which could simultaneously help in the breakdown of SOM, or (2) be the result of the co-metabolism of energy-rich FOM catabolites by SOM

Abbreviations: SOM, soil organic matter; FOM, fresh organic matter; PE, priming effect; LMWC, low molecular weight compounds; HMWC, high molecular weight compounds; SOC, soil organic carbon; BR, basal respiration; SM, substrate mineralization; LF, light fraction of organic matter

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miners that are increasing SOM breakdown. In the second option, Fontaine et al. (2003) suggest a competition between decomposers and miners for FOM. In a subsequent study, the same authors have demonstrated, using cellulose as the PE-inducing substrate, that both mechanisms might coexist in the same soil (Fontaine et al., 2004). Recently, other authors showed (1) that LMWC and complex organic substrates such as crop residue could generate both types of PE and (2) that the balance between the two mechanisms was driven by the nutrient content of the soil solution (Chen et al., 2014).

Investigating the PE-generating process is particularly important for soil carbon sequestration and nutrient recycling since each mechanism of PE generation seems to target a different pool of SOM. "Stoichiometric decomposition" resulting from the release of extracellular enzymes by FOM decomposers helps to break down young SOM that has a structure similar to FOM, such as decaying vegetal tissues with a high C:N:P ratio (Blagodatskaya et al., 2014). In contrast, "nutrient mining" targets an old SOM that is already transformed and rich in nutrients, with a long residence time. Therefore, the PE generated by "stoichiometric decomposition" should be considered a stimulation of carbon and nutrient sequestration, while that generated by "nutrient mining" should be considered a depletion of the SOM stock accompanied by a recycling of nutrients.

The scientific interest in the effect of low molecular weight compounds (LMWC) on SOM destabilization has recently intensified in the context of carbon sequestration. LMWC are the major source of carbon released by plants in the soil *via* their rhizosphere. The current increase in atmospheric CO_2 suggests that photosynthesis will be more intense (Ainsworth and Long, 2005), as will the subsequent soil rhizodeposition (Heimann and Reichstein, 2008). Consequently, there is a need to better understand if and under which conditions LMWC destabilize old SOM, as well as to identify the microbial actors.

In addition to LMWC, high molecular weight compounds (HMWC) such as cellulose can also destabilize SOM (Fontaine et al., 2004, 2011; Guenet et al., 2010, 2012; Blagodatskaya et al., 2014). Conservation agriculture has been proposed as an alternative to conventional cultivation practices with the goal of increasing soil organic matter content and therefore soil fertility. Current practices are, *inter alia*, based on soil amendment with various organic matter including crop residues, which sometimes, for unknown reasons, fail to increase the soil organic carbon stock (Rumpel, 2008). As crop residues are composed of both LMWC and HMWC, it is important to understand how both compounds generate the PE, including under which conditions and by which actors, in order to optimize agroecological practices and to shift the balance between humification and mineralization towards soil C sequestration.

This is especially important in poor, rural, tropical countries such as Madagascar, where soils are naturally nutrient-depleted and mineral fertilizers are too expensive for farmers who have no alternative other than to manage organic wastes to improve soil fertility. Our hypothesis is that soil nutrient status is not the sole key driver of the balance between "stoichiometric decomposition" and "nutrient mining". The quality of the SOM, as well as that of the inducing substrates and the composition of microbial communities, might play an important role in both PE-generating mechanisms. The objective of the present study was, therefore, to investigate the identity of the bacterial groups in Malagasy Ferralitic soils involved in each PE-generating mechanism and the effect of three types of drivers: FOM quality, SOM quality and soil nutrient status.

2. Materials and methods

2.1. Soil sampling

This study was carried out in the agricultural region of Itasy, located in the highlands of Madagascar, 30 km west of Antananarivo, which has a high altitude tropical climate with a mean annual temperature of 18.4 °C and a mean annual precipitation of 1319 mm (https://fr.climate-data.org). Hillsides are subjected to a hot, rainy season from November to April and a cold, dry season from May to October. Three agricultural soils were sampled in September 2015 from plots with different histories and different toposequences to generate samples with variability in C and nutrient contents. Soils were commonly named based on their respective colours, with the red soil (south 19°01′98.8″, east 47°27′40.6″) being a Rhodic Ferralsol, the yellow soil (south 19°02′56.8″, east 47°27′27.6″) being a Ferralic Cambisol and the black soil (south 19°02′10.1″, east 47°27′45.5″) being an Umbric Ferralsol (IUSS Working Group WRB, 2014). Details on the plot histories and toposequences are presented in Appendix 1. In each plot, 5 soil cores 0–10 cm in depth and 1 m apart were sampled using a metal cylinder, pooled together and sieved (2 mm). After gravel and coarse plant debris (> 2 mm) were removed, composite samples were stored at 4 °C for one week prior to further soil incubation and analysis.

2.2. Physicochemical characterization

Soil pH (H_2O) was quantified by suspending soil in water (1:5 ratio) and measuring the pH with a glass electrode and a microprocessor pH meter (Hanna Instruments, USA). Particle size distribution was determined using the Robinson pipette method (Pansu and Gautheyrou, 2007).

Soil organic carbon (SOC) was analysed using the method developed by Walkley and Black (1934). Light fraction soil organic matter (LF) and organic particle size fractions (F > 200 µm; F: 50–200 µm; F < 50 µm) were measured following the procedure described by Gavinelli et al. (1995). The available nitrogen (NH_4^+) content, obtained after KCl extraction, was determined by colorimetry according to the Berthelot reaction (Mulvaney, 1986) and by using an automated continuous flow analyser San^{++} (Skalar Analytique, France). The available phosphorus (P) content was measured using an anion exchange resin (Amer et al., 1955).

2.3. Incubation conditions

The experimental design was a 3 × 4 × 2 factorial design that had 3 replications with the following treatment factors: soil type (black, red or yellow soils), substrate quality (no amendment, glucose, rice or wheat residues) and incubation time (7 days or 42 days). Therefore, each of the three composite soil samples was used to fill four series of six 150-ml flasks with 20 g equivalent dry weight of soil. The soil water content was adjusted to 70% of the saturation threshold using sterile deionized water. After a 7-day preincubation period at 27 °C, the 4 treatments were applied. Two sets of microcosms were amended with 4 mg g^{-1} dry weight of soil containing powdered crop residue, including wheat (*Triticum aestivum* cv. Caphorn: leaves and stems) and rice (*Oryza sativa*: leaves, stems and roots) in quantities corresponding to the amount of straw applied in the field. Details of ^{13}C-crop cultivation and labelling can be found in Appendix 1. One set of microcosms was amended with glucose at a concentration of 1 mg g^{-1} of dry soil (Sigma Aldricht), which roughly corresponds to the amount of the soluble fraction brought by each crop residue (Chen et al., 2014). One set was not amended, but the soil was homogenized as in the three other treatments. Characteristics of the substrates are listed in Table 1.

All microcosms were incubated uncovered in the dark at 27 °C for a maximum of 42 days, with the humidity adjusted with sterile water every two days. Prior to CO_2 analysis (0 d, 7 d and 42 d), the flasks were first flushed with fresh air and then hermetically sealed with plasma plugs, after which the CO_2 was allowed to accumulate for 6 h. Gas phases were sampled for total CO_2 and $^{13}CO_2$ measurements. At 0 d, total CO_2 was only sampled on gas phases of triplicated non-amended conditions in order to measure basal respiration of the three different soils. After 7 d and 42 d, 3 flasks per treatment (soil × substrate) were harvested, and soils were split into two subsamples each: one subsample was stored at 4 °C for no more than 3 days prior to the