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High clay content accelerates the decomposition of fresh organic matter in artificial soils

Hui Wei [a, d], Bertrand Guenet [b], Sara Vicca [b], Naoise Nunan [c], Han Asard [b], Hamada AbdElgawad [b], Weijun Shen [a, *], Ivan A. Janssens [b]

[a] Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, CAS 723 Xingke Rd., Tianhe District, Guangzhou 510650, PR China
[b] Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium
[c] CNRS, UMR7618, BioEMCo, Bâtiment EGER, Campus AgroParisTech, 78850 Thiverval-Grignon, France
[d] Graduate University of the Chinese Academy of Sciences, Beijing 100049, PR China

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ABSTRACT

Clay is generally considered an important stabiliser that reduces the rate of decomposition of organic matter (OM) in soils. However, several recent studies have shown trends contradicting this widely held view, emphasising our poor understanding of the mechanisms underlying the clay effects on OM decomposition. Here, an incubation experiment was conducted using artificial soils differing in clay content (0, 5, and 50%) at different temperatures (5, 15, and 25 °C) to determine the effects of clay content, temperature and their interaction on fresh OM decomposition. CO_2 efflux was measured throughout the experiment. Phospholipid fatty acids (PLFAs), enzyme activities, microbial biomass carbon (MBC), and dissolved organic carbon (DOC) were also measured at the end of the pre-incubation and incubation periods in order to follow changes in microbial community structure, functioning, and substrate availability. The results showed that higher clay contents promoted OM decomposition probably by increasing substrate availability and by sustaining a greater microbial biomass, albeit with a different community structure and with higher activities of most of the extracellular enzymes assayed. Higher clay content induced increases in the PLFA contents of all bacterial functional groups relative to fungal PLFA content. However, clay content did not change the temperature sensitivity (Q_{10}) of OM decomposition. The higher substrate availability in the high clay artificial soils sustained more soil microbial biomass, resulting in a different community structure and different functioning. The higher microbial biomass, as well as the changed community structure and functions, accelerated OM decomposition. From these observations, an alternative pathway to understanding the effects of clay on OM decomposition is proposed, in which clay may not only accelerate the decomposition of organic materials in soils but also facilitate the SOM accumulation as microbial products in the long term. Our results highlight the importance of clay content as a control over OM decomposition and greater attention is required to elucidate the underlying mechanisms.

1. Introduction

Soil contains the largest portion of organic carbon (~1500 Pg C in the first meter of soil) in global terrestrial ecosystems (Post et al., 1982; Batjes, 1996; Jobbágy and Jackson, 2000) and is therefore of great importance to the global carbon balance. Even a small loss from such a large carbon pool may bring about large increases in atmospheric CO_2 concentrations (Jenkinson et al., 1991; Cox et al., 2000). For this reason, the decomposition of soil organic matter (SOM), which is typically approximated by heterotrophic respiration, has been of great concern for decades. Although previous studies have revealed that several factors such as temperature, moisture, soil texture, vegetation type and productivity are important for controlling SOM decomposition (Pastor and Post, 1986; von Lützow et al., 2006; Shen et al., 2009), we remain far from a complete understanding of the mechanisms involved (Davidson and Janssens, 2006; Schmidt et al., 2011). Temperature, for example, has been frequently reported to enhance decomposition quasi-exponentially (e.g., Davidson and Janssens, 2006; Craine

* Corresponding author.
E-mail address: shenweij@scbg.ac.cn (W. Shen).

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et al., 2010); however, variation in the temperature responses cannot always be explained (Kirschbaum, 2006; Schmidt et al., 2011).

Many studies have indicated that clay can protect soil organic matter (SOM) from decomposition, and several mechanisms have been proposed (Krull et al., 2003; von Lützow et al., 2006; Six and Paustian, 2014). One is the physical protection mechanism, i.e., the pore network of clay soils is characterized by a large number of small pores that are not accessible to microbes, and the OM contained in these biologically barren pores is physically protected by the soil architecture and may, therefore, be unavailable to soil microorganisms (Oades, 1988; Krull et al., 2003; von Lützow et al., 2006). For example, it has been suggested that bacteria cannot enter soil pores with diameters less than three times their body size (Kilbertus, 1980). This space limitation implies that more than 90% of the pore space in clay soils is inaccessible to bacteria (Oades, 1988; Van Veen and Kuikman, 1990).

Another mechanism by which clay protects OM is the chemical protection. Clay particles are the most active soil components in the production of organomineral complexes because of their high charge and specific surface area (Krull et al., 2003; von Lützow et al., 2006). Microbial enzymes decompose OM that is embedded in such organomineral complexes less efficiently than free OM. Both of the physical and chemical mechanisms are frequently proposed to explain the large stocks and low decomposition rates of OM in clay soils (Six et al., 2004; von Lützow et al., 2006; Six and Paustian, 2014). However, several recent studies have found that clay had no effect, or even a positive effect, on SOM decomposition (Müller and Höper, 2004; Dilustro et al., 2005; Fissore et al., 2008). Besides the aforementioned physical and chemical protection mechanisms, other mechanisms such as microbial adaptation are probably also important in the processes of SOM stabilization and destabilization (Schmidt et al., 2011; Schimel and Schaeffer, 2012; Cotrufo et al., 2013). The role of microbial processes in SOM stabilization/destabilization has been less studied, compared to the physical and chemical protection mechanisms (Schimel and Schaeffer, 2012; Cotrufo et al., 2013; Wieder et al., 2013).

Furthermore, the clay effects on OM decomposition may interact with other influential factors such as temperature. The adsorption of OM to clay minerals is an exothermic reaction, and desorption is an endothermic reaction. According to Le Chatelier's principle, an increase in temperature is favourable for preserving more reactants in exothermic reactions and for producing more products in endothermic reactions in clay soils. This means that temperature increases are likely to stimulate the desorption of organic materials from and retard their adsorption to clay surfaces, thus enhancing substrate availability (Conant et al., 2011). As a result of this interaction, SOM decomposition in clay soils may be more sensitive to changes in temperature (Evans et al., 2011). However, to our knowledge, clay content–temperature interactions and their effects on SOM decomposition have not yet received much attention.

To improve our understanding of OM decomposition responding to differences in clay content and temperature, as well as to explore the mechanisms underlying these responses from a microbial ecology perspective, we conducted a laboratory incubation using three artificial soils (0, 5, and 50% clay content) at three temperatures (5, 15, and 25 °C) for two months. CO_2 efflux was measured regularly throughout the experiment, and dissolved organic carbon (DOC), microbial biomass carbon (MBC), phospholipid fatty acids (PLFAs) and enzyme activity profiles were measured at the end of the incubation. We aimed to answer the following three questions: 1) How does clay content affect OM decomposition? 2) Is there an interactive effect between clay content and temperature on OM decomposition? 3) How are substrate supply, microbial biomass, and soil community structure and functioning related to the effects of clay content, temperature and their interaction on OM decomposition in our artificial soils?

2. Materials and methods

2.1. Artificial soil mixture

The OM used in the incubation was collected from the lower O horizon of a Scots pine forest in the Belgian Campine region (see details in Janssens et al., 1999; Gielen et al., 2013) after removing the upper-layer undecomposed plant residues, and therefore it was fresh OM including partially decomposed litter and humus. The sample was then air-dried, ground and sieved through a 1 mm mesh. Because the OM was not sterilised, it was also the source of microorganisms. We prepared our samples by mixing commercial bentonite (Sigma–Aldrich), acid-washed white sand (inert, 63–365 μm), and OM homogeneously in a concrete blender. These clay matrices are called artificial soils in our study to differentiate from natural soils, as in previous studies (Guenet et al., 2011; Pronk et al., 2012). Artificial soils with three textures were prepared (control: no clay + 75% sand +25% OM; 5% clay soil: 5% clay + 70% sand +25% OM; 50% clay soil: 50% clay + 25% sand +25% OM). The total organic carbon content (TOC) of these artificial soils was 9%, with a C/N ratio of 22. No significant differences in TOC and the C/N ratio were detected between the clay treatments ($P = 0.954$ for TOC and $P = 0.601$ for C/N ratio). The pH values were 4.6, 5.1, and 6.9 for control, 5%, and 50% clay soils, respectively. The water holding capacity (WHC) of the artificial soils was determined by saturating 35 g subsamples for 24 h in Whatman #42 filter papers that were placed in plastic funnels and then draining them for another 24 h before determining the water content by drying for 48 h in an oven at 60 °C. Lower drying temperature (60 °C instead of 105 °C) was used to avoid the overestimation of water content due to high-temperature-induced extra oxidization of OM, which was a mixture of plant materials including partially decomposed litter and humus. The final water holding capacity (WHC) of the artificial soils were 0.71 ± 0.03, 0.84 ± 0.03, and 2.45 ± 0.15 g g^{-1} soil (dry weight equivalent) for control, 5%, and 50% clay soils, respectively.

We used these artificial soils to represent forest surface soil, which is a considerable terrestrial organic carbon pool with a high susceptibility to global change (Jobbágy and Jackson, 2000; Chen et al., 2012). Artificial rather than natural soil was chosen to control the clay content independently of other soil variables (Conant et al., 2011; Guenet et al., 2011). Although it differs from natural soils in some properties such as aggregates and organomineral complexes, the artificial soil is useful in laboratory incubations, particularly in gradient studies, because artificial soil avoids complicated interactions with confounding factors (Conant et al., 2011; Guenet et al., 2011).

2.2. Soil incubations and CO_2 efflux measurements

Twelve experimental units, which consisted of either 100 g (dry weight equivalent) artificial soil in the case of the control and 5% clay soils, or 50 g (dry weight equivalent) artificial soil in the case of the 50% clay soil in 200 ml glass Erlenmeyer flasks, were established for each temperature treatment, with four replicates for each type. There were three temperature treatments, meaning that there were totally 36 experimental units. Soil water content was adjusted to 60% of WHC by adding deionised water. We used 50 g rather than 100 g dry soil with high clay content (50%) because these soils were heavier and bulkier after wetting; thus, the total weight of the 50% clay soil was similar to those of the other two soils for incubation. All the soil samples were pre-incubated at 15 °C for 30 days to allow