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Establishment of macro-aggregates and organic matter turnover by microbial communities in long-term incubated artificial soils

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ABSTRACT

The study of interactions between minerals, organic matter (OM) and microorganisms is essential for the understanding of soil functions such as OM turnover. Here, we present an interdisciplinary approach using artificial soils to study the establishment of the microbial community and the formation of macro-aggregates as a function of the mineral composition by using artificial soils. The defined composition of a model system enables to directly relate the development of microbial communities and soil structure to the presence of specific constituents. Five different artificial soil compositions were produced with two types of clay minerals (illite, montmorillonite), metal oxides (ferrihydrite, boehmite) and charcoal incubated with sterile manure and a microbial community derived from a natural soil. We used the artificial soils to analyse the response of these model soil systems to additional sterile manure supply (after 562 days). The artificial soils were subjected to a prolonged incubation period of more than two years (842 days) in order to take temporally dynamic processes into account. In our model systems with varying mineralogy, we expected a changing microbial community composition and an effect on macro-aggregation after OM addition, as the input of fresh substrate will re-activate the artificial soils. The abundance and structure of 16S rRNA gene and internal transcribed spacer (ITS) fragments amplified from total community DNA were studied by quantitative real-time PCR (qPCR) and denaturing gradient gel electrophoresis (DGGE), respectively. The formation of macro-aggregates (>2 mm), the total organic carbon (OC) and nitrogen (N) contents, the OC and N contents in particle size fractions and the CO_2 respiration were determined. The second manure input resulted in higher CO_2 respiration rates, 16S rRNA gene and ITS copy numbers, indicating a stronger response of the microbial community in the matured soil-like system. The type of clay minerals was identified as the most important factor determining the composition of the bacterial communities established. The additional OM and longer incubation time led to a re-formation of macro-aggregates which was significantly higher when montmorillonite was present. Thus, the type of clay mineral was decisive for both microbial community composition as well as macro-aggregation, whereas the addition of other components had a minor effect. Even though different bacterial communities were established depending on the artificial soil composition, the amount and quality of the OM did not show significant differences supporting the concept of functional redundancy.

1. Introduction

In the course of soil formation, mineral particles and OM are clustered and glued together into aggregates of various sizes, building up a complex soil structure that is crucial for various soil functions. The current knowledge about aggregate formation is that minerals, polyvalent cations and soil OM lead to a micro-aggregate formation (Edwards and Bremner, 1967) and that these micro-aggregates serve as building blocks for macro-aggregates, enmeshed by fungal hyphae and roots (Tisdall and Oades, 1982). This aggregate hierarchy model was advanced by Oades (1984), who postulated that the OM within macro-aggregates is decomposed by microorganisms, becomes encapsulated with minerals and microbial residues and forms micro-aggregates within macro-

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aggregates. Clay minerals are known to be important for the formation and stabilisation of aggregates in soils (Edwards and Bremner, 1967; Six et al., 2004). However, only few studies have been carried out on the influence of a specific mineralogy on aggregation (Denef and Six, 2005; Denef et al., 2002; Fernández-Ugalde et al., 2013; Reichert et al., 2009). Thus, our knowledge still lacks information regarding the role of different clay minerals in soil aggregation (Fernández-Ugalde et al., 2013). The soil microbiota is assumed to be actively involved in aggregation dynamics by the production and decomposition of microbial residues (Baldock, 2002). A more dominant role in soil aggregation is assigned to fungi, stabilising macro-aggregates, as compared to bacteria, which are assumed to act at a smaller scale (Chenu and Cosentino, 2011; Chenu and Stotzky, 2002; Tisdall, 1994). Thus, microorganisms are seen as architects arranging the surrounding soil environment (Young and Crawford, 2004). The resulting three-dimensional soil matrix contains a network of heterogeneous reactive interfaces controlling transport, availability and fate of solutes, colloids, gases, nutrients and pollutants (Totsche et al., 2010).

On the one hand, microorganisms affect soil particles by aggregation, weathering and modification of their arrangement (Chenu and Stotzky, 2002). On the other hand, the presence of surface-active soil particles, for instance clay minerals, likely influences the microbiota by providing the physico-chemical conditions for microbial growth and genetic transfer, adhesion, adsorption of nutrients, pollutants, metabolites and enzymes, protection against stresses and predators etc., thus, by a variety of different biological, physical, and physicochemical processes (Chenu and Stotzky, 2002; Filip, 1973; Stotzky, 1967, 1986). Advances in molecular techniques have opened new possibilities to study the interactions between minerals and microbial communities. However, only few studies exist so far which consider the different constituents and their interaction with microbial communities. Carson et al. (2009) showed that the structure of bacterial communities in soil is influenced by the mineral substrate and concluded that minerals play a greater role in bacterial ecology than simply providing an inert matrix for bacterial growth. Recently, Heckman et al. (2013) found that the surfaces of metal oxides exerted a strong control on soluble nutrient dynamics and thus on the composition of the microbial community. Charcoal is also known to affect the physical and chemical parameters of soil, e.g. pH and the release of soluble nutrients, which in turn is supposed to influence microbial activity and community structure (Lehmann et al., 2011).

The study of interactions between the soil microbiota, aggregation and mineralogy is needed to understand important soil functions like OM turnover. The complexity of soils makes analyses of these interactions in natural soil systems difficult (Ellis, 2004; Guenet et al., 2011; Vos et al., 2013). Furthermore, the comparability between soils to predict the role of single constituents is hampered, as soils are usually exposed to different environmental conditions. Therefore, artificial soils are regarded as an effective tool for studying the factors controlling soil formation and functioning (Ding et al., 2013; Guenet et al., 2011; Pronk et al., 2012). An artificial soil approach was recently used by Pronk et al. (2012, 2013) to study OM turnover and the formation of aggregates over an incubation time of 540 days. The authors showed that macro-aggregates and organo-mineral associations were formed quickly (90 days) from clean model materials (Pronk et al., 2012). The development was accompanied by the colonisation of initially clean particles by diverse microbial communities as a function of the mineral composition and charcoal (Babin et al., 2013; Ding et al., 2013). In the early phase (90 days) of the artificial soil incubation, charcoal and to a lesser extent clay minerals shaped the composition of the bacterial communities (Ding et al., 2013). After 360 days, a remarkable effect of metal oxides on the bacterial communities was also observed (Babin et al., 2013). These studies demonstrated a dynamic development of the microbial communities over the incubation time, depending on the composition of the artificial soil (Babin et al., 2013; Ding et al., 2013). At the end of the incubation time, a decline of the system was observed concerning microbiota and macro-aggregation, which was attributed to the missing OM input (Pronk et al., 2012). Aggregation is known to be a dynamic process, especially in regard to periodic input of OM (Abiven et al., 2009; Six et al., 2004). Although the development of such artificial systems seems to be highly dynamic, other incubation experiments with model systems were carried out only for time periods up to 1.5 years (Guenet et al., 2011; Heckman et al., 2013; Pronk et al., 2012). Therefore, it is not yet clear how model systems develop over a longer time period, and whether the observed soil composition-dependent differences persist in matured systems.

Although soil processes and properties are controlled by a complex interplay between different soil components, most studies look at soil processes from either the perspective of a soil microbiologist or a soil scientist. Here, we try to cross the interdisciplinary boundaries to find mechanistic links between biotic and abiotic soil factors. Encouraged by the results obtained from the artificial soil studies described above, we conducted an experiment with defined materials (illite, montmorillonite, ferrihydrite, boehmite and charcoal), sterile manure and a microbial inoculant. In our experiment, we implemented a second sterile manure input in order to avoid a declining of the system as observed by Pronk et al. (2012). The incubation conditions were chosen to avoid complications due to variable environmental influences, so that the interpretation of the experimental results could be focused on the effect of artificial soil composition and incubation time under the response of the model system to additional sterile manure supply. We studied the response of established artificial soil systems to additional manure input with regard to microbial community response and macro-aggregation. To take the proposed dynamic processes into account, artificial soils were subjected to a prolonged incubation period of more than two years (842 days).

We assumed the following based on the results of Pronk et al. (2012) and Babin et al. (2013):

(i) The continuing development of the artificial soils will lead to further differentiation of the microbial communities depending on artificial soil composition.
(ii) The additional sterile manure input will re-activate the soil biota resulting in a re-formation of macro-aggregates, independently of the artificial soil composition.
(iii) The CO_2 respiration and shifts in microbial community composition will be a function of the soil composition in response to the additional OM input.
(iv) Soil OM properties will develop differently depending on the microbial community established as determined by artificial soil composition.

2. Material and methods

2.1. Design of artificial soils

Five different compositions indicated by montmorillonite (MT), illite (IL), montmorillonite + charcoal (MT + CH), illite + ferrihydrite (IL + FH) and illite + boehmite (IL + B) were created. All mixtures contained sand-sized (Quartz Sand Haltern, H33) and silt-sized (Millisil W11H) quartz (Quarzwerke GmbH,