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Succession of soil microbial communities and enzyme activities in artificial soils

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ABSTRACT

Soil microorganisms are frequently attached to mineral surfaces or organo-mineral complexes, yet little is known about the microbial colonization of different soil minerals. The use of artificial soils that differ only in their mineral composition (illite, montmorillonite, ferrihydrite, boehmite) and the presence of charcoal, but not in soil texture and organic composition, offered a unique opportunity to study composition, function and succession of soil microorganisms colonizing newly exposed organo-mineral surfaces. Artificial soils were incubated with a microbial inoculum from an arable topsoil at constant temperature (20 °C) and moisture conditions for up to 18 months. The succession of enzyme activities involved in C-, N- and P-cycling gave clear evidence that nutrient limitation drove microbial community structure during the incubation independent of mineral composition. Discriminant analyses of principal components of PLFAs showed that microbial community structure changed over a period of 18 months toward similar communities for all artificial soils at the end of incubation. This was supported by a shift in the soil microbial community from dominance of specific phyla like *Betaproteobacteria*, which is often referred to as copiotrophic organisms, during the first 6 months of the incubation, toward systems with a higher dominance of e.g. *Acidobacteria*, which are suggested to follow the oligotrophic life-strategy. The effect of mineral surface properties on enzyme activities was pronounced during the first 6 months of incubation. Microbial colonization and succession on mineral surfaces was likely affected by mineral properties such as surface charge and, at the end of incubation, availability of beneficial nutrients. Charcoal affected the microbial community only during the first 6 months of incubation with slightly increased colonization by bacteria which are often described as oligotrophic organisms. In contrast, illite and montmorillonite probably provided nutrient rich environments with montmorillonite supplying more exchangeable cations. The artificial soils experiment clearly showed that changes in substrate availability as well as mineral properties are important drivers for the development of microbial communities.

1. Introduction

Soils are heterogeneous mixtures of mineral, organic and biological compounds which are frequently associated in complex hierarchical structures. During the development of soils, aggregates are formed. The surfaces of micro and macro aggregates differ in their physicochemical properties and provide habitats for soil microorganisms. Abundance, diversity and function of soil microorganisms are regulated by environmental factors such as

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substrate and water availability (Killham et al., 1993; Chenu et al., 2001; Monard et al., 2012), habitat properties such as particle and pore size distribution (Ranjard et al., 2000; Sessitsch et al., 2001; Strong et al., 2004) and mineral composition (Roberts, 2004; Gleeson et al., 2005, 2006; Carson et al., 2007, 2009). Previous studies have provided evidence that differences in particle and pore size distribution, in organic matter (OM) quantity and quality as well as mineral composition of soils may select for specific bacterial communities (Ranjard et al., 2000; Sessitsch et al., 2001; Davinic et al., 2012). After physical fractionation of soil samples, more bacteria were found in micro aggregates than in macro aggregates, and the distribution of bacteria depended on the content of organic carbon (OC) and clay (Ranjard et al., 2000). There is also evidence that particle size as well as mineral composition of soils drive not only specific microbial colonization of organo-mineral surfaces, but also modify microbial functions (Kandeler et al., 1999; Stemmer et al., 1999; Sessitsch et al., 2001; Poll et al., 2003).

Minerals form ecological niches which play an important role in biogeochemical cycles (Uroz et al., 2012). However, little information is available regarding the influence of mineral composition on microbial community composition and function. Recent developments in molecular techniques have created new opportunities to study the interactions between minerals and microbial communities, as well as the microbial role in soil functional processes. Previous studies have provided evidence that different soil minerals and their specific surface properties influence microbial colonization and select for different bacterial communities (Roberts, 2004; Gleeson et al., 2005, 2006; Boyd et al., 2007; Carson et al., 2007, 2009); e.g. positively charged mineral surfaces attracted negatively charged microbes, whereas negatively charged surfaces were less colonized. In addition to the electrostatic properties of mineral surfaces, their roughness and chemical composition also impact initial colonization; the colonization of negatively charged silicate surfaces increased with increasing Fe and decreasing Al content of the mineral, as Fe is a nutrient and Al is toxic (Roberts, 2004). Under P and Fe limitation, microorganisms preferentially colonized feldspar containing the limiting nutrients P and Fe (Rogers and Bennett, 2004). Similarly, Carson et al. (2009) reported that mica, basalt and rock phosphate selected for specific bacterial communities depending on differences in their elemental and nutrient concentrations. The presence of specific ribotypes was connected with specific minerals and was driven by the elemental composition of the mineral (Gleeson et al., 2005, 2006).

The complexity of natural soils makes it difficult to find a direct link between mineralogy and soil biota. Therefore, artificial soils offer a unique opportunity to study microbial colonization and functioning of organo-mineral surfaces in a simplified model system (Zhang et al., 2011; Pronk et al., 2012; Ding et al., 2013; Vogel et al., 2014; Wei et al., 2014a,b). Over the last few years, many studies on artificial soils have been based on a microcosm experiment of Pronk et al. (2012) in which artificial soils were composed of quartz, manure as the OM source, and a microbial community extracted from a natural arable soil, with 8 different mixtures of montmorillonite, illite, ferrihydrite, boehmite and charcoal. Besides studies on aggregation and chemistry of these artificial soils (Heister et al., 2012; Pronk et al., 2012, 2013) some results are available on the early microbial colonization of different organo-mineral complexes (Babin et al., 2013; Ding et al., 2013). Over a period of 3 months, Ding et al. (2012, 2013) demonstrated that the diversity of the microbial communities for all artificial soils were lower than for the inoculum used. In addition, soil minerals as well as charcoal shaped the community composition, and the bacterial community structure of charcoal-containing soils differed greatly from other soils at all taxonomic levels studied (Ding et al., 2013). Vogel et al. (2015) found that the mineralization did not correlate with the surface area of the clay minerals used in the artificial soils system. Much less information is available however, about the succession of microbial communities in relation to microbial abundance, diversity and function during prolonged incubation of artificial soils (Steinbach et al., 2015; Vogel et al., 2014).

Therefore, the objective of this study was to determine the succession of microbial communities on organo-mineral complexes, in relation to mineral composition and substrate availability over a period of 18 months. We hypothesized that (1) different minerals and/or charcoal select for specific colonizers. In particular, we hypothesized that (2) incubation time and therefore substrate availability influences microbial colonization of different mineral surfaces, and that (3) microbial succession follows copiotrophic and oligotrophic strategies based on different nutritional needs. To test our hypotheses, we used samples from an artificial soils experiment (Pronk et al., 2012). The structure and activity of the microbial community were determined using phospholipid fatty acid (PLFA) and enzyme analyses. The abundance of 16S rRNA genes, fungal ITS fragment as well as the abundances of seven different taxa were quantified with quantitative PCR (qPCR).

2. Material and methods

2.1. Experimental design

A series of eight different artificial soils was produced as described in detail by Pronk et al. (2012). The artificial soils covered a wide range of complexity (two-component systems to three- to four-component systems), but were restricted to eight combinations most likely found in nature. Quartz (Q; quartz sand, silt-sized quartz and clay-sized quartz) was mixed with one or more combinations of the model components montmorillonite (MT), illite (IL), ferrihydrite (FH), boehmite (B) and charcoal (CH) (Table 1); each treatment was prepared in triplicate. All artificial soils had similar texture with only slight variations in the sand and clay mineral or clay-sized quartz fractions. This derived from variable additions of the model compounds and clay-sized quartz to keep the mass of the size fraction <6.3 μm constantly at 5.6%. Ferrihydrite, boehmite and charcoal were considered as part of this fraction because of their high reactivity and specific surface area. Dried and sterilized horse manure was added as a nutrient and substrate source for microbial growth. The soils were inoculated (60 ml inoculum to each batch of 1 kg) with a microbial community extracted from the topsoil of an Eutric Cambisol (pH 6.5) obtained from the $Ca(NO_3)_2$ treatment of a long-term field trial at Ultuna, Sweden. The inoculum was prepared by shaking a soil suspension (soil (g) to water (ml) ratio of 1:2) for 2 h with gravel and

Table 1
Composition of the artificial soils in % mass contribution of each model component (100% excluding manure). Manure was added at a rate of 4.5% of mass of mineral components, i.e. 45 g kg^{-1}.

Model component	Soil composition							
	MT	IL	FH	MT*IL	MT*CH	IL*FH	IL*B	IL*FH*CH
Quartz sand	41.7	40.0	41.4	40.8	41.7	40.0	40.0	40.0
Silt-sized quartz	52.0	52.0	52.0	52.0	52.0	52.0	52.0	52.0
Montmorillonite	6.3	-	-	3.2	4.3	-	-	-
Illite	-	8.0	-	4.0	-	7.0	7.0	5.0
Clay-sized quartz	-	-	5.6	-	-	-	-	-
Ferrihydrite	-	-	1.0	-	-	1.0	-	1.0
Boehmite	-	-	-	-	-	-	1.0	-
Charcoal	-	-	-	-	2.0	-	-	2.0
Manure	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5