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Separation of soil microbial community structure by aggregate size to a large extent under agricultural practices during early pedogenesis of a Mollisol

Na Li [a], Shui-Hong Yao [b], Yun-Fa Qiao [a], Wen-Xiu Zou [a], Meng-Yang You [a], Xiao-Zeng Han [a,**], Bin Zhang [a,b,*]

[a] Key Laboratory of Mollisols Agroecology, National Field Observation and Research Station of Hailun Agroecosystems, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Harbin 150081, PR China
[b] Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing 100081, PR China

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ABSTRACT

Soil microbial communities may differ with aggregate size as aggregates constitute a complex environment for microorganisms. However, such effects are inconsistent for mature soils and largely unknown at the initial stage of soil formation. By using an eight-year field experiment established on dug parent material (PM) of a Mollisol, our objectives were (1) to examine the effects of aggregate size on soil microbial communities by analyzing phospholipid fatty acids (PLFAs) and (2) to identify the controlling factors of such changes in microbial community structure. The field treatments included two no-tilled soils under perennial crops and four tilled soils under the same cropping system, with or without chemical fertilization and crop residue amendment and were compared to PM and an arable Mollisol (MO) with only chemical fertilization. Total N, soil organic C (SOC), total PLFAs and composition of soil microbial communities were affected by aggregate size and field treatment. Principal component analysis (PCA) of PLFA profiles demonstrated that the microbial community structure was separated by aggregate size classes via PC1 for all studied soils and by field treatment via PC2 in each aggregate size class. The separations via PC1 were driven by fungi, eukaryotes and bacteria that were associated with the >2, 2–0.25 and 0.25–0.053-mm aggregates, respectively. The separations via PC2 were driven by gram positive (G(+)) bacteria and actinomycetes that were associated with the field treatments, being more separated in 2–0.25 mm aggregates than in 0.25–0.053 mm aggregates. These results suggested that the formation of macroaggregates from weathered particles or microaggregates had governed the distribution of microbial functional groups in different sizes of aggregates due to the variations of physical and chemical environment. The variations among field treatments were larger in larger aggregates possibly due to more influence of organic carbon input and tillage on formation of larger aggregates.

1. Introduction

Loss of surface soil is accelerated by soil water erosion and at mining and construction sites, resulting in soil parent materials being closer to the ground surface, or even exposed to the air. This in turn can affect the ability of soils to support food production. Thus, there is a considerable need for large-scale restoration programs to develop strategies for restoration, protection and sustainable use of such degraded soils (Cairns, 1999; Hobbs and Harris, 2001; Schulz et al., 2013). Many large-scale restoration programs have proven successful in terms of above-ground ecosystem properties. However, our understanding of soil development, particularly from the parent materials under managed ecosystems is still very poor (Harris, 2009; Yao et al., 2009). Although agricultural use is one of the most important objectives of restoration in arable regions, and agricultural practices can rapidly influence soil properties and fertility in

* Corresponding author at: Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing 100081, PR China. Tel.: +86 10 82106719; fax: +86 10 82106225.
** Corresponding author.
E-mail address: zhangbin01@caas.cn (B. Zhang).

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contrast to 'natural' successional processes (Knops and Tilman, 2000), such management approaches have rarely been considered as a restoration technique *per se*.

Soil microbial communities generally depend on soil structure or substrate inputs (i.e., crop residues) (Elliott and Coleman, 1988). Soil aggregates form from soil particles and organic materials in a hierarchical way (Tisdall and Oades, 1982). Such aggregation or disaggregation results in a complex environment for micro-organisms in soil (Dexter, 1988). Since the exposure to larger voids will vary between aggregate size classes, aggregates of different sizes may also differ with respect to the size and composition of the microbial community (Petersen et al., 1997). There are few studies on microbial communities that are directly associated with aggregates (e.g., Petersen et al., 1997; Helgason et al., 2010a,b), and most information regarding aggregate microbial communities is indirectly linked to aggregates themselves by evaluation of bulk soil communities (e.g., Väisänen et al., 2005; Peixoto et al., 2006). Some studies demonstrated that soil microbial communities depend on the size of soil aggregates and the location within soil aggregates (Poly et al., 2001; Ranjard et al., 2000; Mummey and Stahl, 2004). Other studies, however, showed that microbial compositions are influenced more by land use, tillage, or season than by aggregate size (Petersen et al., 1997 Schutter and Dick, 2002; Helgason et al., 2010a,b).

Soil aggregation is affected by land use, cropping system and fertilization through organic inputs (Fröberg et al., 2003; Bronick and Lal, 2005; Brant et al., 2006; Chapon et al., 2012). The changes in the composition and activity of soil microbial communities are often attributed to the quality of soil organic matter (e.g., Davinic et al., 2012). Macro-aggregates form through binding of weathered fine parent materials with decomposed organic matters (Tisdall and Oades, 1982). They can contain more labile substrates (Bronick and Lal, 2005) and fungi (Feeney et al., 2006; Rillig and Mummey, 2006) than micro-aggregates. A recent study demonstrated that soil microbial communities can differentiate very quickly (i.e., 2 days) in different aggregate size classes after organic addition, indicating that bacterial community structure is closely linked to soil aggregation (Blaud et al., 2012). With increasing amount of organic inputs, soil organic carbon (SOC) content increases, which may promote the formation of macro-aggregates (Peng et al., 2003; Bronick and Lal, 2005; Yao et al., 2009), and then determine the spatial distribution of microbial communities among different aggregate size in a long run.

The formation of macro-aggregates is impeded by tillage directly through physical disruption, and indirectly by enhancing organic matter degradation (Young and Ritz, 2000). Tillage can also break down fungal hyphae and then reduce fungal biomass (Beare et al., 1997; Frey et al., 1999; Simmons and Coleman, 2008). Helgason et al. (2010a) found significant separation among aggregate sizes of both no-tilled and tilled soils due to fungal association with large aggregates. But they failed to observe the effects of no tillage on the structure soil microbial communities in bulk soil (Helgason et al., 2010b). Tillage is frequently integrated with organic amendments, and both can affect the composition of soil microbial communities (Treonis et al., 2010). Therefore, this inconsistence of the results of shifts in microbial communities among aggregate size classes can be attributed to the complex interactions between soil aggregation and soil microbial communities under different land uses and agricultural practices such as organic amendment and tillage (Young and Ritz, 2000; Helgason et al., 2010a).

Most of the knowledge about the distribution of microbial functional groups among aggregate size classes and its relation to soil management is often gained in the context of well-developed soils. There are complex interactions between soil biota and abiotic conditions at different stages of above-ground ecosystem succession and below-ground soil development (Schulz et al., 2013). Soil microbes play a significant role in soil formation. They drive mineral weathering during early pedogenesis of soil (Chorover et al., 2007) and are involved in organic matter decomposition and nutrient cycling when fresh organic materials are added to soil (Paul and Clark, 1989; Schimel, 1995; Abiven et al., 2007).

By using an eight-year field experiment established on parent material (PM) of a Mollisol, our previous study demonstrated contrasting development of soil microbial community structure in bulk soils under no-tilled perennial and tilled cropping during the early pedogenesis (Li et al., 2014). In this study, our objectives were (1) to examine the effects of aggregate size on soil microbial communities by analyzing phospholipid fatty acids (PLFAs) and (2) to identify the controlling factors of such changes in microbial community structure. When free minerals and OC are ready, the formation of soil aggregates through mineral-organic complex may be the most prevailing process (Tisdall and Oades, 1982; Six et al., 2004) at the initial stage of soil formation, which is hypothesized to cause distinct separations of soil microbial communities among different aggregate size classes irrespective

Table 1
Experimental design and basic soil properties in bulk soil under the different field treatments and the reference soils (parent material, PM and mature Mollisol, MO) (cited from Li et al., 2014).

Field treatment	Land use[a]	Organic incorporation[b]	Mineral fertilization[c]	Organic C input[d] kg ha^{-1}	SBD Mg m^{-3}	pH	SOC g kg^{-1}	TN g kg^{-1}
PM					1.4	6.88	5.1	0.41
MO					1.1	5.47	29.4	2.14
NatF	Natural fallow	Litter and roots	no	947d	1.1a	6.69a	7.7bc	0.66c
Alfa	Alfalfa	Litter and roots	no	1173c	1.1a	6.40a	9.1b	0.84bc
F0C0	Crop rotation	Roots only	no	861d	1.0b	6.54a	7.0c	0.51 d
F1C0	Crop rotation	Roots only	NPK	1311c	1.0b	5.96b	7.9bc	0.67c
F1C1	Crop rotation	Roots and amended soya seeds and maize straw	NPK	2842b	0.9c	5.71bc	10.8a	0.89b
F1C2	Crop rotation	All crop straw, seeds and roots	NPK	3696a	0.9c	5.60c	12.3a	1.14a

[a] Crop rotation is in a sequence of soya bean and maize in different years since 2004. Crop density was 270 thousand ha^{-1} and 86 thousand ha^{-1} for soya bean and maize, respectively.
[b] The amendment rates in F1C1 were 4500 kg ha^{-1} of baked soybean powder and 2250 kg ha^{-1} of maize straw mixed homogeneously. The C:N ratios were 7.4:1 in soya bean seeds, 33.5 in maize seeds, 63.3:1 in maize straw and 59.1 in soybean straw.
[c] Diammonium phosphate was source of N and P and applied at a rate of 300 kg ha^{-1} year^{-1}; potassium sulfate was source of K and applied at a rate of 120 kg ha^{-1} year^{-1}.
[d] The average amount of organic C input per year were estimated based on the sources of organic incorporation. The average C concentrations were 428, 443, 442 and 431 g kg^{-1} in above-ground biomass and root of the grasses, alfalfa, maize and soya bean, respectively. The root: shoot ratios were 2.0 and 0.4 in NatF and Alfa, and the ratio of root: yield was 0.19 and 0.13 in maize and soya bean, respectively.