Science of the Total Environment 635 (2018) 784–792

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Contrasting responses of bacterial and fungal communities to aggregate-size fractions and long-term fertilizations in soils of northeastern China

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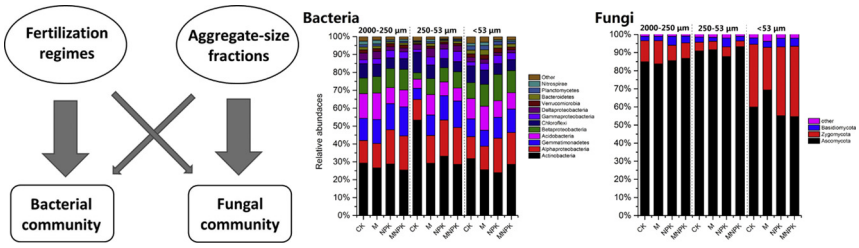
HIGHLIGHTS

- Higher F/B contributes to C sequestration in larger aggregate-size fractions.
- Fungal community is preferentially impacted by aggregate-size fractions.
- Bacterial community is mainly driven by chemical fertilization.
- Fungi play stronger effects on soil C than bacteria at aggregate scale.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 7 January 2018
Received in revised form 10 April 2018
Accepted 12 April 2018
Available online xxxx

Editor: Charlotte Poschenrieder

Keywords:
Aggregate-size fractions
Fertilization
Bacterial community
Fungal community

ABSTRACT

Soils, with non-uniform distribution of nutrients across different aggregate-size fractions, provide spatially heterogeneous microhabitats for microorganisms. However, very limited information is available on microbial distributions and their response to fertilizations across aggregate-size fractions in agricultural soils. Here, we examined the structures of bacterial and fungal communities across different aggregate-size fractions (2000–250 μm, 250–53 μm and <53 μm) in response to 35-years organic and/or chemical fertilization regimes in the soil of northeastern China by phospholipid fatty acid (PLFA) and high throughput sequencing (HTS) technology. Our results show that larger fractions (>53 μm), especially 250–53 μm aggregates, which contain more soil C and N, are associated with greater microbial biomass and higher fungi/bacteria ratio. We firstly reported the fungal community composition in different aggregate-size fractions by HTS technology and found more Ascomycota but less Zygomycota in larger fractions with higher C content across all fertilization regimes. Fertilization and aggregate-size fractions significantly affect the compositions of bacterial and fungal communities although their effects are different. The bacterial community is mainly driven by fertilization, especially chemical fertilizers, and is closely related to the shifts of soil P (phosphorus). The fungal community is preferentially impacted by different aggregate-size fractions and is more associated with the changes of soil C and N. The distinct responses of microbial communities suggest different mechanisms controlling the assembly of soil bacterial and fungal communities at aggregate scale. The investigations of both bacterial and fungal communities could provide a better understanding on nutrient cycling across aggregate-size fractions.

1. Introduction

Soil is usually composed of a wide range of soil aggregate fractions which are assembled by mineral particles and organic matter (Tisdall

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https://doi.org/10.1016/j.scitotenv.2018.04.168
0048-9697/

and Oades, 1982). The physic-chemical conditions within aggregates differ from those prevalent in the bulk soil and different size aggregates (Rillig et al., 2017). Macroaggregates (2000–250 μm) normally contain more labile substrates predominantly derived from plant residues, whereas clay particles are dominated by a high degree of humification of organic matter (Six et al., 2000; Bronick and Lal, 2005; Ying et al., 2017; Zhang et al., 2017a). The different aggregate-size fractions provide spatially heterogeneous habitats for microorganisms, which are characterized by differences in resource availability, moisture content, oxygen concentrations and predation pressure (Ranjard and Richaume, 2001; Jiang et al., 2013; Vos et al., 2013). The differences in microbial communities across different aggregate size fractions are expected to be closely related to biological- and biochemical-mediated transformations of organic matter and soil nutrients, such as C decomposition and storage (Smith et al., 2014; Trivedi et al., 2017), nitrification (Zhang et al., 2017b) and phosphorus cycling (Jiang et al., 2017). On the other hand, soil microbiota also play important roles in the formation and stability of aggregates (Lehmann and Rillig, 2015). Besides the physical effects of enmeshment of macroaggregates (2000–250 μm) by fungal hyphae, extracellular polysaccharides can be produced by hyphae and bacteria, attaching microaggregates (250–53 μm), binding clay and silt (<53 μm) and increasing interparticle cohesion (Ritz and Young, 2004; Daynes et al., 2012; Tisdall et al., 2012). However, the investigation of microbial communities and activities within aggregate size fractions has been poor albeit their essential roles in soil biogeochemical cycling, maintenance of soil fertility and sustainable agriculture.

Fertilization is widely used to improve soil fertility and crop yield across a globe scale. Soil microbes play an important role in maintaining soil productivity through biochemical processes such as residue decomposition and nutrient recycling (Ling et al., 2016). Soil microbial communities are sensitive to fertilization and their responses to manure and/or mineral fertilizers in bulk soils have been well studied over the past years (Lazcano et al., 2013; Hartmann et al., 2015; Suleiman et al., 2016; Fu et al., 2017). The influences of fertilization on soil microbial diversity may be caused by direct effects of nutrient content, or indirect changes in soil and plant properties (Bell et al., 2015). Previous studies indicated that long-term chemical fertilization could observably decrease soil pH which is closely associated with the deceases in bacterial diversity and significant changes in bacterial community composition, while livestock manures could prevent soil acidification and its effects on soil bacteria (Sun et al., 2015). A fertilization experiment in red soil of south China suggested that organic fertilization and fallow management support eutrophic ecosystems with higher intensity of labile-C-degrading genes, while long-term application of nitrogen-containing chemical fertilizers sustain oligotrophic ecosystems with more recalcitrant-C-degrading genes (Xun et al., 2015). Network analysis demonstrated that long-term organic amendments exhibit stronger functional potentials and more interactions within soil community relative to chemical fertilization (Ling et al., 2016). However, most investigations have been conducted on a bulk soil scale. Information is scant regarding soil aggregates on microbial community in agricultural soils subject to long-term fertilization.

Few studies with respect to microbial communities within soil aggregates by phospholipid fatty acid (PLFA) analysis revealed contrasting results in their spatial distribution, community members and nutrient cycles. Some studies reported decreased fungal abundance and fungi/bacteria ratio with decreasing particle size (Poll et al., 2003; Briar et al., 2011; Smith et al., 2014), whereas others found no changes among soil physical fractions (Huygens et al., 2008; Zhang et al., 2016). The contrasting results require further studies to examine heterogeneous distribution of soil microbial community. Furthermore, the development of high throughput sequencing (HTS) technologies has allowed information about soil microbial communities to be obtained at a much finer taxonomic resolution (Smets et al., 2016). Recently study using HTS methods explored the spatial distribution of bacterial community within different aggregate-size fractions and found that effects of management practices on soil C is modulated by soil aggregate sizes and their associated bacterial community (Trivedi et al., 2017). However, much less attention has been paid on the composition of fungal community and their contribution to nutrient cycling within different particle-size fractions.

Therefore, in this study, both PLFA and HTS methods were conducted to explore the responses of soil bacterial and fungal communities within different soil aggregates to 35-years chemical or/and organic fertilization in the Black soil of northeast China. Since large aggregates commonly have more plant residual C and larger pore size which are known to favor fungal colonization, we hypothesized that 1) the total microbial biomass and ratio of fungi to bacteria could be higher in macroaggregates and microaggregates than in silt + clay; 2) the fungal community composition was mainly driven by aggregate-size fractions. We also explored the effects of aggregate-size fractions and fertilization regimes on bacterial community compositions. Finally, we determined the driving factors for the changes in soil bacterial and fungal communities associated with soil aggregates which could be helpful for a better nutrient management of agricultural soils.

2. Methods and materials

2.1. Site description and experimental design

The long-term field fertilizer experiment was located in Harbin, Heilongjiang Province, China (45°40′N, 126°35′E). The rotation system of wheat-soybean-maize has been established in this station since 1980, and maize was planted in 2015. The soil is a typical Black soil (Mollisol according to USDA classification) with the texture of clay loam. This region has a typical monsoon climate, with a mean annual temperature of 3.5 °C, annual evaporation of 1315 mm and annual precipitation of 575 mm. Four treatments with three replicates were randomly implemented in 12 plots (36 m^2 each). Treatments consisted of no fertilizer (control, CK), organic manure (M), fertilizer N + P + K (NPK) and organic manure plus fertilizer N + P + K (MNPK). Dosages of inorganic fertilizers were 150 N (all in kg ha^{-1}), 75 P_2O_5 and 75 K_2O for wheat and maize plots; and 75 N, 150 P_2O_5 and 75 K_2O for soybean plots. The N, P and K were applied as urea, calcium superphosphate, and potassium sulfate, respectively. Horse manure was the organic amendment applied at approximately 18,600 kg ha^{-1} for M and MNPK treatments in maize plots.

2.2. Soil sampling and particle-size fractionation

Soil samples were collected from 6 soil cores at a depth of 0–20 cm for each plot (4 treatments × 3 replications) in July 2015. The fresh >soils were passed through an 8 mm sieve by gently breaking up soil clods along natural planes of weakness. The aggregate was fractionated using a wet sieving method (Elliott, 1986). A series of sieves were used aggregate-size fractions: (i) 250–2000 μm (macroaggregates); (ii) 53–250 μm (microaggregates); (iii) <53 μm (silt + clay fractions). Briefly, fresh soils were submerged in deionized water for 5 min, then aggregates were separated by manually moving the sieve up and down about 3 cm in water for 50 times during a 2 min period. The separated aggregates were used for various chemical, PLFA and molecular analysis. The samples for PLFA and molecular analysis were freeze-dried and then stored at −80 °C. Those samples for soil chemical analysis were dried at 50 °C for 24 h and stored at room temperature.

2.3. Soil geochemical factors

Soil pH was determined at a soil/water ratio of 1:2.5 (w/v) by using a pH meter. Total carbon (TC) and total nitrogen (TN) contents were