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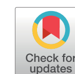
Soil aggregates regulate the impact of soil bacterial and fungal communities on soil respiration



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A R T I C L E I N F O

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A B S T R A C T

Soil aggregate size significantly impacts microbial communities and soil respiration. Soil total porosity and pH can regulate the distribution of soil bacteria and fungal communities within aggregates, thereby influencing soil respiration. However, it is unclear how it affects the microbial community composition distributed in soil aggregates, especially for fungal communities. The roles of soil total porosity and pH in controlling the microbial composition of soil aggregates are also unknown. In this study, we used high-throughput sequencing of the 16S rRNA and ITS gene regions to target bacterial and fungal members of aggregate samples of four sizes (2–4 mm, 1–2 mm, 0.25–1 mm and < 0.25 mm). Our results showed that high respiration occurred in soil aggregates of 2–4 mm and 1–2 mm when there was high soil total porosity and low soil pH than in aggregates of 0.25–1 mm and < 0.25 mm. Moreover, soil aggregates of 2–4 mm and 1–2 mm were dominated by four bacterial families (*Oxalobacteraceae*, *Sphingomonadaceae*, *Cytophagaceae* and *Gemmatimonadaceae*) and two fungal families (*Lasiosphaeriaceae* and *Rhizophlyctidaceae*), while the 0.25–1 mm and < 0.25 mm aggregates were dominated by two bacterial families (*Bacillaceae* and *Clostridiaceae*) and one fungal family (*Nectriaceae*). Our results suggest that soil organic carbon and total porosity positively influenced the bacterial Shannon index, which led to a further positive influence on soil aggregate respiration, while soil pH positively affected the soil fungal Shannon index, leading to increased negative control of the respiration of soil aggregates.

1. Introduction

Soil aggregates, which are composed of primary particles and binding agents, are the basic units of soil structure (Bronick and Lal, 2005). Soil aggregates are conventionally sub-divided into macro-aggregates (> 0.25 mm) and micro-aggregates (< 0.25 mm). Soil organic carbon (SOC) consists of various functional pools that are stabilized by soil aggregates (von Lutzow et al., 2007). Generally, SOC mineralization (soil respiration) in macro-aggregates is higher than that in micro-aggregates (Fernandez et al., 2010; Noellemeyer et al., 2008; Rabbi et al., 2014). However, respiration of soil macro-aggregates is reportedly lower than (Drury et al., 2004), or the same as (Razafimbelo et al., 2008), that of micro-aggregates. Moreover, our latest study revealed that soil respiration in 1–2 mm aggregates is higher than that in other sized aggregates (Yang et al., 2017). Currently, the only explanation for this is that the 1–2 mm aggregates contain the highest microbial biomass (Jiang et al., 2011).

Soil aggregates provide different habitats (such as aerobic and anaerobic micro-sites) that are required to support the activities of a diverse microbial community (Gupta and Germida, 2015). The use of a biochemical phospholipids fatty acid analysis (PLFA) technique (Davinic et al., 2012; Helgason et al., 2010) has helped to describe the spatial stratification of microbial populations between different aggregate size classes. Some studies have reported that microbial biomass and activity can be higher in macro-aggregates (> 0.25 mm) (Helgason et al., 2010; N. Li et al., 2015; Zhang et al., 2015) but also concentrated in micro-aggregates (< 0.25 mm) (Jiang et al., 2013; Zhang et al., 2013). Similarly, Wang et al. (2017) recently reported that microbial PLFAs are higher in > 2 mm and 0.25–1 mm aggregates but not 1–2 mm aggregates. These findings make it difficult to explain why soil respiration in macro-aggregates is higher than that in micro-aggregates, and the limited taxonomic resolution of this PLFA technique did not allow us to identify the specific microbial groups that shift in abundance across the aggregate sizes (Rousk et al., 2010). Most studies have used cloning and sequencing analyses to focus on the bacterial communities of aggregates (Gupta and Germida, 2015). However, macro-aggregates are generally considered to be dominated by fungi (Frey, 2005), and we know very little about their fungal community dynamics.

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Furthermore, it is still not known how the distribution of bacteria and fungi in different aggregates regulates soil respiration at the aggregate-size scale.

Soil microbial communities are influenced by various environmental factors, including SOC (Carney et al., 2007; Deng et al., 2016; Don et al., 2017; Spohn et al., 2016), pH (Bartram et al., 2014; Joa et al., 2014; Rousk et al., 2010; Shen et al., 2013; Tripathi et al., 2012; Xiong et al., 2012), electrical conductivity (Ma et al., 2016; Min et al., 2016), soil texture (Girvan et al., 2003; Lauber et al., 2008), and salinity (Lozupone and Knight, 2007). Soil pH is a primary factor controlling bacterial diversity and its community composition (Shen et al., 2013; Xiong et al., 2012); however, most previous studies have focused on the effects of soil pH on soil bacterial communities, while ignoring soil fungi. In addition to soil pH, soil total porosity, which is the best indicator of soil structure quality (Pagliai and Vignozzi, 2002), can also influence soil microbial communities. However, no related studies have been conducted to date. Additionally, investigations of soil total porosity under different tillage treatments currently comprise a hotspot in tillage research (Tangyuan et al., 2009), but it is still not clear how soil total porosity regulates microbial composition and diversity, especially in no-tillage grassland systems.

The objectives for this study were (i) to identify differences in physicochemical properties of soil aggregates, especially soil respiration, total porosity and pH; (ii) to directly compare the variability in bacterial and fungal communities in different-sized soil aggregates; and (iii) to identify the internal factors that influence soil aggregate respiration by analyzing both soil physicochemical properties and soil bacterial and fungal communities. To accomplish this, we used Illumina MiSeq high-throughput sequencing of the 16S rRNA gene and the internal transcribed spacer (ITS) gene region to target the bacterial and fungal members of each size of soil aggregate sample.

2. Materials and methods

2.1. Soil sample and aggregate preparation

The soil in this study was collected from a large plot (5 m × 5 m) of natural grassland located in Guyuan National Grassland Ecosystem Research Station in the agro-pastoral transition region of northern Hebei Province in China (41°46′ N, 115°41′ E, elevation 1380 m) in May of 2016. The site has a calcic-orthic Aridisol soil with a loamy-sand texture (Yang et al., 2017).

The top layer (0–15 cm) of soil was quickly transported to the laboratory, where plant roots and leaves were carefully removed by hand, after which the soil were spread in a thin layer and air-dried. The dried soil was sieved to separate large macro-aggregates (2–4 mm), macro-aggregates (1–2 mm), meso-aggregates (0.25–1 mm) and micro-aggregates (< 0.25 mm). The method used for aggregate size separation was dry sieve according to Elliott (1986) and Tian et al. (2015). The moderate undisturbed soil was shaken through four sieves (4, 2, 1 and 0.25 mm) for 2 min. We removed the > 4 mm soil because there were few of these aggregates in grassland soil. Thereafter, the large macro-aggregates (2–4 mm) were collected from the 2 mm sieve, macro-aggregates (1–2 mm) from the 1 mm sieve, meso-aggregates (0.25–1 mm) from the 0.25 mm and micro-aggregates (< 0.25 mm) passed through the 0.25 mm sieve (Tian et al., 2016). Some basic characteristics of the soil aggregates are shown in Table 1. Soil pH was determined after shaking a soil water (1:2.5 wt/vol) suspension for 30 min. Soil organic carbon (SOC) concentration was measured using an auto-analyzer (TOC, Elementar, Germany), and Soil total N (TN) was measured using the FOSS Kjeltec 2300 Analyser Unit (FOSS, Hillerød, Sweden). Soil total porosity was calculated from bulk density and measured particle density (i.e., 2.65 g cm^{-3}) with the following equation:

$$\text{Soil total porosity} = \left(1 - \frac{\text{Soil bulk density}}{2.65}\right) \times 100\%$$

where soil bulk density was determined using oven-dried soils (Regelink et al., 2015). In brief, we choose three replicates of 500 g dry aggregates and undisturbed (CK) soil in 1000 mL jars, and adjusted the moisture content to 30%, the maximum field water capacity of soil. After standing for 24 h, a foil sampler with a volume of 100 cm^{-3} was used to obtain the samples, and drying at 105 °C for 24 h.

2.2. Soil aggregates incubation and respiration measurement

The air-dried soil samples (100 g dry weight) of each aggregate size class (2–4, 1–2, 0.25–1, and < 0.25 mm) and undisturbed soil (CK) were placed in a thin and loose layer on the bottom of 1000 mL jars. Each aggregate size and CK had three replicates. The moisture content was adjusted to 30%, the maximum field water capacity of soil in our study. The soil was then pre-incubated at 30 °C for five days to remove the flush of C mineralization caused by re-wetting (Wei et al., 2016).

The samples were then incubated in the dark at 25 °C for 24 h. Small vials with 5 mL of 1 M NaOH were placed in the incubation jars to trap CO_2 after adding distilled water to the soil. In addition, three incubation jars containing only NaOH were used as blanks to correct for the CO_2 trapped from the air inside the vessels. The soil respiration (μg CO_2-C g^{-1} soil day^{-1}) was estimated by titrating 2 mL of each trap and 2 mL 1 M $BaCl_2$ (1:1) with 0.1 M HCl and phenolphthalein indicator (1% w/v in ethanol) using a Digital Buret continuous E (VITLAB, Germany) according to Butterly et al. (2016). At the end of the incubation period, soil aggregate samples were collected immediately and stored at −20 °C for microbiological sequences. Although air drying of soil sample is not representative of the communities that originally existed in the soil, it can represent the difference in the distribution of microbes in our incubation conditions.

2.3. DNA extraction and PCR amplification

Genomic DNA was extracted from each soil aggregate sample with three replicates using an E.Z.N.A.® stool DNA Kit (Omega Bio-tek, Norcross, GA, USA) according to the manufacturer's instructions. The quality of extracted DNA was checked by 1% agarose gel electrophoresis and spectrophotometry (optical density at 260 nm/280 nm ratio). All extracted DNA samples were stored at −20 °C for further analysis. The V3–V4 hypervariable gene regions of the 16S rRNA and the fungal ITS gene regions were subjected to high-throughput sequencing by Beijing Allwegene Tech, Ltd. (Beijing, China) using the Illumina Miseq PE300 sequencing platform (Illumina, Inc., CA, USA). The V3–V4 regions of the bacterial 16S rRNA gene were amplified with the universal

Table 1
Physicochemical properties of total soil or aggregates.

Samples	Soil respiration (μg C g^{-1} soil day^{-1})	Soil total porosity (%)	Soil pH	SOC (g kg^{-1})	TN (g kg^{-1})	C/N	Proportion (%)
CK	17.31 ± 0.38d	50.40 ± 0.22d	8.32 ± 0.01b	11.80 ± 0.89b	1.53 ± 0.03c	7.96 ± 0.10a	–
2–4 mm	29.55 ± 0.28b	70.38 ± 0.19a	8.24 ± 0.01c	13.27 ± 0.09ab	1.67 ± 0.03bc	7.68 ± 0.06a	12.71 ± 1.07c
1–2 mm	38.58 ± 0.34a	63.86 ± 0.21b	8.21 ± 0.01c	11.87 ± 0.22b	1.73 ± 0.03b	6.75 ± 0.12b	5.76 ± 0.32d
0.25–1 mm	22.08 ± 0.31c	51.34 ± 0.07c	8.45 ± 0.01a	5.20 ± 0.23c	1.07 ± 0.07d	5.20 ± 0.14c	38.26 ± 1.49b
< 0.25 mm	16.44 ± 0.47d	48.41 ± 0.01e	8.28 ± 0.01b	14.17 ± 0.28a	1.90 ± 0.06a	7.83 ± 0.06a	42.09 ± 0.98a

The numerical values are the means ± standard errors. Different letters in columns indicate significant differences between aggregate size classes ($P < 0.05$).

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