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Soil aggregate size mediates the responses of microbial communities to crop rotation

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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 microorganisms play an essential role in the redistribution of soil aggregate sizes due to the micro-environmental changes. Yet, little is known regarding how individual microbial taxa within different-sized aggregates respond to agronomic practice. This study integrated physical, chemical, and molecular techniques (i.e., high-throughput DNA sequencing and qPCR) to assess the influence of corn-tobacco rotation on the soil microbial community at the soil microenvironment scale, i.e., within mega- (> 2 mm), macro- (0.25–2 mm) and micro-aggregate (< 0.25 mm) fractions. The soil samples (0–20 cm) analyzed in this study originated from corn and tobacco, which were cultivated under three different fertilization regimes. The results demonstrate that corn-tobacco rotation substantially impacted the distribution of aggregate sizes, and the shift in soil microbial communities associated with soil aggregates was related to changes in soil total carbon (TC), the C/N ratio and pH. The indicator microbial taxa (i.e., those were sensitive to crop rotation) varied with aggregate size. When compared with tobacco soil, the corn soil showed higher relative abundances of probably more copiotrophic taxa across large-sized aggregates, also with more bacteria in mega-aggregates and more fungi in macro-aggregates. Changes in total microbial communities associated with mega- and macro-aggregates in response to crop rotation were driven mainly by alterations in bacterial and fungal communities, respectively. Overall, the results of this study demonstrate that soil aggregate size strongly affected the microbial community composition on agricultural fields, promoting the differential responses between bacteria and fungi to crop rotation in specific size of aggregates.

1. Introduction

Soil microbial analyses are typically performed on whole-soil samples using methods that tend to homogenize variability, resulting in a loss of information regarding *in situ* species interactions and microbial niches. In contrast, examining aggregates of different size classes and stabilities separated from whole soils provides investigators with insight into relationships between distinct microbial assemblages and soil microhabitats. Physicochemical properties of aggregate fractions vary with aggregate size, which promotes distinct microbial niches within each aggregate [1–6].

Soil aggregate formation is a dynamic process, and the composition of the microbial community is assumed to be an important factor controlling this process [2,7,8]. Indeed, microorganisms modify their habitats by gathering soil particles around them, a behavior likely intended to create a more favorable habitat [9]. Microorganisms can also directly consume the organic binding agents that hold aggregates together, resulting in aggregate decomposition [10]. Current conceptual models of aggregate formation emphasize the mechanisms by which soil particles, plant roots and fungal hyphae hold together to form large soil fractions (> 0.25 mm), after which small fractions (< 0.25 mm) containing a large quantity of extracellular polymeric substances produced by microorganisms are released due to disaggregation of the larger aggregates [11–15]. The process of aggregate formation, which is an important regulator for soil organic matter (SOM) kinetics and soil fertility, is assumed to be closely linked to changes in microbial communities [16]. Aggregates of different size classes in soil create a composite of ecological niches differing in terms of physicochemical

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Table 1
Changes in the distributions of mega-, macro- and micro-aggregates between the corn and tobacco soils in a crop rotation experiment.

Crops	Aggregates			MWD (mm)
	Mega-aggregates (> 2 mm) (%)	Macro-aggregates (0.25–2 mm) (%)	Micro-aggregates (< 0.25 mm) (%)	
Corn	71.86 ± 5.29 B	27.34 ± 5.15 A	0.80 ± 0.26 A	1.75 ± 0.05 B
Tobacco	61.15 ± 3.42 A	37.18 ± 2.89 B	1.67 ± 0.64 B	1.65 ± 0.04 A

Note: Data presented are means ± sd (n = 12). Different uppercase letters within the same row indicate significant differences between corn and tobacco soils at $P < 0.01$(*t*-test).

properties which promotes the colonization of different microbial assemblages within each aggregate [2,8]. Different species of crops vary in their exudate composition, which may selectively recruit different soil microorganisms in the same soil [17]. Moreover, crop rotation can generate positive environmental impacts, specifically an increase in microbial diversity and fungal abundance [18–21], variations in which may be reflected in their associated aggregates [22]. In contrast to the detailed understanding of the effects of microbial activity on aggregate formation, little is known regarding how specific microbial taxa within different-sized aggregates respond to crop rotation, especially for fungi. A sufficient understanding of the biological factors affecting both aggregate formation and degradation will help in implementing agronomic practices to maintain good soil structure.

We used a unique experimental rotation system at a corn-tobacco rotation cropping experimental site in Guizhou Province, China, where corn and tobacco were separately grown on two adjacent fields with yearly rotation. We sampled soils under the two crops separately at a single time point, thereby eliminating phenological differences between the vegetation cover in different crop-planting seasons. Our aim was to determine whether the microbial (bacterial and fungal) communities under these two different crops are fundamentally distinct from each other and how yearly changes in microbial communities across all sizes of soil aggregates in the two crop soils related with yearly fluctuations in aggregate size distribution. We hypothesized that crop rotation would have a significant impact on soil aggregate size distribution and microbial community in aggregates and that the variability in the microbial community would be related to aggregate size distribution. Furthermore, we hypothesized that both bacteria and fungi in aggregates of different size classes would differ in their responses to crop rotation.

2. Materials and methods

2.1. Experimental layout and sample collection

The study was conducted at the Corn-Tobacco Rotation Cropping System Experiment site (26°52′24.8″N, 107°06′40.8″E), founded by the Tobacco Scientific Research Institute of Guizhou Province, China. The average precipitation at this site is 1197 mm $year^{-1}$, with an average temperature of 15.3 °C. The soil is classified as yellow mud soil with a clay loam texture (25.0% clay, 39.5% silt and 35.5% sand). The crop rotation experiment began in 2008 and consisted of two fields (#1 and adjacent #2) with four (145 $m^2 \cdot plot^{-1}$) plots each. Corn/tobacco rotations were conducted on the two fields with different initial crops. Tobacco was the initial crop in field #1, whereas corn was the initial crop in field #2. Seeds of flue-cured tobacco (*Nicotiana tabacum* L.) variety 'K326' and corn (*Zea mays* L.) variety 'Qianxing No. 4' were provided by Tobacco Scientific Research Institute of Guizhou Province. Tobacco was transplanted at the end of April and then completely harvested in September. Corn was sown at the end of May and harvested in September. A fallow period followed crop harvest. Different fertilization treatments, i.e., control without fertilizer (CK), nitrogen fertilizer (N), combined application of inorganic fertilizer (NPK) and combined application of inorganic fertilizer plus organic amendments (NPKM), were applied to the four plots in each field every year. The application rates of N, P and K were the same in all three of the treatments for each field. The fertilization schedules were 120–60-60 and 75-75-150 N-P_2O_5-K_2O kg·ha^{-1} for the corn and tobacco seasons, respectively. Cow dung compost (7500 kg· ha^{-1}) was applied uniformly in the NPKM treatment for both crops. Inorganic N, P, and K fertilizer was applied as urea, superphosphate, and potassium sulfate, respectively. Sampling was conducted in August 2015 from the four plots in each field. Three spatially distinct intact soil blocks (each composed of five soil samples (0–20-cm depth) collected along each sub-plot) were collected from each plot using a shovel after the removal of surface residues. These soil blocks were separately placed in rigid plastic boxes, stored at approximately 4 °C, and transported to the laboratory.

2.2. Aggregate fractionation

Soil aggregate samples, including mega-aggregates (> 2 mm), macro-aggregates (0.25–2 mm) and micro-aggregates (< 0.25 mm), were obtained using an Endecotts Analytical Sieve Shaker Type OCTAGON200 (Endecotts Ltd Technology, London, UK) based on the modified dry-sieving method described by Bach and Hofmockel [23] (see Methods S1 for detailed descriptions). A portion of each sample was saved and immediately stored at −20 °C for DNA extraction; the remainder was kept at 4 °C for physical and chemical analyses. The mean weight diameter (MWD = Σ (percentage of sample weight on sieve × the mean diameter of the size classes)) was calculated to determine changes in soil structure due to crop rotation, and a high MWD value indicated high stability of soil structure and a high proportion of large-sized soil aggregates.

2.3. Soil chemistry and microbial enzyme activity analyses

Soil total carbon (TC) and nitrogen (TN) contents were measured by direct combustion using a Vario EL III Element Analyzer (Elementar Analysensysteme Co., Hanau, Germany). Soil pH and electric conductivity (EC) were determined from aqueous suspensions of the soil samples (1:5, w/v, soil/water ratio) using a pH meter (PE-10, Sartorious, Germany) and a conductivity meter (MP515-02, SANXIN, China), respectively. Microbial hydrolytic-enzyme (i.e., including esterase, protease, lipase, etc.) activity was measured using a fluorescein diacetate (FDA) assay based on the method of Green et al. [24], with slight modification (see Methods S2 for detailed descriptions).

2.4. Biomolecular analysis

Soil DNA was extracted from fresh soil using PowerSoil DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, USA) according to the manufacturer's instructions. The extracted DNA was quantified and assessed for purity (ratio of A260/A280) using a spectrophotometer (NanoDrop, 2000, Thermo Scientific, USA). All DNA samples were diluted to 10 ng·μl^{-1} and stored at −80 °C for subsequent molecular analysis. Primers 338 F (5′-CTCCTACGGGAGGCAGCA-3′) and 806 R (5′-GGACTACHVGGGTWTCTAAT-3′) [25] and primers ITSF (5′-GCATCGATGAAGAACGCAGC-3′) and ITSR (5′-TCCTCCGCTTATTGATA

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