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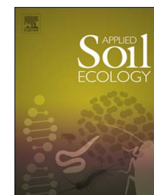

Shifts in microbial communities with increasing soil fertility across a chronosequence of paddy cultivation in subtropical China

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A B S T R A C T

An understanding of microbial community assembly and succession are keys to uncovering mechanisms underlying soil fertility development. The dynamics of microbial communities during a paddy soil chronosequence were investigated by phospholipid fatty acid profiling and amplicon high throughput sequencing. The upper 20 cm were sampled from soils after 5, 15, 30 and 100 years of paddy use and from adjacent barren land. Enzyme activities and contents of soil organic carbon, nitrogen and phosphorus of paddy fields strongly increased compared to barren land, and continued to increase at least up to 100 years of paddy cultivation. The increasing soil trophic status favored bacteria over fungi, and fast-growing copiotrophic bacteria gradually replaced slow-growing oligotrophic bacteria. The genus *Ignavibacterium* with versatile metabolism was identified as an indicator of the bacterial community in year 30 and 100. The variations of bacterial α-diversity tended to stabilize, but species richness continued to increase after 30 years of paddy use. The β-diversity indicated that bacterial community structure in paddy fields differed from that in barren land. The soils of 5 and 15 years of paddy cultivation clustered into one group separated from the group formed from the year 30 and 100. Redundancy analysis indicated that two stoichiometric ratios: C/N and C/P were the major factors affecting microbial community succession. We conclude that long-term paddy cultivation resulted in changes in biochemical properties and variations in trophic pattern of microbial communities, corresponding to increasing soil fertility.

1. Introduction

Paddy soils are anthropogenic soils (Antrosols or Technosols according to WRB 2014) and are a major resource for food production. Important pedogenic processes and transformations associated with anthropogenic activities have been identified and are well described concerning paddy soil genesis (Chen et al., 2011; Cheng et al., 2009; Kogel-Knabner et al., 2010; Wang et al., 2015). During the process of paddy cultivation, soil fertility evolution is defined as change in the ability of a soil supplying nutrients to crops (Shang et al., 2014). Soil fertility is mainly regulated by plants and microorganisms (Hartman et al., 2008), and in turn soil properties are the major factor shaping microbial communities (Cline and Zak, 2015; Cui et al., 2012; Wang et al., 2015). However, it is hard to disentangle the relationship between nutrient accumulation and microbial community succession during paddy soil development.

Most previous studies have reported the profiles of soil properties at a given stage of paddy cultivation, and this may conceal the dynamics of soil development (Su et al., 2015). Chronosequence approach provide insight into the rates and directions of soil ecosystem evolution spanning multiple time-scales due to the advantage of space-for-time substitution (Jangid et al., 2013; Jones et al., 2009). The phyla *α-Proteobacteria* and *Verrucomicrobia* are major indicators for two stages of bacterial community succession in paddy soils: a rapid-succession with clear increases in bacterial diversity within the first several decades and thereafter, a long gradual-succession stage lasting for centuries (Cui et al., 2012). Many researchers have depicted the dynamics of soil microbial community succession along chronosequence, and have

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provided various explanations for these successions (Dini-Andreote et al., 2014; Jones et al., 2009). The shifts in bacterial communities were closely aligned with ecosystem development, pedogenesis and vegetative succession (Jangid et al., 2013). Distinct ecological niches are common for soil bacteria, which were suited for either fast-growing copiotrophic bacteria or slow-growing oligotrophic bacteria (Cederlund et al., 2014).

Numerous factors contribute to the succession of microbial communities, including soil nutrients, soil type, vegetable coverage and management (Cederlund et al., 2014; Girvan et al., 2003; Lauber et al., 2009; Sul et al., 2013). The shifts in the soil physical structure, as well as variations in pH and salinity predominate in bacterial community temporal succession in an undisturbed salt marsh chronosequence (Dini-Andreote et al., 2014). It remains unclear what are the main factors controlling the dynamics of microbial community succession in soil under long-term paddy cultivation.

The mechanism underlying the microbial community succession in distinct soil types might be inconsistent (Cline and Zak, 2015; Dini-Andreote et al., 2014; Huang et al., 2015). So, it is necessary to fully explain soil fertility evolution in a particular soil type to provide instructive guidance for paddy cultivation. In subtropical China, paddy soils derived from Quaternary red clay are generally deficient in available nutrients, and fertilization is always used to increase fertility (Li et al., 2000; Zhong and Cai, 2007). Most studies have reported the role of soil nutrient accumulation with the duration of paddy cultivation, but only few have assessed the successional patterns of microbial communities along paddy chronosequence (Cheng et al., 2009; Han et al., 2015).

We investigated soil microbial community evolution along a paddy chronosequence. For this purpose, four distinct paddy fields and adjacent barren land were identified: estimated as 0, 5, 15, 30 and 100 years of cultivated paddy soil from subtropical China. We hypothesized that soil nutrients were predominant in shaping microbial communities along the paddy chronosequence. We expected that oligotrophic phylotypes would dominate the initial stage of succession (0–15 Years) and be gradually replaced by copiotrophic bacteria during later succession (30–100 Years) with higher soil organic matter (SOM) levels. To validate this, the soil fertility conditions were quantified using nutrient contents: carbon (C), nitrogen (N), phosphorus (P) and potassium (K). Phospholipid fatty acid (PLFA) analysis was used to evaluate the soil microbial community succession along the paddy chronosequence. The 16S rRNA genes were used to identify bacterial community succession along the soil chronosequence. The activities of enzymes β-xylosidase (βX), β-glucosidase (βG), *N*-acetyl-glucosaminidase (NAG) and acid phosphatase (AP) were used to reflect the potential of SOM decomposition because these enzymes integrate information about microbial activity and physicochemical conditions (Blagodatskaya et al., 2016; Razavi et al., 2015; Sinsabaugh et al., 2014, 2008).

2. Materials and methods

2.1. Site description

An investigation was conducted at the Ecological Experimental Station of Red Soil in Yujiang County of Jiangxi Province, China (28°15′30″N, 116°55′30″E). This region is a typical subtropical monsoon climate with mean annual temperature of 17.6 °C and annual precipitation of 1795 mm. The sample plots were several hundreds of meters apart and were originally barren land that were used to cultivate double-cropping rice (*Oryza sativa* L.) over various periods of time spanning one century. All field plots had identical water and fertilizer managements: the plow horizon extended to 17–25 cm depth; routine irrigation and chemical fertilizers (all in kg ha^{-1}: 79 N, 79 P_2O_5 and 79 K_2O) were applied in each growing season; and straw of early rice was incorporated into soil after harvesting (Li et al., 2005). Ages of the 15-, 30- and 100-year soils were checked with published literature (Li et al., 2005, 2003). Ages of the 5-year soil were identified based on historical information with much help from experienced local experts. Each paddy chronosequence and the adjacent barren land consisted three field plots selected at random from local region.

2.2. Soil sampling and analyzing chemical properties

Each sample consisted five surface soil (0–20 cm) cores collected at randomly from each field plot. All soils were derived from Quaternary red clay. After removing root debris, each bulk sample was shock-frozen in a dry ice box and transported to the laboratory. One portion of each sample was freeze-dried and stored at −80 °C for PLFA and amplicon high throughput sequencing analyses and the other portion was stored at field moisture content at 4 °C for later determination of enzyme activities and microbial biomass C. The air-dried at room temperature was prepared for chemical analysis.

The chemical properties of soils were determined using the conventional methods described by Lu (1999). Soil pH was assayed using a pH meter (FE30, Mettler-Toledo, CH) with 1:2.5 soil:water suspension. Soil organic C (SOC) was determined by $K_2Cr_2O_7$—H_2SO_4 oxidation. Total and available N were measured as Kjeldahl-N; total P and available P were assayed by HF–$HClO_4$ digestion and sodium bicarbonate extraction (molybdenum blue method), respectively; total K and available K were determined by HF-$HClO_4$ digestion and ammonium acetate extraction (flame photometer), respectively.

2.3. Soil enzyme activity assays

The activities of βX, NAG, βG and AP were quantified fluorometrically using MUB-linked substrates: 4-MUB-β-D-xylopyranoside, 4-MUB-*N*-acetyl-β-D-glucosaminide, 4-MUB-β-D-glucoside and 4-MUB-phosphate, respectively (DeForest, 2009; German et al., 2011; Saiya-Cork et al., 2002). First, soil suspension was prepared by adding 1 g of fresh soil to 125 mL of 50 mM acetate buffer (pH 5.0) and homogenized for 2 min with an OMNI mixer (OMNI, LA, USA). Next, 200 µL of soil suspension was added to wells that each contained 50 µL of 10-µM MUB (4-methylumbelliferone) solution, 200-µM MUB-linked substrate, and acetate buffer. They severed as sample assay, quench standard, and soil control. Then 200 µL of acetate buffer was dispended in wells that each contained 50 µL of MUB solution, substrate solution, and acetate buffer. They served as reference standard, substrate control, and blank control. The reaction mixtures were thoroughly mixed before incubating in darkness at 20 °C for 2 h. After incubation, 10 µL of 1.0 M NaOH solution was added to each well to stop the reaction. Fluorescence immediately was measured using a microplate fluorometer (SpectraMax i3x, Molecular Devices, CA, USA) with 365-nm excitation and 450-nm emission filters (Saiya-Cork et al., 2002). Absolute enzymatic activities were expressed in units of nmol h^{-1} g^{-1} and calculated by the following equations (DeForest, 2009):

$$\text{Activity}(\text{nmol h}^{-1}\text{g}^{-1}) = \frac{\text{Net fluorescence}\times 125\text{mL}}{\text{Emission coefficient}\times 0.2\text{mL}\times\text{Time(h)}\times\text{Soil mass(g)}} \tag{1}$$

where

$$\text{Net fluorescence} = \left(\frac{\text{Sampl eassay} - \text{Soil control}}{\text{Quenchcoefficient}}\right) - \text{Substratecontrol} \tag{2}$$

$$\text{Emission coefficient(fluorescence nmol}^{-1}) = \langle\text{H2}\rangle\langle\text{H2}\rangle\frac{\text{Reference standard}}{0.5\text{nmol}} \tag{3}$$

$$\text{Quench coefficient} = \frac{(\text{Quenchstandard} - \text{Soil control})}{\text{Reference standard}} \tag{4}$$

The 125 mL in the first equation refers to the volume of soil

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