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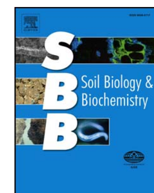

Soil pH correlates with the co-occurrence and assemblage process of diazotrophic communities in rhizosphere and bulk soils of wheat fields

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ABSTRACT

Biological nitrogen fixation contributes to the pool of plant-available N in both bulk soil and the rhizosphere. Here we investigated the co-association and assemblage process of diazotrophic community members in both rhizosphere and bulk soil of wheat fields. The diazotrophic community structure in the rhizosphere was significantly different and comprised a less competitive and more stable network structure when compared with that of the bulk soil. Deterministic versus stochastic community assemblage processes were quantified using betaNTI scores, demonstrating that deterministic processes decreased in importance with distance from plant roots. Soil pH was correlated with diazotrophic community structure and diversity, and community structure showed greater connectivity and stability in soils with neutral pH relative to those in acidic or alkaline soils. Stochastic processes dominated the assemblage of the diazotrophic community in soils with neutral pH, while deterministic processes dominated in acidic or alkaline soils. These results suggest that soil pH may play an essential role in the interaction and assemblage processes of the diazotrophic community in the rhizosphere and bulk soils, which could enhance our understanding of biological nitrogen fixation in agricultural soils.

1. Introduction

Biological nitrogen fixation (BNF) is one of the most significant steps of the nitrogen cycle in both ocean (Zehr et al., 1997, 2003) and terrestrial ecosystems (Orr et al., 2011; Silva et al., 2013; Zhou et al., 2016). In agricultural ecosystem, about 24% of nitrogen in crop biomass originated from non-symbiotic N_2 fixation (Ladha et al., 2016). Microorganisms capable of nitrogen fixation (diazotrophic organisms) that harbor the nifH gene have broad phylogenetic distribution (Zehr and McReynolds, 1989; Silva et al., 2013). Surveys of diazotrophic diversity have been conducted in a wide range of environments, including marine (Langlois et al., 2005; Turk et al., 2011), estuarine sediments (Affourtit et al., 2001), terrestrial geothermal springs (Hall et al., 2008; Hamilton et al., 2011), and terrestrial soils (Hamelin et al., 2002; Wang et al., 2017). Soil pH (Levy-Booth et al., 2014; Tu et al., 2016), soil organic matter (Wakelin et al., 2010; Gupta et al., 2014), soil moisture (Penton et al., 2016), and soil carbon: nitrogen ratio (Wang et al., 2017) have been shown to be dominant drivers of soil diazotrophic community structure. Collectively, these studies have revealed patterns in the distribution and diversity of diazotrophs in both natural ecosystems and agricultural bulk soils. However, diazotrophs often form close associations with the plant rhizosphere, which acts as a biological hotspot whose physicochemical properties differ substantially from the surrounding bulk soil (Philippot et al., 2013). While there have been studies of diazotrophic communities in the rhizosphere (Gupta et al., 2014), neither the physical nor chemical parameters that constrain the structure of diazotrophic communities within the rhizosphere of typical agricultural ecosystems have been examined.

In rhizosphere, plants exude organic compounds that support microbial activity near the roots, which, in turn, provide beneficial services to the plant (Dennis et al., 2010; Turner et al., 2013). A multistep model for root microbiome assembly from soil has been proposed and supported by research in rice (Edwards et al., 2015) and grapevines (Zarraonaindia et al., 2015). These studies have also shown that the composition of bacterial (Donn et al., 2015; Fan et al., 2017) and fungal (Zhang et al., 2017) communities varied significantly between rhizosphere and bulk soil, with bacterial diversity decreasing from the bulk soil towards roots. Co-occurrence networks provide evidence of the

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correlative changes in relative abundance between biomarkers, providing additional metrics to examine the relationships within the microbial community (Butland et al., 2005). Mendes et al. (2014) found a less complex network topology in rhizosphere when compared with bulk soil in a short-term plantation system. Similarly, Fan et al. (2017) detected a less complex, more hub based bacterial co-occurrence topology in the rhizosphere of the North China Plain. This reduced complexity supports the concept that the rhizosphere is a highly selective environment, which promotes specific taxonomic co-occurrences that could be indicative of reduced metabolic flexibility. One key metabolic process occurring within the rhizosphere is nitrogen fixation, and rhizospheric diazotrophs have wide ecological distribution and adaptability, While nitrogen fixation is of particular interest for improving productivity of sugarcane (Fischer et al., 2012) and commercial crops such as corn, rice, and wheat (Okon et al., 1977; Revers et al., 2000; Venieraki et al., 2011), the composition and co-occurrence of diazotrophic membership in different root-associated compartments of agricultural soils remains largely unknown.

Microbial community structures are shaped by a combination of deterministic and stochastic processes (Ofiţeru et al., 2010). Deterministic community assembly results from the predictable filtering of species by both environmental and biotic conditions (Leibold and McPeek, 2006), while stochastic community assembly occurs through the essentially random processes of dispersal, birth, death, and drift (Bell, 2001). As habitat heterogeneity declines at smaller scales, especially towards a strong selective force (e.g. rhizosphere), a more apparent contribution of stochastic processes over deterministic factors will be presented at these scales (Legendre et al., 2009; Chase, 2014). However, the scale at which this apparent shift becomes relevant for microbial community composition is still unclear (O'Brien et al., 2016). Previous studies have explored the relative importance of stochastic versus deterministic microbial community assemblage processes between rhizosphere and bulk soil. For example, a soybean cultivation study demonstrated that microbial community selection in the rhizosphere occurred via deterministic niche filtering, while the bulk soil microbial community seemed to be controlled by stochastic processes (Mendes et al., 2014). Despite the ecological and economic impact of diazotrophs (Werner and Newton, 2005; Brink, 2016), no attempt has yet been made to determine whether these microbes follow similar rules of community assembly in agricultural systems.

The North China Plain is an important agricultural area in China, with a traditional long-term (about 40 years) wheat-maize rotation system (Chen et al., 2004). Wheat (*Triticumaestivum* L.) is one of the main grain crops globally, but productivity increases per year have slowed to 0.9% (Fischer and Edmeades, 2010) in response to issues with field management, diseases, and poor nitrogen nutrition. It is possible that targeted manipulation of nitrogen fixing microbial community could lead to a more environmentally and economically sustainable production systems. In our study, we collected soils across the North China Plain from three compartments: namely bulk soil, loosely bound soil, and tightly bound soil, providing a rough gradient of root proximity (Donn et al., 2015). Two hypotheses were proposed in the current study. First, the diversity and co-occurrence topology of the rhizospheric diazotrophic community will be simpler when compared to the bulk soil. Second, the rhizospheric diazotrophic communities will demonstrate deterministic assemblage processes when compared to the bulk soil.

2. Materials and methods

2.1. Sample collection

Nine sampling sites were chosen from the typical wheat planting fields by GIS map across a broad area (~800,000 km^2) (32° N ~ 38° N; 110° E ~ 118° E) on the North China Plain (Fig. S1; Table S1) with wheat-maize rotation. The soil type in most sampling sites were Epiaquepts, Haplustalfs, Humaquepts and Calciustepts according to soil taxonomy of the USA (Table S2). Samples were collected during the wheat filling stage (22nd −27th of May 2015). At each sampling site, five replicate locations were measured within a ~100 km^2 square plot. A group of ten to twelve wheat plants were extracted in every place by digging around the group to keep the root systems as intact as possible. Loosely bound soil samples were collected by gently shaking off the soil which lightly adhered to the root, and the tightly bound soil samples were collected by brushing the soil which tightly adhered to roots. The topsoil (0–15 cm), beside each group and ~50 cm away from plants, was collected using an auger corer as bulk soil (Fan et al., 2017). All samples were packed into polyethylene bags and shipped on ice packs (4 °C) to the laboratory. The soils were sieved through 2 mm meshes, handpicked to remove fine roots, residues, and stones. Each sample was then divided into two parts: one was stored at −40 °C for DNA extraction within two weeks, and the other one was stored at 4 °C for soil chemical analyses.

2.2. Soil physical and chemical analysis

Soil moisture was measured gravimetrically by drying 5 g fresh soil until the soil reached a constant weight. Soil texture was tested by using Laser Particle Sizer (LS13320) with air dried soil (Table S2). Soil for total carbon (TC), total nitrogen (TN), total phosphorus (TP) and total potassium (TK) analyses was air dried, sieved (1 mm mesh), determined by combustion (CNS-2000; LECO, St. Joseph, MI, USA). Soil pH was determined by pH monitor (Thermo Orion-868) with a fresh soil to water ratio of 1:5 (Table S3).

2.3. High throughput sequencing and bioinformatics analysis

A half gram of fresh soil was used for DNA extraction using the Power Soil DNA kit (MO BIO Laboratories, Carlsbad, CA, USA) following the manufacturer's instructions. Primers nifHF (5′-TGYGAYCCNAARGCNGA-3′) and nifHRb (5′-ADNGCCATCATYTCNCC-3′) (Gaby and Buckley, 2012) were used for amplification of the nifH gene. These amplified PCR products were sequenced on the Illumina MiSeq PE 300 platform. Sequences obtained from this research were submitted in the NCBI Sequence Read Archive (SRA) with accession number SRP 113262.

After sequencing, nifH nucleotide sequences were analyzed using the QIIME pipeline (http://qiime.sourceforge.net/) (Caporaso et al., 2010). The low-quality sequences that had a quality score < 20, contained ambiguous nucleotides, or did not match the primer and barcode, were removed. The remaining sequences were further converted to amino acid sequences using the FunGene Pipeline of the Ribosomal Database Project (Wang et al., 2013). Sequences whose translated proteins did not match the nifH protein sequence or that contained termination codons were discarded. The remaining sequences were aligned against the nifH gene database (Gaby and Buckley, 2014), and both failed and chimeric sequences were also removed. The remaining high-quality sequences were clustered into operational taxonomic units (OTUs) with UCLUST (Edgar, 2010) running in de novo mode at 95% amino acid similarity, and all singleton OTUs were deleted. As the nifH gene provides sufficient phylogenetic resolution (Pinto et al., 1995), it has been used frequently in ecological studies. A phylogenetic tree was estimated based on aligned representative sequences by using FastTree (Price et al., 2010).

2.4. Statistical analysis

SPSS20.0 was used to perform ANOVA, pairwise *t*-test and covariance analysis to calculate significant differences in the dominant microbial taxon composition, alpha diversity and soil variables. NMDS were performed for the diazotrophic community data by calculating the Bray-Curtis dissimilarity. The NMDS, SIMPER analysis and Mantel test

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