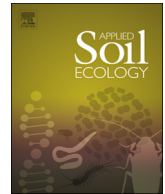




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Long-term phosphorus application to a maize monoculture influences the soil microbial community and its feedback effects on maize seedling biomass

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ABSTRACT

Both indigenous arbuscular mycorrhizal (AM) fungi and phosphate solubilizing bacteria (PSB) are involved in phosphorus (P) mobilization and turnover in agroecosystems. Understanding the diversity and community structure of AM fungi and PSB is important for potentially optimizing their role in mining P for sustainable agriculture. Yet the characteristics of both AM fungi and PSB in response to P input, in particular the influence of different indigenous microbial communities on plant growth has been little studied. Here, we collected soil samples from the top 20 cm of the profile of a soil receiving three fertilizer P rates, comprising nil, optimal (44 kg P ha^{-1}) and excessive (131 kg P ha^{-1}) P to evaluate the AM fungal community structure and abundance of relevant PSB groups at three sampling times (June, July and September) using 454 pyrosequencing and quantitative-PCR (q-PCR), respectively. In addition, a pot experiment was conducted to investigate the feedback effects of different fractions of indigenous soil microbes on maize seedling growth. The results showed that overall sampling time had a greater impact than P application rate on the community structure of AM fungi and PSB abundance. At each sampling time the AM fungal communities were significantly affected by the fertilizer P rate. The overall abundance of soil microbes and selected taxa were slightly affected by sampling time but not by fertilizer P. Shoot biomass and P nutrition were significantly affected by the microbial community fraction but not by the fertilizer P rate. Changes in AM fungal communities did not lead to significant differences in maize growth. However, long-term absence of P inputs tended to build up microbial communities which greatly suppressed maize growth. Shoot biomass showed a mean decline of 24.4% when grown in inoculated soil compared to sterilized soil. Our results indicate that current P management has not led to negative influences on soil microbial communities. Evidence highlights the need to understand the interactions between plants and microbiome in mining P in order to make maximum use of the most effective indigenous soil microbes for sustainable agriculture.

1. Introduction

The productivity of 30–40% of arable land globally is constrained by P supply (Von Uexküll et al., 1995). As P is poor in solubility and mobility in the soil due to the strong adsorption of P to iron and aluminum cations at low pH and calcium at high soil pH (Hinsinger, 2001), continuous provision of adequate P is essential to ensure adequate crop productivity in agroecosystems. In past decades large amounts of P fertilizer have been applied to intensive agricultural soils. For example, the consumption of chemical P fertilizers in China has increased approximately 100 times between 1960 (0.05 Mt) and 2010 (5.3 Mt) but crop yields have not increased at the same rate (Li et al., 2015). This has led to low P use efficiency (< 20%) and a high risk of severe eutrophication of surface waters (Sharpley and Tunney, 2000). On the

other hand, P rocks are non-renewable and finite resources, and the existing global P reserves are estimated to be likely depleted within 50–100 years (Cordell et al., 2009). China is now the largest producer of P rock (40% of total, 2013) and P cycling has been intensified. It is estimated that the remaining accessible high-quality Chinese phosphate rock reserves will suffice only until 2050 (Zhang et al., 2008), but more efficient P management might postpone the depletion of P reserves for > 20 years (Liu et al., 2016b). Integrated P management to increase P use efficiency and better exploit soil accumulated P resources is therefore imperative.

Soil microbes hold great promise for new management options to counteract excessive fertilization and increase P fertilizer use efficiency, leading to more environmentally-friendly agriculture (Adesemoye and Kloepper, 2009; Mauchline and Malone, 2017). Microbes are vital

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constituents of the rhizosphere and play key roles in the biogeochemistry of P. Microorganisms can directly (e.g. by alteration of sorption equilibria or through the induction of metabolic processes including the efflux of protons and organic anions or phosphatase activity), and/or indirectly (e.g. by extension of root systems due to mycorrhizal associations or increased root growth via hormonal stimulation) affect the capacity of plants to acquire P from the soil (Richardson and Simpson, 2011). In agroecosystems repeated application of mineral P fertilizer in the long term may directly or indirectly shift soil biological properties, in terms of both microbial community composition and functioning. The most intensively-studied soil microorganisms include arbuscular mycorrhizal (AM) fungi (Smith and Read, 2008). AM fungi interact with 80% of terrestrial plant species including the majority of agricultural crops (Brachmann and Parniske, 2006). The predominant role of AMF is attributed to increased host plant P nutrition in soils of low P status as a consequence of their high affinity P mechanisms (Smith and Read, 2008). The potential to incorporate the management of AMF as a 'green tool' and natural biofertilizer to maximize crop P use efficiency, reduce fertilizer P use and increase crop yields in reduced-input agroecosystems has been highlighted (Berruti et al., 2016).

Evidence from intensive agriculture indicates that root colonization by AM fungi in the topsoil is more responsive to P fertilization than the change in the AM fungi community in the subsoil (Wang et al., 2016). Root colonization rates in agricultural fields decreased under increased P fertilization (Balzergue et al., 2011; Wang et al., 2016) while the structure and abundance of the AM fungi community is relatively variable. P fertilization reduces, or has no effect on, AM fungal diversity in soil or roots. For example, P fertilizers (> 20 years) significantly decreased AM fungal diversity in an arable soil in north China (Lin et al., 2012). By contrast, the application of P fertilizers (50 kg P ha⁻¹ yr⁻¹) for 5 years had no significant influence on AM fungal community composition in a continuous maize field (Mathimaran et al., 2007). The community composition (but not the richness of AM fungi in maize roots) was significantly affected by P inputs (Wang et al., 2016). Mycorrhizal responsiveness and community structure in host roots may be more closely linked with plant P demand (Ryan et al., 2000) and phenology (Johnson et al., 2014) and the resource-trade relationships (C-P) among the symbionts (Kiers et al., 2011), and the soil AM fungal community may be relatively more responsive to soil P fertilization *per se* and corresponding changes in soil properties. Here, the question remains as to whether or not AM fungi communities at the optimal P supply rate in the soil pool are more comparable to those at nil or low fertilizer P inputs than those at excessive fertilizer P rates.

In addition to AM fungi, a large number of phosphate-solubilizing bacteria (PSB) demonstrate the capability to solubilize organic or insoluble inorganic P *in vitro* (Richardson and Simpson, 2011). In fact, PSB have long and widely been used as biofertilizers to increase soil P availability, although the success of inoculation is context-dependent. It remains to be elucidated whether P solubilization capability is a widespread and general trait of the soil microbial community which is independent of soil P status, or a trait linked to groups of soil taxa (Wakelin et al., 2012). Recent evidence shows that selection for P-solubilizing phenotypes *in vitro* were negatively correlated to soil P levels in three pastures of different fertilizer history, and the dominant taxa were *Pseudomonadaceae* and *Actinobacteria* (Mander et al., 2012). A molecular study shows that the overall soil microbial (bacterial and fungal) community was not significantly affected by soil P status, while *Actinobacteria* (but not *α-Proteobacteria* or *Pseudomonas*) communities were, and it has been suggested that this can be used as an indicator of a microbial P-solubilizing trait (Mander et al., 2012).

The selection pressure of long-term P fertilization on the soil microbial community may affect the functioning of the soil microbiome. Previous studies show that AM fungi from N- or P-deficient (71 years) soils grew larger but reduced barley growth to a greater extent compared to AM fungi isolated from non-deficient soils (Antunes et al.,

2012). Bainard et al. (2013) addressed differences in total soil microbial and AM fungal communities from conventional and tree-based intercropping agricultural systems. The results show that negative effects of the non-AM fungal microbes were stronger than the beneficial effects of the AM fungi in these cropping systems. The adaptation of soil microbes to P fertilization may strongly affect their feedback effects on plant growth. However, little is known about the relative importance of AMF and other soil microbial groups on crop growth after long-term P fertilization selection on soil microbial communities.

The present study was conducted at a long-term P fertilization experimental site on the North China Plain where excessive P fertilization has been reported (net average P surplus 53 kg ha⁻¹ yr⁻¹) (Vitousek et al., 2009). Hence, holistic investigations into soil microbial communities in response to P fertilization might allow us to better understand P cycling in cropping systems in order to predict effective P management strategies. We tested the hypothesis that long-term optimal P supply may sustain AM fungal diversity and functioning, which is comparable to that at nil P (selection towards mutualism), while high P supply reduces AM fungal diversity and reduces AM functioning (selection towards parasitism). The abundance of selected microbial taxa (*Firmicutes* and *Actinobacteria*) may be less responsive to P status due to strong carbon limitation (low soil organic carbon content) in the arable soil with inorganic P input. We also investigated the feedback effects of different microbial fractions on the growth of maize plants. We hypothesized that maize would be more responsive to the inoculation of soil microbes from optimal P supply relative to that at nil or excessive P supply.

2. Materials and methods

The present study comprised two experiments. The first was a field experiment in which we took advantage of an existing 8-year-old P fertilization trial with continuous maize monoculture. Soil samples were taken to analyze the AM fungal diversity and community composition and the abundance of PSB groups. The second was a pot experiment designed to assess the impacts of different fractions of the soil microbiome derived from different P rates on the yield and P uptake of maize.

2.1. Field experiment

2.1.1. Study site and experimental design

The study site was located at China Agricultural University's Shangzhuang Experimental Station, Beijing, China (39°59'N, 116°17'E). The climate is warm and sub-humid with an average annual temperature of 13.2 °C and precipitation ranging from 213 to 840 mm. The soil type is a calcareous alluvial soil with a silt loam texture typical of the region. The soil had a pH of 8.3 (1:5, soil: water suspension), contained 12 g kg⁻¹ organic carbon, 0.63 g kg⁻¹ total N, Olsen-P 3 mg kg⁻¹, 15 mg kg⁻¹ mineral N content (Nmin) and available K 110 mg kg⁻¹ (NH₄OAc-K). The experiment was a long-term P fertilizer trial which was established in 2007. The experiment was composed of a gradient of P fertilization with annual inputs of 0, 5, 11, 22, 33, 44, 66 and 131 kg P ha⁻¹ as calcium superphosphate. The soil received annual basal fertilizers (N and K) at rates of 225 kg N ha⁻¹ (as urea, 75 kg N ha⁻¹ each, before sowing, at elongation and silking stages, respectively) and 66 kg K ha⁻¹ (as potassium sulfate). An additional 66 kg K ha⁻¹ was top dressed at silking to meet the nutrient requirement for maize production. There are three replicate plots per treatment arranged in a randomized complete block design. Each plot has an area of approximate 35 m² (5 m × 7 m), and the layout of the experimental site was shown in Fig. S1. The field is plowed before sowing each year and was irrigated with a sprinkler a few days before sowing in the study year. The spring maize was planted in monoculture (M-M). The seeds (cv. Zheng dan 958) were sown in May 2014 at a density of 70,000 seeds ha⁻¹ with a row spacing of 60 cm and intra-row spacing

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