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Spatiotemporal differences in the arbuscular mycorrhizal fungi communities in soil and roots in response to long-term organic compost inputs in an intensive agricultural cropping system on the North China Plain

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Abstract

Purpose Fertilizer management is important for minimizing nutrient losses from intensive agroecosystems. An increasing amount of organic fertilizer has been applied to overcome the problems associated with mineral fertilizers. Thus, an understanding of the diversity and community structure changes in arbuscular mycorrhizal fungi (AMF) in response to long-term organic fertilizer management can be potentially significant in the development of nutrient management strategies.

Materials and methods Here, a study was conducted to investigate the vertical distribution of AMF in a calcareous field and the temporal structure of AMF in maize roots with different levels of continuous fertilization over a 13-year period. T-RFLP and clone library construction were used to investigate AMF community in this study. Canonical correspondence analysis was performed to determine the significance of environmental variable that may affect the AMF community composition.

Results and discussion Our results showed that the Shannon-Weiner and evenness indexes of soil AMF community decreased, while AMF richness was not significantly affected. Organic compost application reduced root colonization, while the negative influence of conventional inorganic fertilization was minor. The effect was significant at 13 leaf collar stage of maize. Crop phenology especially growth stages might override fertilizer supply in determining the community composition of active root inhabiting AM fungi. Significant differences in the community structure of soil AMF were observed between control and organic compost treatments in surface soil, and the community shift was primarily attributable to soil organic matter and nutrient contents (total nitrogen and carbon, Olsen-P, and exchangeable K). Vertical distribution of AMF was significantly related to soil electrical conductivity and pH values.

Conclusions Our results indicated that AMF community assemblage was complex and dependent on fertilization-mediated changes in soil properties, soil depth, and crop phenology. The modification of AMF communities by fertilization may have great impact on soil health and ecosystem services in intensive agroecosystems.

Keywords Arbuscular mycorrhizal fungi · Intensive agriculture · Maize · Long-term organic compost input · North China Plain

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1 Introduction

The application of inorganic fertilizers to agricultural soils has greatly increased in China over the past three decades, whereas it has tended to decrease in northwest Europe (Richter and Roelcke 2000; Ju et al. 2004). Farmers tend to increase the application rates of inorganic fertilizers or organic manures to overcome soil nutrient deficiencies and achieve higher crop yields on the North China Plain (NCP, Ju et al. 2005). Over the period 1980–2008, the crop yields (mainly maize and wheat) on the NCP increased by a factor of 2.8 (2200–6200 kg ha^{-1}), grain production increased by a factor of 2.6 (23–59 million tons), and the application rate of chemical fertilizers increased by a factor of 5.1 (68–350 kg ha^{-1}) (Pei et al. 2013). For example, the average amount of N applied over the winter wheat–summer maize cropping system cycle increased from 143 kg N ha^{-1} in 1967 to approximately 384 kg N ha^{-1} in 1988 and 670 kg N ha^{-1} in 2000 (Zhen et al. 2006). The excessive use of chemical fertilizers as an "insurance" for reliable yields leads to high soil productivity in most situations; however, it also causes severe environmental problems and soil degradation (Ueji and Inao 2001; Toshisuke et al. 2008). Excessive P inputs can result in severe eutrophication of surface waters (Zhang et al. 2004), while excessive N application leads to groundwater pollution caused by NO_3^--N (Zhu and Chen 2002; Ju et al. 2006), air pollution by N deposition (Liu et al. 2003), and soil acidification (Guo et al. 2010). Hence, appropriate nutrient management to increase the nutrient use efficiency and minimize damage on the environment is of strategic importance for the development of sustainable agriculture.

Recently, increasing interest has been focused on incorporating compost nutrient management into sustainable agricultural intensification in China (Chadwick et al. 2015). Low-input and organic agricultural systems are also considered as alternative solutions to conserve natural resources and reduce environmental degradation (Mäder et al. 2002). A wealth of data is available from long-term observation experimental sites in China and other countries (Ai et al. 2012; Maillard and Angers 2014), and these data show that the continuous application of NP fertilizer and organic materials, including straw (Lu et al. 2009) and compost (Rasool et al. 2008), significantly improves the crop yields and soil quality, particularly the soil organic matter (SOM) content (Demelash et al. 2014). Balanced fertilization, especially with the addition of organic compost, also changes the soil microbial community and enhances the efficient metabolism of microorganisms due to the increase of nutrient availability (Lin et al. 2012).

AM fungi (AMF) are members of Glomeromycotina, which form the most common and widespread terrestrial plant symbioses (Smith and Read 2008). They are believed to support plant growth by increasing the supply of immobile soil nutrients, notably P, enhancing the tolerance or resistance to soil pathogens and abiotic stresses and improving the soil structure (Helgason and Fitter 2009). AMF are often reported to play a vital role in nutrient-deficient natural ecosystems and also in low-put agriculture (Smith and Read 2008; Douds and Millner 1999). Meanwhile, positive and complex functions were observed in nutrient-rich agroecosystems (Liu et al. 2014, 2016; Oehl et al. 2017). The demand for certain nutrients in agricultural soils is reflected by changes in the AMF community composition or diversity (Lin et al. 2012). For example, it has been demonstrated that the use of inorganic fertilizer (e.g., N and P fertilizer) negatively affects AM abundance and diversity (Liu et al. 2012; Watts-Williams and Cavagnaro 2012). Such changes in community diversity give a level of functional redundancy (Powell and Rillig 2018). There are a number of factors that may cause this effect, excessive soil nutrient contents, change in soil pH, and to the indirect effect of fertilization on plant community and productivity (Liu et al. 2012). However, the responses of AMF and shifts in the community under such anthropogenic disturbances have not been thoroughly investigated and remain ambiguous (Rillig and Mummey 2006; Van Der Heijden et al. 2008). As a main substrate and energy source for microbes, organic manure application may indirectly affect the growth and composition of AMF by mediating soil microbial communities and activities (Yang et al. 2018). Organic sources of nutrients, such as farmyard manure, compost, and crop residues, differed in its components and decomposition properties and are shown to exert an unpredictable effect on AMF (Gosling et al. 2006). Organic manure can slowly release nutrients for plants and microbes and help in maintaining a medium-high nutrient availability (Scotti et al. 2016; Yang et al. 2017), which may benefit AM fungi. Although AM fungi are not saprotrophic fungi, some studies have shown that AM fungi can directly take advantage of organic matter (Govindarajulu et al. 2005). In addition, compost addition usually promotes plant growth and enhances carbon allocation to soil fungi (Donn et al. 2014), thus can indirectly affect AM fungi. Previous research showed that the application of manure or other organic fertilizers usually had positive effects on AM fungal diversity and modified the AM fungal community composition (Oehl et al. 2004). However, negative or neutral effect of compost addition on AM biomass and diversity was sometimes reported in field or greenhouse studies (Copetta et al. 2011; Cozzolino et al. 2016). In a review paper, Cavagnaro (2015) found that 8% of publications detected a negative effect of compost addition on AM root colonization. Most of these studies are based on independent short-term responses as well as mineral or organic fertilizer responses, which may cause biased and one-sided consequences.

In this study, because soil fertility degradation may occur with the replacement of organic fertilizers by inorganic fertilizers, a long-term experiment was set up at the Quzhou Experiment Station on the NCP. The NCP is one of the most

intensive grain-producing agricultural regions in China which has cultivated approximately 35 million ha of crops. The winter wheat–summer maize rotational cropping system is the dominant crop system (> 14 million ha) (Michalczyk et al. 2014). This system accounts for 50% of the national total yields of winter wheat and 33% of summer maize (Wang et al. 2012). Therefore, the crop yields and agricultural sustainability of the NCP have great implications for food security in China. We undertook a comprehensive comparison of the AMF response to long-term (13 years) fertilizer regimes, especially organic compost inputs, by using a T-RFLP method. The vertical distribution of the AMF community in soil and its temporal structure in maize roots under different fertilization regimes were also measured. Our aims were to investigate (1) the AM fungal community structure and diversity in a wheat/maize rotation field under different fertilizer regimes after 13 years and (2) the vertical distribution of soil AMF and the temporal structure of root AMF. The null hypothesis was that long-term organic compost application would result in distinct shift in AMF diversity and composition, and the alteration of AMF communities was closely associated with soil physicochemical properties, in particular, soil nutrient contents.

2 Materials and methods

2.1 Experimental field

The investigation was conducted at the long-term experiment site (from 1998) of China Agricultural University, which is located at the Quzhou Experimental Station, Quzhou County, Hebei Province, China (36°52′N, 115°02′E). The soil is typic fluvaquents (Soil Survey Staff 2014). The physical and chemical properties of the soil in the top 30 cm prior to planting were as follows: total N, 0.67 g kg^{-1}; Olsen-P, 5 mg kg^{-1}; exchangeable K, 74 mg kg^{-1}; organic matter content, 10.3 g kg^{-1}; and soil pH (1:2.5 soil/water, *w*/*v*), 8.5. The cropping system is a typical winter wheat–summer maize rotation. The field was plowed down to 20 cm. Winter wheat (*Triticum aestivum* L. cv. Liangxing 99) was planted in mid-October and harvested in mid-June; maize (*Zea mays* L. cv. Ne 15) was sown in mid-June and harvested in mid-October. The mean yields of wheat and maize were 6.5 and 8.0 t ha^{-1}, respectively. After harvest, the straw was removed from the fields. In this study, only samples collected in the maize season were investigated.

2.2 Experimental design

The experiment had a randomized complete block design with three replicates. The size of each plot was 8 m × 4 m. The planting density of maize was approximately 67,500 individual seeds per hectare, which had a 60-cm row width. This experiment consisted of four fertilizer regimes, namely, the control (CK, no fertilizer input), high organic compost input (High Org., traditional compost at 15000 kg ha^{-1} at maize season), low organic compost input (Low Org., 7500 kg ha^{-1}), and conventional chemical fertilization (Con. F., ammonium bicarbonate at 750 kg ha^{-1} (450 kg ha^{-1} in wheat season and 300 kg ha^{-1} in the maize season), urea 300 kg ha^{-1} (150 kg ha^{-1} in the wheat season and 150 kg ha^{-1} in the maize season), calcium superphosphate 750 kg ha^{-1} (450 kg ha^{-1} in the wheat season and 300 kg ha^{-1} in the maize season); ammonium bicarbonate and calcium superphosphate were fertilized in spring as basal fertilizers before sowing, and urea was applied as topdressing). The component of the traditional compost was 60% crop straw, 30% animal manure, 5% cottonseed cake, and 5% bran. Crop straw was cut into 3–5 cm and mixed homogenously with dry animal manure, cottonseed cake, and bran. The mixture was piled up and topped-sprayed with animal manure, afterwards covered with plastic cloth for fermentation. The temperature of the compost heap was maintained below 60 °C with a regular daily plowing of 1–2 times. The composting lasted for 30 days and ended when the C/N ratio < 20.

Before sowing, wheat straw was removed from the field, and all fertilizers were broadcast and mixed with the surface soil by disking before maize seeding. Irrigation, herbicides, and pesticides were used according to the local practice when necessary. Grain yield was determined by manually harvesting and drying (60 °C) ears from two rows per plot.

2.3 Soil and plant sampling

Soil samples were collected in October 2011 after the maize harvest, i.e., 13 years after the establishment of the experiment. Soil samples from different depths (0–20, 20–40, and 40–60 cm) were collected using a soil core sampler with a 3-cm internal diameter. Each plot was divided into four quadrants in each of which the soil samples were obtained. The four soil cores collected from each plot were mixed to generate one composite sample at each soil depth. The sieved (< 2 mm) soil samples were divided into two portions and were stored at − 20 °C for the molecular analysis and ambient temperature for the soil physicochemical property analysis, respectively.

Maize root samples were collected at growth stages V6 (6-leaf collar, 20 July, 32 days after sowing), V13 (13-leaf collar, 5 August, 48 days after sowing), and RS (kernel dough, 19 September, 93 days after sowing). Three maize plants were sampled along a transect at three sampling points with 1 m intervals. The shoots and roots were separated, and the roots of three maize plants from each plot were mixed to form a composite sample. Maize roots were excavated intact to a

depth of 40 cm, transported to the laboratory, washed thoroughly with distilled water, and cut into 1 cm segments. The root samples were divided into two portions similar to the soil samples, with one part stored at − 20 °C for molecular analysis and the other retained for the determination of AMF colonization indexes.

2.4 Soil and plant physicochemical properties

The physicochemical properties of the soil and plant samples were determined with conventional methods, including the glass electrode method for soil pH, the Dumas combustion method for total N, an electrical conductivity meter for soil electrical conductivity (EC), soil digestion with hot acid dichromate for soil organic matter (Bremner 1996), and 0.5 M $NaHCO_3$ extraction for available P (Olsen-P, Olsen et al. 1954). Detailed procedures and instrumental information can be obtained from previous studies (Liu et al. 2014, 2016). A Mehlich 3 solution extraction method was used for soil Na and Zn concentration determinations using inductively coupled plasma optical emission spectroscopy (ICP-AES, OPTIMA 3300 DV, Perkin-Elmer, Waltham, MA) (Mehlich 1984).

2.5 Assessment of AMF colonization, spore density, and hyphal length density

We used a classic Trypan blue staining method (Phillips and Hayman 1970), in which 30, 1 cm long, root segments from each sample were randomly selected and mounted onto microscope slides to determine the AMF colonization. The percentage of root length colonized by Glomeromycotina was quantified using the magnified intersection method with 200 intersections (McGonigle et al. 1990); other mycorrhizal indicators (root length colonization, %RLC; arbuscular colonization, %AC; hyphal colonization, %HC) were also determined. AMF spores in soil (2 mm sieved) were counted using the method described by Daniels and Skipper (1982). The hyphal length density was determined according to Jakobsen et al. (1992).

2.6 DNA extraction, amplification, and T-RFLP analysis

The frozen soil (0.5 g) was subjected to soil DNA extraction using a FastDNA Spin Kit for Soil (Bio101, Carlsbad, CA). Frozen maize roots (0.05 g, ground and homogenized with liquid nitrogen) were used for maize root genomic DNA extraction using a Fast Plant Kit (Tiangen, Beijing, China) following the manufacturers' instructions. The total DNA concentration in each soil and root sample was quantified spectrophotometrically using a NanoDrop ND-8000 (NanoDrop, Wilmington, DE). The fluorescently labeled primer pairs NS31-HEX/AM1-FAM (Dickie and FitzJohn 2007) and conventional NS31/AM1 (Helgason et al. 1998) were used to amplify the AMF SSU rDNA gene (~ 550 bp) for the T-RFLP analysis and subsequent clone-sequencing analysis. To overcome the inhibiting effect of the polysaccharide components in the roots on PCR amplification, a nested PCR procedure combining AML1 and AML2 (Lee et al. 2008; first PCR) was used for the root sample amplification. The PCR reaction system and thermal cycling conditions for the soil and root samples were performed as previously described (Liu et al. 2014, 2016).

The automated sequencer detected all fluorescent DNA fragments. If there is a strong secondary structure or partial digestion, a signal that does not correspond to a true T-RF can be detected. T-RFLP requires matching unknown T-RFLP profiles to a database of known T-RFLP patterns to identify which species or taxa are in a sample (Dickie et al. 2002). In the present experiment, we used the clone sequencing method to construct an AMF T-RFLP profile database. The restriction enzymes HinfI and Hin1II (both Promega) were used for PCR product digestion (Dickie and FitzJohn 2007), and detailed information on enzymic digestion can be found in our previous studies conducted in adjacent fields (Liu et al. 2014, 2016). We screened the T-RF fragments obtained in this study, and only those ranging from 45 to 450 bp with a minimum peak height of 50 relative fluorescent units (accounting for 1% of the total peak profile) were considered effective (Johnson et al. 2003). A clone-sequencing method was also used to construct the AMF T-RFLP profile database, which had a good correction effect for matching unknown T-RFLP profiles to identify the species or taxa in the samples.

2.7 Cloning, sequencing, and phylogenetic analysis

Only surface soil samples (0–20 cm depth) were used to construct the AMF T-RFLP profile database. The target length of the cloned region was ~ 550 bp, which encompassed part of the SSU rDNA gene. Twelve soil samples (4 fertilizer treatments, 3 replicates) were amplified, and the 3 replicated PCR products of each fertilizer treatment were pooled together to form one clone library. Four soil sample clone libraries of the AMF 18S rRNA genes were constructed to distinguish the identity of the T-RFs in this study. Cloning was conducted by the method of Liu et al. (2014), and purified PCR products were cloned into the pGEM-T Easy Vector System (Promega) following the manufacturer's instructions.

Ninety-six positive clones were randomly picked in each clone library using the blue/white screening method and sequenced by the ZhongKeXiLin Biotechnology Company (ABI 3730XL, Beijing, China), and a neighbor-joining tree was constructed based on 79–97 effective sequences. Reference sequences were obtained from the GenBank database. After sequencing, each positive clone was used as a

template for PCR amplification using fluorescently labeled primer pairs (NS31-HEX/AM1-FAM) and enzymic digestion for the T-RFLP analysis.

A ChromasPro software was used to simulate the enzymic digestion effects of HinfI and Hin1II on the AMF sequences. Unknown T-RFLP profiles were matched with the profiles of sequenced clones, and all T-RFs within 1.5 bp were required to be detected for a positive match. Only those T-RF profiles that matched sequenced clones were used. This step allowed us to conclude with confidence that all peaks taken into account were true T-RFs even when they were of low intensity.

Sequences were examined using a BLAST search (Altschul et al. 1997) to determine whether sequences were derived from Glomeromycota (http://www.ncbi.nlm.nih.gov/). Sequence groups and phylogenetic analyses were implemented using previously described methods (Liu et al. 2014, 2016). *Endogone pisiformis* (X58724) was used as outgroup, and the AM fungal sequences used in this study were submitted to GenBank under the accession numbers KY232314–KY232645.

2.8 Data analysis and statistics

Only those T-RFs that matched clone library sequences were defined as valid T-RFs, and the T-RF matrix was binary transformed using the presence/absence of individual T-RFs. Percentage of T-RFs was used for AMF community composition analysis in the soil and roots. The AMF community richness (S) was represented by the total number of T-RFs in each sample. One-way ANOVAs followed by Duncan's multiple range test were used to test for significant differences ($p < 0.05$) among the soil physicochemical properties and colonization and diversity indexes of the AMF, and two-way ANOVAs were used to analyze the main and interactive effects of different fertilization regimes and soil depth on each soil chemical property and AMF colonization. Significant differences among treatments in figures and tables were tested using Duncan's multiple range test ($p < 0.05$) and indicated by different lowercase or capital letters. Two-way ANOVAs were used to analyze the main and interactive effects of experimental treatments on each environmental properties. Pearson's correlations were used to assess the relationships between AMF diversity indexes and soil chemical variables of maize yields in 2011. All statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL). The canonical correspondence analysis (CCA) was performed to analyze the influence of the fertilization regime and soil physicochemical properties on the soil AMF community. Ordination analyses and hypothesis testing were conducted in CANOCO for Windows (version 4.5) with binary-transformed data. Forward selection tests were conducted using 499 permutations, and the Monte Carlo permutation test with $p < 0.05$ was used.

3 Results

3.1 Soil physicochemical properties

Maize yields in 2011 were the highest in the High Org. treatment (10,600 ± 366 kg ha^{-1}). The yields were 9400 ± 312 in Low Org. and 8100 ± 216 in the Con. F. treatment, and the lowest was 5200 ± 337 in CK, respectively. Soil depth and fertilizer forms all had effects on the soil nutrient properties (Table 1). In this study, long-term fertilizer inputs had significant positive effects on soil nutrient parameters. Soil total carbon (TC) content in the High Org. group was 42.2 mg kg^{-1}, which was 12.0% higher than in the CK, 9.71% higher than Con. F., and 1.44% higher than Low Org. Soil TC content in the 0–20 cm had the highest value, which was 42.9% higher than that in the 20–40 cm ($p = 0.000$) and 51.8% higher than that in the 40–60 cm ($p = 0.000$). Soil TN content in the High Org. treatment was 3.50% higher than that in the Low Org. treatment, 20.5% higher than that in the CK, and 16.5% higher than that in the Con. F. treatment. The TN contents among the vertical layers were also changed ($p = 0.002$) and showed a similar tendency to TC. The top soil layer (0–20 cm) had the highest soil TC and TN contents, and the positive effect decreased with increasing soil depth ($p = 0.000$).

Soil pH reached a relatively stable level, and no significant difference was observed among the fertilization regimes ($p = 0.965$). However, differences were observed among soil profiles. Soil pH value was highest at 20–40 cm depth, which was 4.29% higher than that at 0–20 cm ($p = 0.001$) and 3.06% higher than that at 40–60 cm depth ($p = 0.009$). No significant differences in EC contents were observed among fertilization treatments ($p = 0.882$). However, the highest soil EC value (735.7 μs cm^{-1}) was observed in the deepest soil layer (40–60 cm) of CK, which was 160.86% ($p = 0.002$) higher than that in the 0–20 cm.

The long-term organic compost inputs also had effect on soil Olsen-P, exchangeable K content ($p = 0.001$), and SOM content ($p = 0.021$) (Table 1). Soil Olsen-P content showed a trend of High Org. > Low Org. > Con. F. > CK, and the differences among treatments were significant ($p = 0.028$). Soil Olsen-P was stable in the upper soil layer and showed the following trend of 0–20 cm > 20–40 cm > 40–60 cm ($p = 0.000$). The exchangeable K content showed a relatively similar trend as the Olsen-P. Zn concentrations in the High Org. and Low Org. groups were higher than that in the CK and Con. F. treatments. Soil depth significantly affected cation concentrations. Element concentrations (e.g., Fe, Mn, Zn, Cu, K, and Mg) showed a decreasing trend with the increasing soil profile (0–20 > 0–40 > 40–60 cm; $p = 0.000$–0.001), while Ca and Na concentrations were opposite (40–60 > 20–40 > 0–20 cm; $p = 0.000$ and 0.027).

Table 1 Soil physicochemical properties under different fertilizer treatments

Treatment	Soil depth (cm)	Total carbon (g kg^{-1})	Total nitrogen (g kg^{-1})	pH value	Olsen-P (mg kg^{-1})	Exchangeable K (mg kg^{-1})	Organic matter (g kg^{-1})	Soil electrical conductivity (μs cm^{-1})
CK	0~20	15.3 ± 0.11c	1.22 ± 0.02b	8.40 ± 0.05abc	5.88 ± 0.50d	110 ± 15.8cd	11.4 ± 0.45b	220 ± 39.6c
	20~40	11.6 ± 0.23de	0.75 ± 0.02cde	8.53 ± 0.14abc	3.01 ± 0.18d	78.3 ± 7.91de	3.10 ± 0.13cd	304 ± 105b
	40~60	10.8 ± 0.28e	0.61 ± 0.06e	8.19 ± 0.26abc	2.50 ± 0.50d	61.2 ± 12.6e	1.70 ± 0.92d	736 ± 402a
Con. F.	0~20	15.9 ± 0.02c	1.34 ± 0.03b	8.18 ± 0.04abc	29.3 ± 4.81c	152 ± 20.7b	13.3 ± 0.85b	233 ± 9.24a
	20~40	11.5 ± 0.41de	0.72 ± 0.06cde	8.51 ± 0.10abc	4.58 ± 0.43d	73.1 ± 10.3de	3.50 ± 0.86cd	275 ± 22.7a
	40~60	11.1 ± 0.43e	0.60 ± 0.07e	8.26 ± 0.18abc	2.74 ± 0.06d	69.1 ± 8.64de	2.18 ± 1.06cd	630 ± 226a
Low Org.	0~20	17.5 ± 0.17b	1.50 ± 0.03a	8.13 ± 0.05bc	73.7 ± 9.68b	179 ± 10.8b	16.1 ± 0.26a	238 ± 16.0a
	20~40	12.6 ± 0.61d	0.84 ± 0.08c	8.55 ± 0.10ab	11.3 ± 0.67d	95.5 ± 5.27de	4.89 ± 1.93c	227 ± 31.3a
	40~60	11.5 ± 0.59de	0.66 ± 0.08de	8.32 ± 0.21abc	3.92 ± 1.04d	84.9 ± 24.6de	1.72 ± 0.92d	632 ± 353a
High Org.	0~20	19.1 ± 0.39a	1.63 ± 0.06a	8.08 ± 0.04c	105 ± 3.16a	289 ± 4.75a	17.1 ± 1.21a	239 ± 12.7a
	20~40	11.8 ± 0.38de	0.79 ± 0.03cd	8.61 ± 0.05a	22.3 ± 3.66c	144 ± 6.59bc	4.05 ± 0.55cd	220 ± 3.53a
	40~60	11.3 ± 0.38e	0.69 ± 0.06cde	8.41 ± 0.18abc	6.63 ± 0.47d	83.6 ± 11.5de	1.99 ± 0.82cd	430 ± 189a
Analysis of variance								
Fertilization		***	**	ns	***	***	*	ns
Soil depths		***	***	**	***	***	***	*
Fertilization × soil depths		**	*	ns	***	***	ns	ns

Data are presented as the mean ± SE ($n = 3$). Different letters indicated significant differences among the treatments and soil depth. Two-way ANOVAs (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; *ns*, non-significant) were used to analyze the main and interactive effects of the chemical or organic fertilizer application and soil depths on each soil chemical property. CK: no fertilization; Con. F.: conventional chemical fertilization treatment; Low and High Org. represent the low and high amount of organic compost input treatments, respectively

3.2 AMF colonization and hyphal growth

Root length colonization (%RLC), arbuscular colonization (%AC), and hyphal colonization (%HC) in maize roots were strongly influenced by the growth stage and fertilization regime (Table 2) and showed various responses. At V13, fertilization (Con. F., Low Org., and High Org.) decreased the %RLC, %AC, and %HC, with a greater decrease observed in the organic compost input treatments, especially when applied with high amounts. At V6, the %RLC, %AC, and %HC were relatively low, and no significant differences were observed among the fertilization treatments. At the RS stage, high colonization levels were increased, and no significant difference was observed among different treatments. In general, the %RLC increased over maize growing season. However, the highest values in the CK and the other treatments were observed at stages V13 and RS, respectively. The %AC and %HC also showed similar trends. Maize growth stage had significant effects on the hyphal length density and spore density ($p < 0.05$ and $p = 0.001$, respectively), with the spore density tended to increase at the RS stage.

3.3 Structure of the soil AM fungal community

In this study, long-term fertilizer application (fertilizer forms and rates) did not have any effect on soil AMF richness (Fig. 1), although the Low Org. and Con. F. treatments reduced the richness at 40–60 cm depth. T-RFLP analyses in combination with cloning and sequencing were used to analyze the AMF community. Twenty-one T-RFs (97, 105, 107, 116, 140, 141, 142, 143, 144, 157, 158, 164, 165, 168, 169, 189, 190, 191, 257, 258, and 259 bp) were detected in the T-RFLP profiles (Table S3, Electronic Supplementary Material). The T-RFLP fingerprints showed that the fungal community was greatly affected by fertilization and varied with soil depth. The fungal community in the High Org. treatment had higher richness, especially at the top soil profile, compared with that of Con. F. and Low Org. treatments (Table S3, Electronic Supplementary Material). The T-RFs of 97, 116, 165, and 189 bp were present in all soil samples, whereas other T-RFs (105, 143, and 191 bp) were detected only in the CK and High Org. groups. The 140 bp T-RF could be detected cross all soil depths in the Con. F. and Low Org. treatments but was absent in certain soil layers in the CK and High Org. treatments.

Soil chemical properties showed different correlation characteristics with AMF diversity indexes (Table S4). Soil variables (TC, TN, Olsen-P, EK, and OM) were positively correlated with AMF evenness, while only Olsen-P showed significant positive correlation with Shannon-Weiner diversity. Maize yields were negatively correlated with only evenness ($p = 0.005$). The relationship between soil chemical variables with T-RFLP profiles was explored using a CCA analysis (Fig. 2). Soil TN, TC, OM, AP (Olsen-P), pH, and EC showed significant effects on the AMF community. Soil pH was

Table 2 Percentage of root colonization, spore density, and hyphal length density over maize growth stages under different long-term fertilization regimes

Growth stage	Treatment	Root length colonization (%RLC)	Arbuscular colonization (%AC)	Hyphal colonization (%HC)	Hyphal length density (m g^{-1})	Spore density (g^{-1} soil)
V6	CK	11.70 ± 1.99a	2.14 ± 0.31a	1.60 ± 0.76a	1.01 ± 0.06a	4.69 ± 0.97a
	Con. F.	13.06 ± 0.69a	1.68 ± 0.36a	1.81 ± 0.92a	0.95 ± 0.13a	6.12 ± 0.55a
	Low Org.	8.03 ± 1.32a	1.04 ± 0.42a	0.78 ± 0.38a	0.85 ± 0.10a	4.90 ± 0.36a
	High Org.	11.01 ± 4.12a	2.38 ± 1.01a	2.86 ± 2.46a	0.70 ± 0.13a	4.76 ± 0.13a
V13	CK	63.75 ± 2.07a	30.65 ± 1.76a	32.23 ± 3.65a	0.66 ± 0.26a	6.58 ± 0.82a
	Con. F.	33.84 ± 2.27b	14.20 ± 1.05b	15.22 ± 1.46b	0.47 ± 0.02a	5.42 ± 0.70ab
	Low Org.	24.92 ± 0.25c	6.05 ± 0.63c	10.88 ± 0.74b	0.65 ± 0.18a	5.52 ± 0.17ab
	High Org.	19.67 ± 3.98c	7.42 ± 2.06c	8.11 ± 2.16b	0.52 ± 0.16a	4.38 ± 0.21b
RS	CK	51.69 ± 4.75a	19.00 ± 3.24a	26.84 ± 4.39a	1.02 ± 0.22a	7.40 ± 1.31a
	Con. F.	60.04 ± 4.12a	29.91 ± 4.85a	33.90 ± 4.34a	0.68 ± 0.11a	7.72 ± 1.23a
	Low Org.	48.17 ± 12.66a	15.75 ± 5.61a	25.63 ± 8.30a	0.69 ± 0.10a	7.32 ± 1.00a
	High Org.	47.72 ± 6.51a	19.04 ± 5.18a	23.11 ± 4.30a	0.50 ± 0.14a	7.60 ± 0.43a
Analysis of variance						
Organic fertilization level		**	***	***	ns	ns
Growth stage		***	**	*	*	***
Organic fertilization level × growth stage		**	**	*	ns	ns

Data are presented as the mean ± SE ($n = 4$). Different letters indicated significant differences among the treatments and growth stage. Two-way ANOVAs (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; *ns*, not significant) were used to analyze the main and interactive effects of fertilization treatments and growth stages on each colonization property. CK: no fertilization; Con. F.: conventional chemical fertilization treatment; Low and High Org. represent the low and high amount of organic compost input treatments, respectively. V6, V13, and RS refer to the 6-leaf collar, 13-leaf collar, and kernel dough stages during maize growth period, respectively

negatively correlated with AMF community in the top soil, while most soil AMF T-RFs at deeper soil layers tended to have positive correlation with soil EC.

3.4 Structure of AMF community in maize roots

No differences in AMF evenness were observed in roots cross maize growth stages ($p > 0.05$), although the values in the CK were significantly higher than those in the Con. F. and Low Org. treatments (Table S1, Electronic Supplementary Material). The T-RF richness increased over maize growing period (Fig. 1). Root AMF richness and Shannon index at V6 were lower than at stages V13 and RS, while the difference between the latter two stages was not significant. The fertilization effects on the Shannon diversity index and evenness were reduced, and significant effects were observed only at V13. However, the growth stages had significant effect on diversity indices of Shannon-Wiener ($p < 0.01$), richness ($p = 0.001$), and evenness ($p > 0.05$) (Table S1, Electronic Supplementary Material).

Maize growth stage, but not long-term fertilization, had significant effect on AMF community richness in maize roots (Fig. 1). Fifteen T-RFs (97, 105, 116, 140, 141, 157, 158, 164, 168, 169, 189, 190, 191, 258, and 259 bp) were detected (Table S3, Electronic Supplementary Material). The frequency of the 189 bp and 259 bp T-RFs was higher in maize roots than in soil (Fig. S2, Electronic Supplementary Material). The structure of AMF community in maize roots was significantly affected by maize growth stage but not by fertilization regime (Fig. S2; Table S3, Electronic Supplementary Material). The T-RFs of 97, 116, 141, 258, and 259 bp were the most frequently detected phylotypes in roots over maize growing period. The T-RFs of 157, 164, and 189 bp could be found in all root samples except in certain treatments at stage V6 (Con. F. and High Org. for 157 bp; CK for 164 bp; CK and Low Org. for 189 bp). The 158 and 190 bp T-RFs were found only in certain treatments at stages V6 and V13 but not at the RS stage. The 168 bp T-RF was absent in the CK and Low Org. treatment. The 169 bp T-RF was found only in the CK and Con. F. treatments at stages V13 and RS. Three T-RFs (105, 140, and 191 bp) were occasionally found in certain treatments.

3.5 Phylogenetic analysis of AMF in the surface soil

Four clone libraries were constructed in this study. Rarefaction curves based on the analyzed sequences in each clone library nearly reached a plateau, which indicated that the number of sequences was sufficient to characterize the AMF phylotypes presenting in the soil and roots (data not shown). Twenty-eight discrete clusters were obtained from the phylogenetic analysis; hence, 28 potential taxonomic units (each with bootstrap

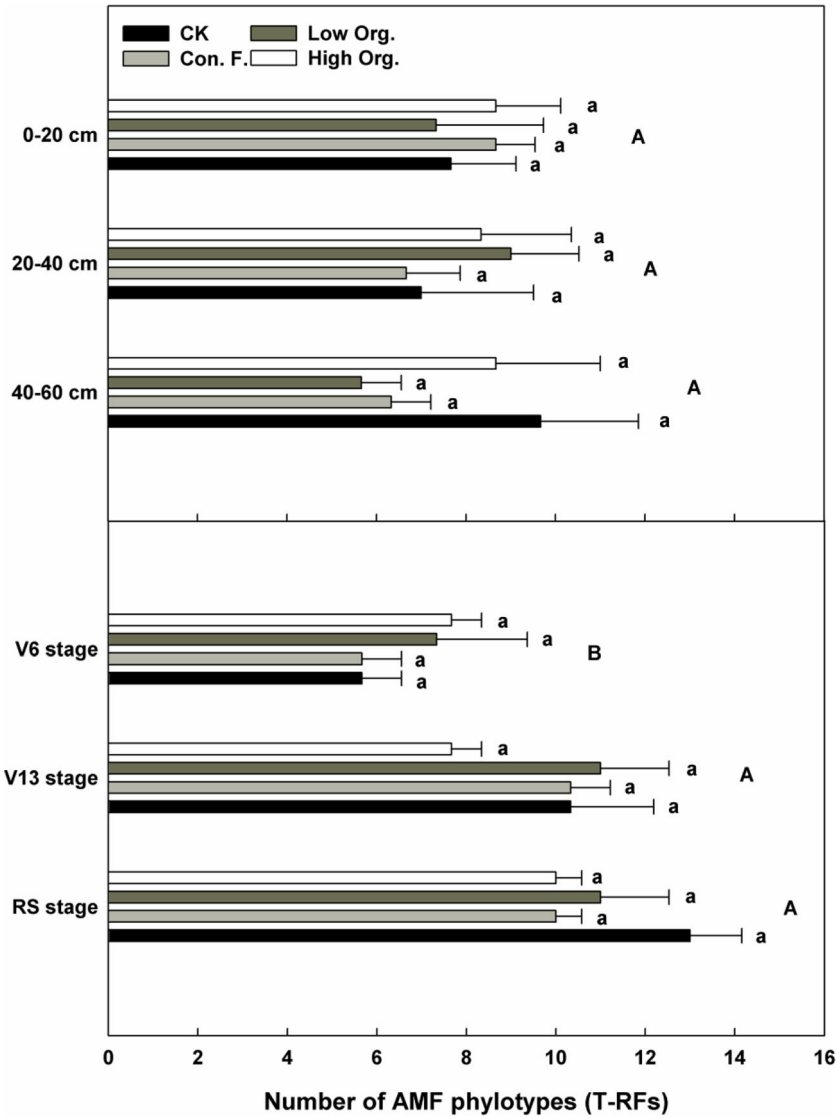

Fig. 1 Richness of the fungal T-RFs in the soil at different depths and the maize roots at different growth stages in the different fertilization treatments
Bars represent the mean ± SE ($n = 3$). Significant differences among the treatments and soil depths were tested using Duncan's multiple range test ($p < 0.05$) and are indicated by different lowercase or capital letters

support > 50%) were represented in the clone libraries. The 28 phylotypes are shown on the phylogenetic tree (neighbor-joining tree) with sequence identities from 97 to 100%, and they are represented by *sp*1–*sp*28. 18 of the 28 OTUs belonged to *Glomus*, 4 to *Funneliformis*, 3 to *Diversispora*, 1 to *Sclerocystis*, 1 to *Rhizophagus*, and 1 to *Acaulospora*. Of the effective clones sequenced from the clone library, *Glomus* (31.6–78.5%), *Funneliformis* (16.5–50.5%), and *Diversispora* (2.5–13.7%) were predominant, with *Acaulospora*, *Sclerocystis*, and *Rhizophagus* showing lower abundances.

Similar to previous studies (Liu et al. 2014, 2016), most T-RFs were assigned to Glomerales (including the *Glomus* groups A and B), and three T-RFs (141, 142, 169 bp) were partly assigned to Diversisporales. Of the three T-RFs, the 141 and 169 bp T-RFs belonged to the Diversisporaceae and 142 bp T-RF belonged to the Acaulosporaceae. Of the T-RFs assigned to Glomerales, the 116 bp T-RF was the most frequent T-RF, and it belonged to *Glomus* group A which includes *Fun*2 (*Funneliformis caledonius*), *Glo*15 (*Glomus viscosum*), *Fun*4 (*Funneliformis constrictus*), and *Glo*13 (uncultured *Glomus*). The 165 bp T-RF was *Glo*3 (*Glomus macrocarpum*). The 157 bp T-RF was affiliated with *Glomus indicum* (*Glo*1), and the 107 bp was *Sclerocystis sinuosa* (*Scl*1). The other T-RFs were associated with more than one sequence group.

4 Discussion

4.1 Influence of long-term organic compost application on soil AMF community composition

The AMF community composition in the soil was differentiated according to the fertilizer type and soil depths, and this variation might be related to environmental conditions (Entry

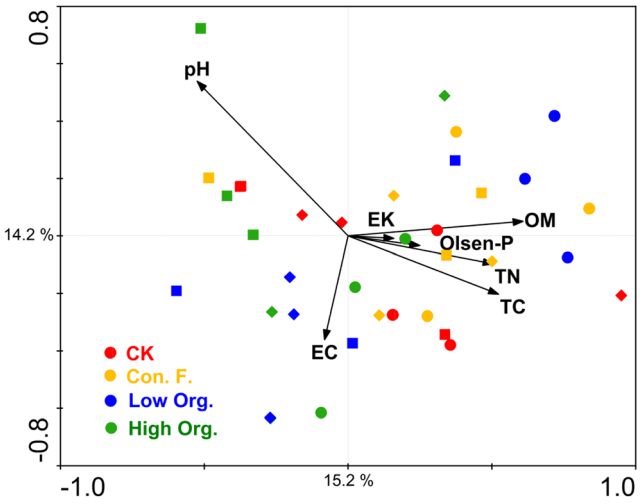

Fig. 2 Canonical correspondence analysis (CCA) of the AMF community composition in the soil in response to vectors of significant soil chemical properties. CK represents no fertilization; Con. F. represents conventional chemical fertilization treatment; and Low Org. and High Org. represent the low and high amount of organic compost treatments, respectively. Solid circles 0–20 cm; solid squares 20–40 cm; and solid diamonds 40–60 cm. The first and second axes explain 15.2% and 14.2% of the variance, respectively. The Monte Carlo test of significance of the first canonical axis and all canonical axes are $p = 0.0140$ ($F = 3.508$) and $p = 0.002$ ($F = 2.645$), respectively

et al. 2002), including nutrient levels and soil pH (Wang et al. 2011). The differences in the AMF community among the treatments occurred at the surface soil layer and were positively correlated with organic matter, total nitrogen, total carbon, Olsen-P, N/P ratio, and exchangeable K (Table 1 and Fig. 2). Soil pH was negatively correlated with AMF community at the top soil, while most soil AMF T-RFs at deep soil layers attended to have positive correlation with soil EC (Fig. 2). Increasing evidence indicates that soil fertility has strong effects on AMF species selection (Johnson 1993; Smith and Smith 2011). We also found that in addition to a surplus of Olsen-P and N_{min} caused by fertilization, an increase of organic matter also resulted in changes in the AMF community composition. Soil pH or pH-driven changes in soil chemical properties are also important in shaping AMF communities in both natural and agricultural ecosystems (Yang et al. 2014; Bainard et al. 2014). However, this diversity change was not accompanied by a loss of AMF species in soil, although the relative percentage varied and the soil AMF pool remained stable. In this study, the soil electrical conductivity had a significant impact on the vertical distribution of AMF, and the AMF community composition at the 40–60 cm soil depth was differentiated from that of the upper two soil layers, which is consistent with the results of our previous studies (Liu et al. 2014, 2016) and a recent study in a semi-arid prairie ecosystem (Bainard et al. 2014). Moreover, the inherent level of soil salinization may exert effect on soil AMF community. The relationship between AMF and soil chemical factors (soil pH, electrical conductivity, and nutrient indicators) was phylogenetically conserved at the genus level, and this variation within the AMF genera might have an important ecological significance (Bainard et al. 2014). In this study, *Sclerocystis sinuosa* and *Aca*1 (uncultured *Acaulospora*) could be detected only in the organic compost treatment, which indicated that these AMF were likely sensitive to the presence and amount of organic compost.

4.2 Temporal dynamics of AMF composition in maize roots as affected by long-term organic compost application

The AMF community variation and colonization characteristics are strongly controlled by host nutrient status and soil nutrient availability (Smith and Read 2008; Kahiluoto et al. 2001). Similarly, in this study, mycorrhizal colonization and community composition were altered due to long-term organic compost application. Long-term organic compost applications (High Org. and Low Org.) caused an accumulation of phosphorus at the 0–20 cm soil depth (available *p* values at this soil depth were 105.3 and 73.7 mg P kg^{-1}), which was much higher than the critical *p* values for maize production in this region (3.9 to 17.3 mg P kg^{-1}; Xu et al. 2009). In general, root colonization by AMF is inversely related to soil available P and plant P nutrition (Kahiluoto et al. 2001). Our results indicate that long-term organic compost application leads to low root infection by AMF, while high P accumulation may possibly inhibit the potential activity of indigenous AMF in the soil. Root colonization and AM-specific Pi transporter genes are significantly upregulated when soil Olsen-P is below a critical level (10 mg kg^{-1}) (Deng et al. 2014).

The concentrations of soil N_{min} and other nutrients in the organic compost treatment were higher than the critical nutrient demand in this region (Peng et al. 2013). Our result is similar to the findings conducted in the Huang-huai-hai Plain, which showed that an excessive nutrient supply might cause a functional redundancy of AMF colonized in plant roots, and mycorrhizal plants are more dependent on mycorrhizae (including external mycelium) in P-poor than in P-rich soils (Hu et al. 2009). The negative effects of fertilization on %RLC, %AC, and %HC tended to be more pronounced at the V13 stage (Table 2), indicating that crop phenology is important for determining root colonization (Liu et al. 2016). The relatively higher and more active fine roots in V13 may affect the dependency of maize on mycorrhizal fungi to acquire nutrients. Similar to AMF colonization, the spore density and hyphal length density were significantly affected by the growth stage and less by the long-term fertilization status (Table 2). These results are in similar to a previous study showing that plant growth period had significant effect on AMF sporulation (Bhadalung et al. 2005). One possible explanation is that AMF colonization is more sensitive to long-

term fertilization and crop phenology than AMF spore production in that the colonization structure is more closely associated with the host plant.

4.3 AMF communities in the soils and roots

Previous studies reported that the application of organic composts had negative impacts on AMF diversity (Jacquot et al. 2000; Gryndler et al. 2008), while several other studies highlighted the positive influence of organic compost application on AMF populations and diversity (Douds and Reider 2003; Oehl et al. 2004; Gosling et al. 2006). Furthermore, a comparative pot experiment reported that in general, AMF appear to thrive in soil with organic matter additions (Albertsen et al. 2006). According to our results, the effects of long-term organic compost application on AMF community diversity are complex and varied spatiotemporally. Long-term organic compost application did not have significant effect on T-RF richness in maize roots or soil overall (Fig. 1), although it did significantly reduce the Shannon-Weiner diversity (α-diversity) and evenness (Table S1, Electronic Supplementary Material). In a study conducted in the Huang-huai-hai Plain, long-term fertilization (> 20 years, especially organic fertilizer application) had significantly negative effects on the richness and diversity of the soil AMF community (Wang et al. 2011). Lin et al. (2012) also found that long-term organic fertilization decreased the AMF diversity and richness in an arable soil in North China. The reduction in the diversity index might be caused by a restrained evenness index, which likely implies the promotion of dominant AMF species leading to a lower Shannon-Weiner index. Hence, the soil AMF community developed towards a relatively clustered direction. The between-treatments AMF diversity (β-diversity) was also significantly separated between soil layers and treatments (Fig. 2), and small differences were observed compared with the findings of previous studies (van Diepen et al. 2011; Xiong et al. 2014). Changes in α-diversity and β-diversity should not occur concurrently, and this deviation may represent an additional effect of a concentrated AMF community. Our study also showed that the soil AMF pool did not result in species loss after long-term organic compost applications, which might explain the mismatch between taxonomic diversity and functional diversity (van Diepen et al. 2011).

In this study, the decline in soil AMF community richness and the Shannon-Weiner index was not observed in the deep soil layers (20–40 and 40–60 cm) (Table S1, Electronic Supplementary Material), which is inconsistent with the results of previous studies in other agricultural ecosystems (Oehl et al. 2005; Tian et al. 2013). This discrepancy might be related to the diverse mobility of nutrients (N and P) (Qu et al. 2014; Schachtman et al. 1998). Organic sources of nutrients with different acting components showed different decomposition characteristics and an unpredictable effect on AMF (Gosling et al. 2006). For instance, farmyard manure, compost, and crop residues did not seem to suppress AMF and might even stimulate fungal growth (Joner 2000; Alloush and Clark 2001). However, overuse of organic amendments, especially high-P-containing manure like chicken manure, may exert negative impacts on AMF (Douds et al. 1997; Jordan et al. 2000). Thus, the vertical distribution of AMF communities in response to fertilization regimes is of great interest when the AMF groups found in deeper soil layers show sensitivity, because AMF at deeper soil depths may be as diverse and functionally important as those in the surface horizons (Fierer et al. 2003; Oehl et al. 2005). Even in the deepest soil profile (40–60 cm), 8–17 T-RFs were identified, which means that the deeper soil layers also had a high microbial diversity and played an important role in soil diversity maintenance (Fierer et al. 2003; Higo et al. 2013). Soil AMF community and root AMF colonization responded differently to long-term organic manure applications. The alterations of AMF by the dosages of organic inputs are consistent with the results of Alguacil et al. (2011). Previous studies showed that changes in community structure are typically correlated with shifts in functional behavior (van Diepen et al. 2011; Fierer et al. 2013; Griffiths and Philippot 2013).

In this study, in total, 28 OTUs were observed in the soil samples, which indicated good coverage for Glomerales (*Glomus* group A/B) and Diversisporales. Most AMF generic-specific types found in our field have been demonstrated to be dominant in this region based on spore analyses (Tian et al. 2011). Studies conducted in North China also found that *Glomus*, *Funneliformis*, and *Rhizophagus* in Glomerales were the dominant AMF genera (Lin et al. 2012; Dai et al. 2013). Two T-RFs were detected in all samples: 97 bp (*Glo*15/17; *Fun*1) and 116 bp (*Glo*11/12/13/15; *Fun*2/3/4; *Rhi*1) (Table S3; S4, Electronic Supplementary Material). These two fragments are likely to occupy broad ecological niches and actively mediate symbiotic systems between AMF and plant roots. The changes in the environment caused by fertilization, organic compost dosage, and fertilizer forms also had effects on the abundance of the AMF T-RFs (Fig. S2, Electronic Supplementary Material). The relative abundance of the 116 bp T-RF in Low Org. group showed a significant increase relative to the other treatments (differences among the remaining 3 treatments were not significant), and the mineral fertilizer application (Con. F.) had a stimulating effect on the abundance of the 140 and 168 bp T-RFs (uncultured *Glomus*), which is consistent with the experimental that was performed with N and P fertilizer application treatments in the adjacent fields (Liu et al. 2014, 2016). In a recent study, *G. mosseae* and *G. caledonium* were relatively more abundant with increasing amounts of applied organic fertilizer, whereas *Paraglomus* sp. was abundant in low dosages of organic fertilizer (Yu et al. 2013). Other studies also found that organic

fertilizers promote *Glomus* species in agricultural soils (Gryndler et al. 2006; Vestberg et al. 2011). AMF from the *Glomus* genus can survive and reproduce easily via mycelium, mycorrhizal spores, or fragments (Giovannetti et al. 1999; Daniell et al. 2001). Therefore, *Glomus* could be more resistant and resilient to disturbances in the ecological environment than other genera and likely have an important role in executing ecological functions (Giovannetti et al. 1999; Daniell et al. 2001). In addition to the AMF belonging to Glomerales, long-term organic compost application also had effects on T-RFs (141, 142, and 169 bp) that are affiliated primarily with Diversisporales, but the effects were not statistically significant (Fig. S2, Electronic Supplementary Material). The results from clone libraries further validated our hypothesis that AMF differ in their responses to organic compost applications. Certain AMF were considered to be sensitive to nitrogen accumulation, including *Glomeraceae* (Bhadalung et al. 2005) and *Scutellospora*, whereas other AMF were sensitive to the organic compost dosage, such as *Sclerocystis sinuosa* which was observed only in the Low Org. group and not found in other treatments. *Aca*1 (uncultured *Acaulospora*) was detected only in the High Org. treatment. Different AMF had contrasting responses to organic matter which might indicate differential life strategies of AMF. In addition to the soil, the roots of crops harbor diverse functionally active AMF communities. Although few studies have examined the AMF communities in both the soil and roots, the AMF diversity in soil is generally considered to be higher than that in the roots (Martínez-García et al. 2011; Chen et al. 2014). Differences in AMF communities between soil and roots (Hempel et al. 2007) are caused by the seasonal nature of AMF communities (Liu et al. 2009) and may also be related to the phenological development and nutrient requirements of the crops (Tian et al. 2011, 2013). Therefore, more systematic investigations of the AMF communities in soils and roots in response to long-term fertilization might provide a better understanding of the potential functions of mycorrhizal fungal species and communities. A total of 28 AMF sequence groups were detected in this trial, and this number is considerably higher than the 20–22 species identified in other arable lands in China (Gai et al. 2004; Wang et al. 2008) and in our previous N fertilization (22 sequence groups) and P fertilization (27 sequence groups) studies at the same site (Liu et al. 2014, 2016). Our results are consistent with a long-term field experiment that found diverse AMF species in arable lands (Oehl et al. 2004).

5 Conclusions

Long-term organic compost applications led to relatively high residual nutrients in the soil. The responses of AMF communities in maize roots and soil to long-term fertilization are complex. Here, we found that long-term organic compost applications reduced root AMF colonization. High inputs suppressed the potential activity of indigenous AMF in the soil, but not the diversity or community structure of AMF in maize roots. The temporal changes in the AMF community in maize roots indicated that crop phenology might override the effect of fertilizer in determining the community composition of active root-inhabiting fungi. However, a shift in the AMF community at the surface soil was mainly attributable to soil nutrient availability, and a moderate input of organic compost tended to increase the diversity of AMF. The vertical distribution of AMF in the soil was significantly related to soil EC and pH. Recently, the replacement of inorganic fertilizers by manure is attracting more attention in Chinese agriculture to increase soil quality and promote ecosystem services. Our results imply that the modification of AMF communities by different fertilizations may have great impact on soil health and ecosystem services in intensive agroecosystems.

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