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Changes of the organic carbon content and stability of soil aggregates affected by soil bacterial community after afforestation

F.Z. Zhao[a,b,*], X.D. Fan[a], C.J. Ren[c], L. Zhang[d], X.H. Han[c,**], G.H. Yang[c], J. Wang[a,b], R. Doughty[e]

[a] Shaanxi Key Laboratory of Earth Surface System and Environmental Carrying Capacity, Northwest University, Xi'an, Shaanxi 710127, China
[b] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Water and Soil Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, Shaanxi, China
[c] College of Agronomy, Northwest A&F University, Yangling, 712100, Shaanxi, China
[d] Shaanxi Land Construction Group, Shaanxi LCG Land Project Technology Institute, Key Laboratory of Degraded and Unused Land Consolidation Engineering the Ministry of Land and Resources of China, Xi'an, Shaanxi 710075, China
[e] Department of Microbiology and Plant Biology, Center for Spatial Analysis, University of Oklahoma, Norman, OK 73019, USA

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ABSTRACT

Soil aggregation is one of the most important factors affecting soil organic carbon (SOC) stabilization, and the stability of aggregates depends in part on soil microbial diversity and composition. Interactions between the soil bacterial community and SOC content in soil aggregates after afforestation are poorly understood. In this study, we investigated difference in the diversity of soil bacterial with high-throughput 16S rRNA sequencing, as well as the SOC content in soil aggregates representing a chronosequence of 42, 27, and 17 years of *Robinia pseudoacacia* L. succession (RP42, RP27, and RP17), and in farmland (FL) soil for comparison (millet (*Setaria italica*) and soybean (*Glycine* max) rotation).The SOC content in RP17, RP27, and RP42 plots were significantly higher than that of FL by an average of 85.57%, 142.37%, and 76.69% in large macro-aggregates (> 1 mm), small macro-aggregates (0.25–1 mm), and micro-aggregates (< 0.25 mm), respectively. The Simpson index for the FL plot was significantly higher than that of the RP17, RP27, and RP42 plots, whereas the Shannon index followed the opposite trend. The dominant bacterial phyla detected were *Proteobacteria*, *Acidobacteria*, and *Actinobacteria* in each afforested and FL sites. These data revealed significant correlations between soil aggregate characteristics, such as SOC content, mean weight diameter (MWD), and geometric mean diameter (GMD), with the relative abundance of *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Nitrospirae*, *Verrucomicrobia*, and *Planctomycetes*. These relationships suggested that the effects of afforestation on SOC stabilization in soil aggregates are modulated by both soil aggregate size and also soil bacterial diversity. We demonstrate that the interaction between soil aggregate size and soil microbes might be a key factor in effective soil conservation, restoration, sustainability of agroecosystems, and erosion prevention.

1. Introduction

Afforestation is a key management technique used to mitigate the effects of climate change (Naveed et al., 2016) and plays an important role in regulating ecosystem function and biodiversity (Bhagwat et al., 2008), ecosystem restoration (Deng and Shangguan, 2017), and preventing soil degradation (Zhu et al., 2017). In the past few decades, global efforts to promote afforestation have rapidly increased (Carson et al., 2010). As of 2015, ~278 million ha of land were being utilized as plantations, which were equivalent to 7% of the global forest area (Carson et al., 2010). Consequently, afforestation is important for both soil nutrient cycling and carbon (C) sequestration in terrestrial ecosystems. Afforestation also influences soil microbial communities and soil aggregate stability (Duchicela et al., 2012). Although previous studies have investigated the effects of afforestation on soil microbial communities (Carson et al., 2010; Garcia-Franco et al., 2015; Cavagnaro et al., 2016; Deng et al., 2016; Ren et al., 2016b) and soil aggregate stability (An et al., 2013; Garcia-Franco et al., 2015), some details remain uncertain. For example, much is unknown about the stability of soil organic carbon (SOC) in soil aggregates after

* Correspondence to: FZ Zhao, Shaanxi Key Laboratory of Earth Surface System and Environmental Carrying Capacity, Northwest University, Xi'an, Shaanxi 710127, China.
** Corresponding author.
E-mail addresses: zhaofazhu@nwu.edu.cn (F.Z. Zhao), hanxinhui@nwsuaf.edu.cn (X.H. Han).

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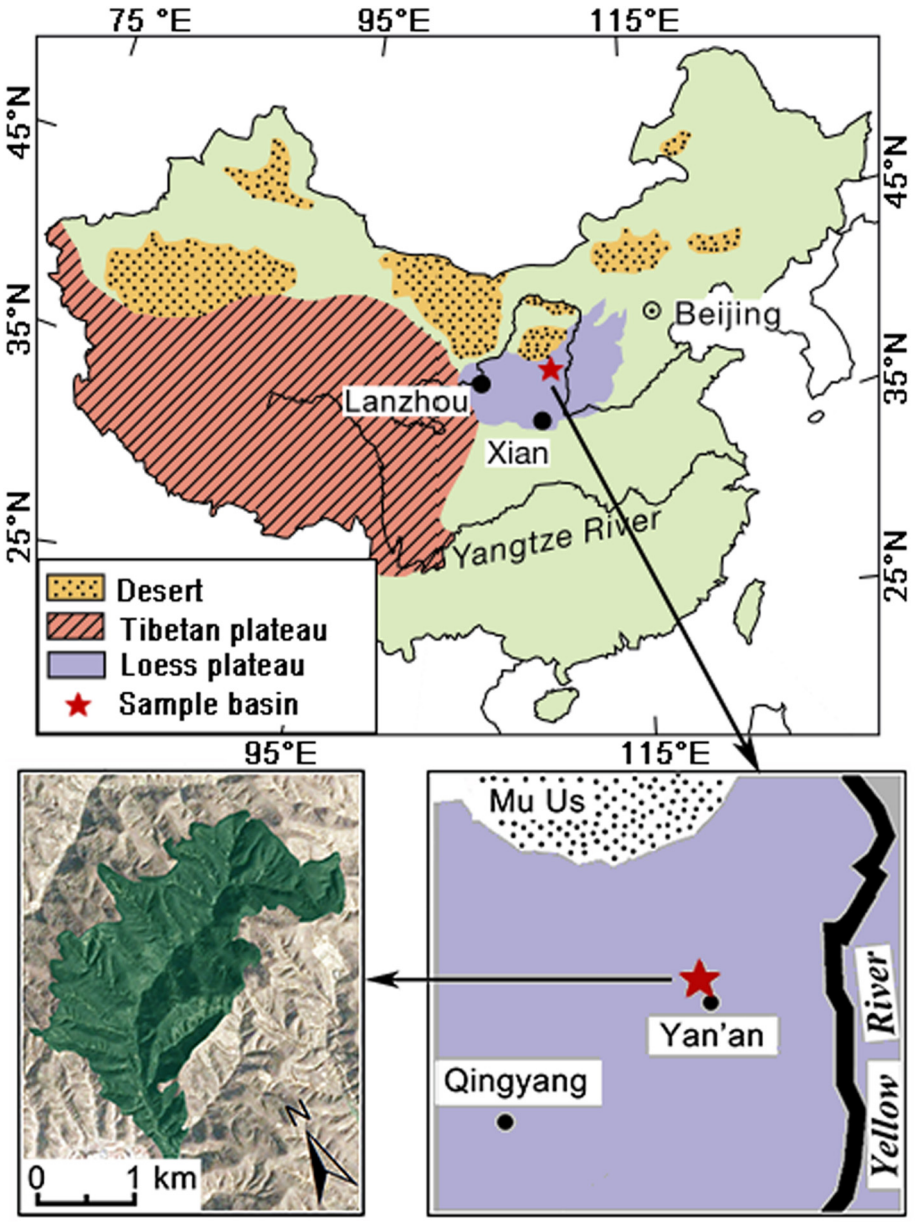

Fig. 1. Location of the Loess Plateau and the study basin.

afforestation. Since soil aggregate stability depends on soil microbial activity, variations in soil aggregate stability after afforestation may be caused by changes in the soil bacterial community. Therefore, the effects of afforestation on soil microbial activity, SOC content in soil aggregates, and soil aggregate stability must be investigated in order to quantify terrestrial C dynamics and predict soil quality (Dou et al., 2016; Mueller et al., 2017; Mukherjee et al., 2014). To further our knowledge of soil productivity and forest ecosystems after afforestation, a clear understanding of the relationships between afforestation, soil microorganisms, and soil aggregate stability is urgently needed.

Measures of soil aggregate stability, including the mean weight diameter (MWD) and geometric mean diameter (GMD), are important ecosystem indicators that are strongly related to soil services such as carbon storage (Xie et al., 2017; Zhang et al., 2017), organic matter stabilization (Chaplot and Cooper, 2015; Mueller et al., 2017; Wei et al., 2017), and erosion prevention (Six et al., 2000; del Pino and Ruiz-Gallardo, 2015; Zhu et al., 2017). Variations in soil aggregate stability are clearly linked with changes in soil microbial communities (Duchicela et al., 2012; Lee-Cruz et al., 2013; Six et al., 2006). A recent study found that different aggregate size classes support distinct microbial habitats, which in turn, support colonization by different microbial communities (Trivedi et al., 2017). This finding suggests that the microbial contribution to SOC accumulation is governed by the interactions between the microbial community structure and soil aggregate stability. Since litter input is a major source of labile organic C for microbial activity, promoting the binding of clay and silt-size particles to form micro-aggregates within macro-aggregates may increase soil stability (Garcia-Franco et al., 2015). Bacteria are involved in stabilizing soil particles (Dorioz et al., 1993), and several studies have shown that soil aggregates of different sizes, as well as different locations within soil aggregates, can be selected for colonization by different bacterial communities (Blaud et al., 2012; Davinic et al., 2012; Fall et al., 2004; Hemkemeyer et al., 2015). Since the interactions between bacteria and soil aggregate stability remain unclear, a better understanding of the impact of afforestation on soil bacterial and soil aggregate stability is essential for sustainable forest management and production.

The Loess Plateau in China covers approximately 62.4 × 104 km^2

and has a long history of agricultural land use and severe soil erosion (Chen et al., 2006). Historically, the native vegetation in the area was destroyed to meet the food supply needs of an expanding population, which eventually resulted in severe soil erosion and land degradation (Fu et al., 2010)., Thus, an environmental protection policy, the Grain to Green Program (GTGP), was implemented by the Chinese central government to counteract soil erosion and other environmental problems. The purpose of the GTGP was to convert low-yield sloped croplands (> 25°) into forests, shrubs, or grasslands (An et al., 2013). In recent years, numerous studies have been conducted to investigate changes in the soil carbon and nitrogen dynamics associated with the soil microbial community after large-scale afforestation (Zhang et al., 2016a; Y. W. Zhang et al., 2016b; H. Zhang et al., 2016c). However, these studies have not investigated the interactions between soil aggregate stability and soil bacterial communities. Therefore, in this study we investigated soil aggregates (Blaud et al., 2014) and soil bacterial communities at sites representing 45 years of *Robinia pseudoacacia* L. (RP) succession after afforestation of former farmland (FL) in the Loess Plateau. We hypothesized that soil bacterial diversity significantly increased after afforestation with corresponding increases in SOC content, mean weight diameter (MWD), and geometric mean diameter (GMD) of soil aggregates, and that this increase in soil bacterial diversity affected the stability of soil aggregates. We also expected that measures of soil aggregate stability (MWD and GMD) and SOC content would be highly correlated with soil bacterial diversity. Our objectives in this study were to (1) evaluate changes in the soil aggregate stability index (MWD, GMD) after afforestation, (2) characterize soil bacterial communities following afforestation, and (3) demonstrate the relationships between soil bacterial communities and soil aggregate SOC content, MWD, and GMD.

2. Materials and methods

2.1. Study area

The study was carried out in the Wuliwan Watershed (36°46′42″–36°46′28″ N, 109°13′46″–109°16′03″ E) located in Ansai County, Shaanxi Province, northern China (Fig. 1). The Wuliwan watershed is an experimental site of the Chinese Academy of Science (CAS). The climate is semi-arid, with a mean annual precipitation of 505 mm, which mainly falls from July to September. The average monthly temperature ranges from −6.2 °C in January to 37.2 °C in July, with a mean annual temperature of 8.8 °C. The soil is classified as loessial soil (Calcaric Cambisols, WRB classification, 2014), which is deposited by wind erosion. Agricultural management in this region has not changed significantly since the 1970s, and millet is mainly planted on sloping lands without irrigation. The main crops grown in rotations at these former FL sites were millet (*Setaria italica*) and soybean (*Glycine* max), and water resources for crop growth were dependent entirely on rainfall since irrigation was not possible. After 30 years of afforestation in the watershed, the area of forest has increased significantly from 5% to 40% (Zhao et al., 2016). Beginning in late 1970s, sloped cropland was replanted with RP to control soil erosion (Wang et al., 2012).

2.2. Experimental design and soil sampling

Prior to afforestation, all sites were essentially FLs, and had been subjected to millet (*Setaria italica*) and soybean (*Glycine* max) rotation for > 20 years (Ren et al., 2016b). In June 2016, based on land-use history, three replicates for each stand age (~1 ha) were randomly chosen, including 42-, 27-, and 17-year-old RP (RP42yr, RP27yr, and RP17yr), with an area of sloped FL selected for comparison (Zhao et al., 2016). Within each of the replicate sites, three plots (25 × 50 m) with similar slopes, gradients, and altitudes were sampled (Table 1). Three (5 × 15 m) sub-plots were established in each plot. After carefully removing the litter layer by hand from the topsoil, soil samples were obtained at 0–10 cm soil depth using a soil auger (5 cm ⌀) from ten points within an "S" shape in each subplot and then homogenized to provide one final soil sample per subplot. Overall, 36 samples (four land use types × three plots × three sub-plots) were collected. The samples were sieved through a 2-mm screen, and roots and other debris were removed (Ren et al., 2016a). A portion of each soil sample was air dried and stored at room temperature prior to analysis to facilitate aggregate separation. A portion of each soil sample was immediately transported to the laboratory for molecular analysis (on ice, and then stored at −80 °C). In this study, we only focused on soil bacteria due to the high number of studies that have assessed the relationship between fungal communities and soil aggregates, and because we know relatively very little about the bacterial community and aggregates in Loess Plateau after afforestation (Zhang et al., 2016b).

2.3. Soil aggregate distribution and aggregate SOC

Soil aggregate size separation was performed according to An et al. (2013) with minor modifications. Air-dried soil (100 ± 0.02 g) was submerged in deionized water in a 1-mm sieve. After slaking for 5 min, the sieve was moved up and down 50 times in 2 min before the wet soil samples were collected in each respective pre-weighed pan (> 1 mm large macro-aggregate; 0.25–1 mm small macro-aggregate; < 0.25 mm micro-aggregates together with free silt + clay sized fraction) (Nie et al., 2014). The contents of each pan were dried at 60 °C and weighed to determine the proportion of soil in each size fraction. The soil in each fraction was weighed, ground, and the SOC was determined using the $K_2Cr_2O_7$ oxidation method (Zhang et al., 2014a; H. Zhang et al., 2014b). Total soil organic carbon (TOC) was determined by Elementar TOC analyzers (Liqui TOC II, Germany).

The mean weight diameter (MWD) and geometric mean diameter (GMD) of soil aggregate fractions were calculated as follows (Chaplot and Cooper, 2015; Obalum and Obi, 2014):

$$\mathrm{MWD} = \sum_{i=1}^{n} (X_i \bullet W_i)$$

where X_i is the average diameter of aggregate fraction, and W_i is weight ratio of each size fraction.

$$\mathrm{GMD} = \mathrm{EXP}\left[\sum_{i=1}^{n} (W_i \bullet \ln(X_i))\right]$$

where W_i is the weight ratio of fraction and X_i is the average diameter of each size aggregate fraction.

2.4. DNA extraction, PCR, and sequencing

DNA from each soil bulk sample was extracted in triplicate using the E.Z.N.A. soil DNA kit (OMEGA, USA) according to the manufacturer's instructions. This extraction method has been reported in our previous study (Ren et al., 2016a). For 16S rRNA, the universal Eubacterial primers, 515F (5′-GTGCCAGCMGCCGCGG-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′), were used to amplify the 16S rRNA V4 region (Mukherjee et al., 2014). The bacterial amplification reaction mixture contained 0.4 μL of each primer, 0.4 μL FastPfu polymerase (China, Beijing TransGen Biotech Co., Ltd), and 1.25 μL template DNA (10 ng). The target DNA was amplified by the following protocol: denaturation at 95 °C for 3 min, then amplification for 27 cycles at 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 45 s, followed by a final extension at 72 °C for 10 min. PCR was carried out three times for each sample and then pooled to provide a final PCR product. To improve the quality and concentration of the PCR product, each mixture (containing 16S rRNA amplicons) was subjected to electrophoresis on 2% agarose gels, and bands with DNA fragments of the expected size (301–400 bp for 16S rRNA) were excised and purified with the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, U.S.). The purified PCR

Table 1
The geographical information and soil properties of four *R. pseudoacacia* sites.

Sites	Farmland	RP17yr	RP27yr	RP42yr
Location	36.865 N, 109.351 E	36.859 N, 109.349 E	36.868 N, 109.351 E	36.871 N, 109.34 E
Elevation (m)	1205	1303	1298	1293
Coverage (%)	–	70	75	85
SBD(g·cm-3)[a]	1.14 ± 0.02 A	1.17 ± 0.01 A	1.20 ± 0.01 A	1.24 ± 0.01 A
Clay (%)	8.12 ± 0.21 A	8.55 ± 0.14A	9.54 ± 0.13 A	10.11 ± 0.12 A
pH	8.48 ± 0.02 A	8.65 ± 0.01 A	8.67 ± 0.11 A	9.38 ± 0.01 A
SWC (%)[b]	9.34 ± 0.74 C	14.32 ± 0. 98 B	15.38 ± 0.79 B	22.12 ± 1.21 A

Capital letters indicate significant difference among different land use types ($P < 0.05$); the error bars are the standard error.
[a] SBD is soil bulk density of soil.
[b] SWC is soil water content.

products were finally solubilized in ddH_2O. A total of 36 PCR products representing six replicates per treatment were obtained, and an equal amount each sample sent to Personal Biotechnology Co., Ltd., Shanghai, China for further analysis on Illumina's MiSeq platform.

Reads were de-multiplexed, quality-filtered, and processed using QIIME, according to the following three criteria: (Caporaso et al., 2012). Sequence analysis was performed using USEARCH v5.2.32 to filter and eliminate noise from the data by clustering similar sequences with < 3% dissimilarity. Microbial Ecology pipeline software was used to select 16S rRNA operational taxonomic units (OTUs) by combining reads of clustered OTUs with 97% similarity. Finally, the complete dataset was sent to the Sequence Read Archive (SRA) database under the accession number. Sequences generated in this study were deposited in National Center for Biotechnology Information (NCBI) with accession number SRP102758 (https://submit.ncbi.nlm.nih.gov/subs/sra/).

2.5. Statistical analysis

One-way ANOVA and least significant difference (LSD) multiple comparison ($P < 0.05$) were used to analyze the significant effects of afforestation on soil bacteria phyla and microbial diversity among treatments, characteristics of SOC in aggregates and its distribution, and the abundance of dominant bacterial phyla. The Shannon index and Simpson index were used to determine the impact of soil bacterial abundance and alpha diversity (alpha diversity is the mean species diversity in sites or habitats at a local scale). The Shannon–Wiener index and Simpson index are one of many indices of species diversity and are based on the concept of evenness or equitability (i.e., the extent to which each species is represented among a sample). The Shannon–Wiener Index and Simpson index are indices that are not greatly affected by sample size, and can be shown to be relatively sample-size independent (Fedor and Spellerberg, 2013; Somerfield et al., 2008). Non-metric multi-dimensional scaling (NMDS) was used to compare soil bacterial communities between treatments based on Bray-Curtis similarity in PRIMER v.7. All statistical analyses were conducted in the SPSS 22.0 software package.

3. Results

3.1. Changes in SOC, TOC and stability of soil aggregates following afforestation

Significant differences were found in the SOC content of soil aggregates of different sizes following afforestation ($P < 0.001$). The SOC content in soil aggregates was highest in fractions of size 1 to 0.25 mm, and lowest in fractions of size < 0.25 mm (Fig. 2a). Comparisons between the different land-use plots showed that RP plot soil aggregates of > 1 mm, 0.25–1 mm, and < 0.25 mm in size had on average, 85.57%, 142.37%, and 76.69% higher levels of SOC than in the FL plot, respectively. The SOC content in soil aggregates in plot RP42 was significantly higher than that in soil aggregates from the RP 27 and RP17 plots by an average 24.60% and 72.42%, respectively ($P < 0.05$). However, SOC content in soil aggregates from plot RP27 was lower than that in soil aggregates from plot RP17 by an average 36.25%. SOC content in afforested plots was significantly higher than that of FL plot by an average of 34.99% and 51.22%, respectively ($P < 0.05$) (Fig. 2b). Among the RP plots, values of MWD and GMD were highest for soil aggregates from the RP27 plot, being higher than that for the RP42 and RP17 plots by 15.80% and 6.96%, respectively. The TOC content of soil aggregates was highest in the RP42 plot, being higher than that of soil aggregates from the RP27, RP17, and FL plots by 78.27%, 5.39% and 138.9% respectively. The TOC content of soil aggregates from the RP27 plot was lower than that of soil aggregates from the RP17 plot by 40.88%.

3.2. Changes in diversity of the soil bacterial community after afforestation

A total of 1,886,754 quality sequences, ranging from 45,779 to 67,570 bacterial sequences per sample (an average of 52,409 sequences per sample), were obtained from the 36 samples (nine replicates for each of the four land-use types – FL, RP42, RP27 and RP17). The read lengths for bacterial sequences ranged from 153 to 464 bp. The alpha diversity of the soil bacterial community was highly variable in soil aggregates from afforested soil at the phylum level (as measured by the Simpson index and Shannon index; Fig. 3). The Simpson index for the FL plot was significantly higher than that of the RP17, RP27, and RP42 plots ($P < 0.05$), which were 0.0042, 0.0041 and 0.0038, respectively. The Shannon index exhibited the opposite trend, and increased significantly from 6.59 for the FL plot to 6.75, 6.76, and 6.82 for the RP17, RP27, and RP42 plots, respectively ($P < 0.05$). Among the RP plots, the Shannon index was highest in RP42 but lowest in RP17, while the Simpson index had the opposite trend. Soil bacterial communities in the FL plot were different to those in the RP plots (Fig. 4). Significant differences in soil bacterial communities were revealed at the OTU-level based on taxonomic metrics according to the NMDS plots (Bray–Curtis similarity) (Adonis: $R = 0.965$, $P = 0.0001$).

3.3. Impact of afforestation on soil bacterial community structure and composition

The dominant bacterial phyla found in the soil aggregates analyzed were *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Bacteroidetes*, *Nitrospirae*, *Verrucomicrobia*, and *Planctomycetes* (Fig. 5). The relative abundance of phylum *Acidobacteria* was higher in the FL plot than in the afforested plots, whereas *Proteobacteria* were relatively more abundant in afforested soil than in the FL plot. The relative abundance of bacteria identified in each land-use type (> 1%) differed significantly ($P < 0.01$) between the four land-use types (Table S1). Except for *Verrucomicrobia*, each bacterial phylum had

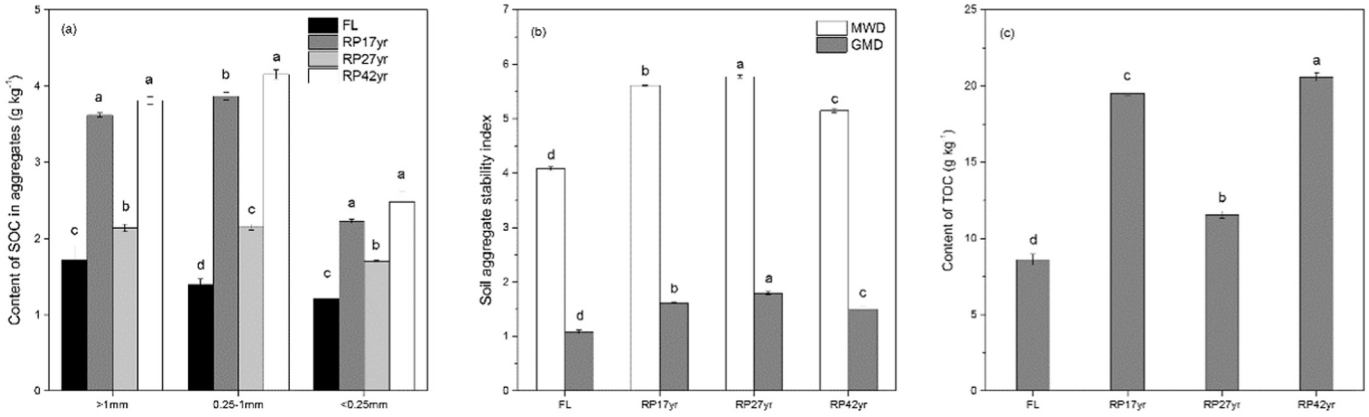

Fig. 2. (a) Content of soil organic carbon (SOC) and its distribution in soil aggregates (g/kg^{-1} soil); (b) variation of soil aggregate stability index (MWD, GMD); (c) content of total soil organic carbon (TOC) after afforestation. Numerical values are means ± standard errors. Bars with different letters indicate significant differences following afforestation ($P < 0.05$). Notes: 42, 27, and 17 years of *Robinia pseudoacacia* L. indicated as RP42, RP27, and RP17.

significantly different relative abundances across land-use types ($P < 0.001$).

3.4. Relationships between SOC content, soil aggregate stability index, and soil bacterial communities

Linear regression analysis revealed a significant correlation between SOC in soil aggregates and the abundances of *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Nitrospirae*, *Verrucomicrobia* and *Planctomycetes*, (Fig. 6). In particular, the abundance of *Acidobacteria*, *Chloroflexi*, *Nitrospirae*, and *Planctomycetes* showed a significant positive correlation with SOC in large macro-aggregates (> 1 mm), small macro-aggregates (0.25–1 mm), micro-aggregate (< 0.25 mm). However, there was no correlation between the abundances of *Bacteroidetes* and *Gemmatimonadetes* with the SOC content in these aggregate size classes. Significant correlations between MWD and GMD with abundances of *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Bacteroidetes*, *Nitrospirae*, and *Planctomycetes* ($P < 0.01$) were also detected, though no such relationships were seen between MWD and GMD with abundances of *Verrucomicrobia* (Fig. 7). These results suggested that the dominant bacterial phyla in the soil bacterial community can significantly affect the MWD, GMD, and SOC content of soil aggregates.

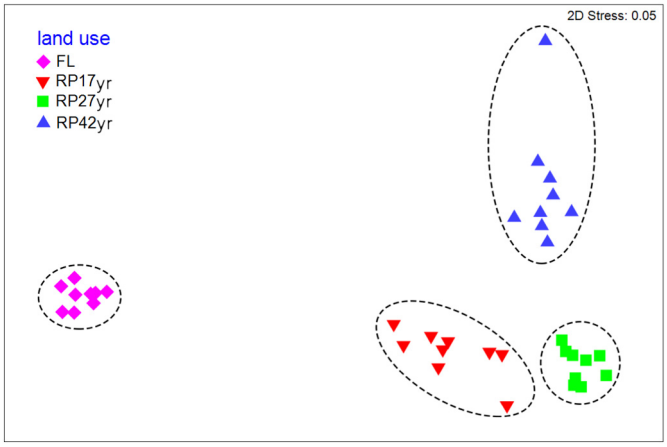

Fig. 4. Soil bacterial community comparisons by NMDS plots based on Bray-Curtis similarity following afforestation. Notes: 42, 27, and 17 years of *Robinia pseudoacacia* L. indicated as RP42, RP27, and RP17.

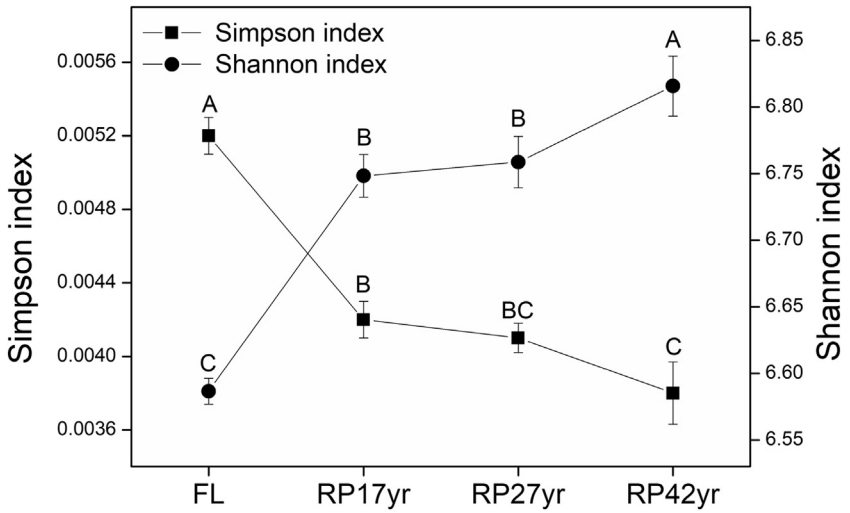

Fig. 3. Impact of afforestation on alpha diversity (Shannon index and Simpson index). Different uppercase letters indicate significant differences between each land use types. Notes: 42, 27, and 17 years of *Robinia pseudoacacia* L. indicated as RP42, RP27, and RP17.

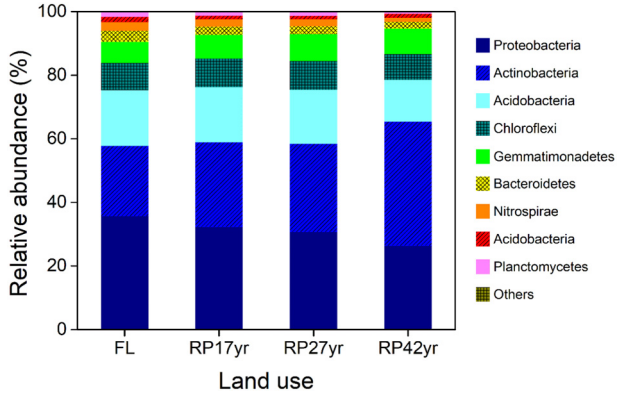

Fig. 5. Soil bacterial community composition at phylum level following afforestation. Notes: 42, 27, and 17 years of *Robinia pseudoacacia* L. indicated as RP42, RP27, and RP17.

4. Discussion

4.1. Soil aggregate stability increased after afforestation

Afforestation is one of the major factors that affect TOC content of soil and is an efficient means of increasing soil aggregate stability (An et al., 2013). We found that aggregate stability and TOC content was much higher in the afforested plots than in the FL plot (Fig. 2b), which suggested that soil quality improved after afforestation. Several studies reported that changes in plant composition due to afforestation could greatly influence soil properties, such as pH and organic input, thereby affecting TOC content and soil aggregate stability (Cavagnaro et al., 2016; Ren et al., 2016b). However, changes in TOC content and soil aggregate stability could also be attributed to the accumulation of litter and residue in forested sites, which increases the diversity of the soil microbial community and subsequently influences soil structure. The latter explanation is consistent with a recent study conducted by Zhu et al. (2017), which reported that the improvement in vegetation structure and species diversity of afforested sites might influence the soil microenvironment to promote soil microbial activities and alter soil

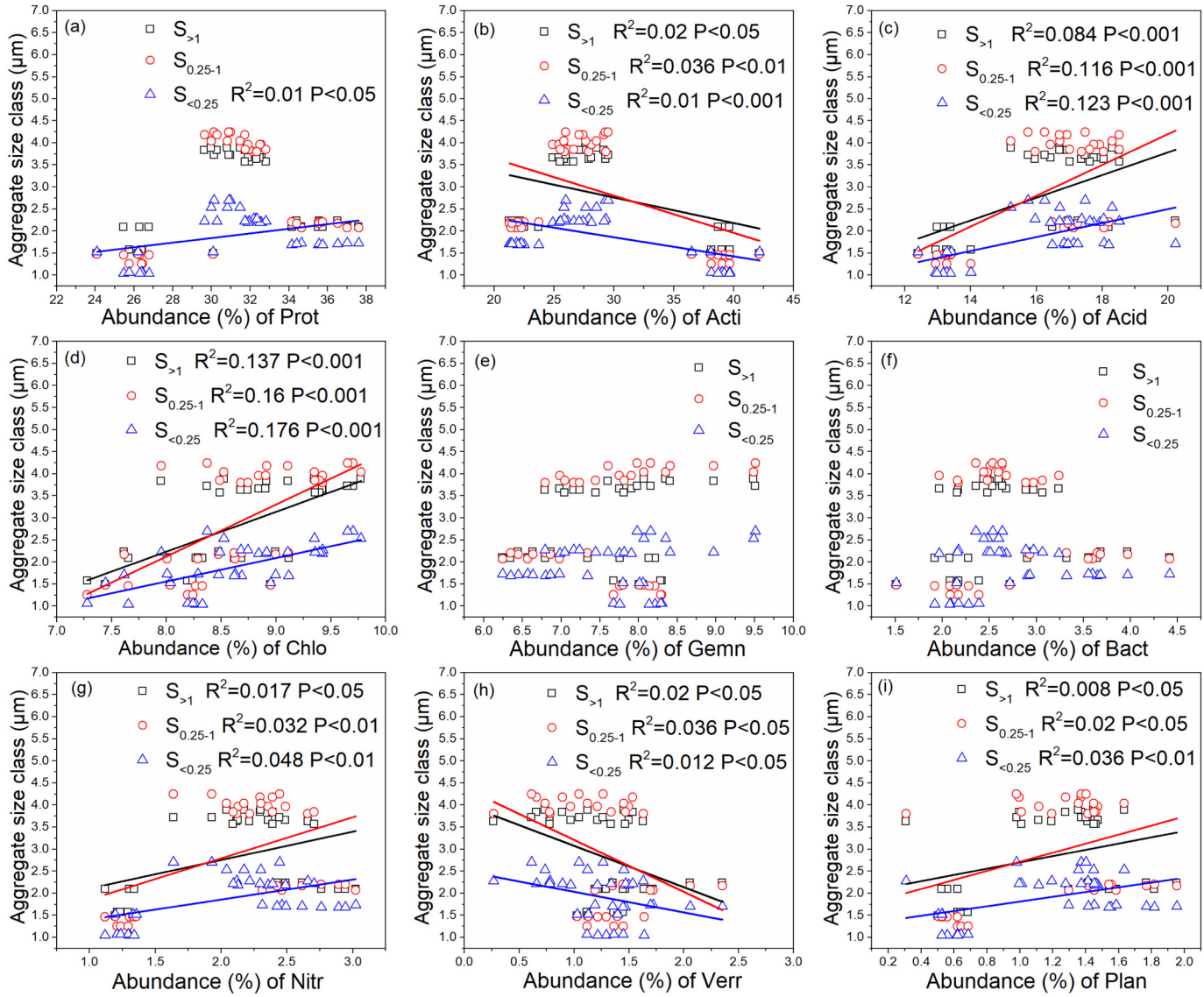

Fig. 6. Relationship between the SOC in large macro-aggregates (> 1 mm), small macro-aggregates (0.25–1 mm), micro-aggregate (< 0.25 mm), and the abundance (% abundance) of Proteobacteria (a), Actinobacteria (b), Acidobacteria (c), Chloroflexi (d), Gemmatimonadetes (e), Bacteroidetes (f), Nitrospirae (g), Verrucomicrobia (h), and Planctomycetes (i) after afforestation.

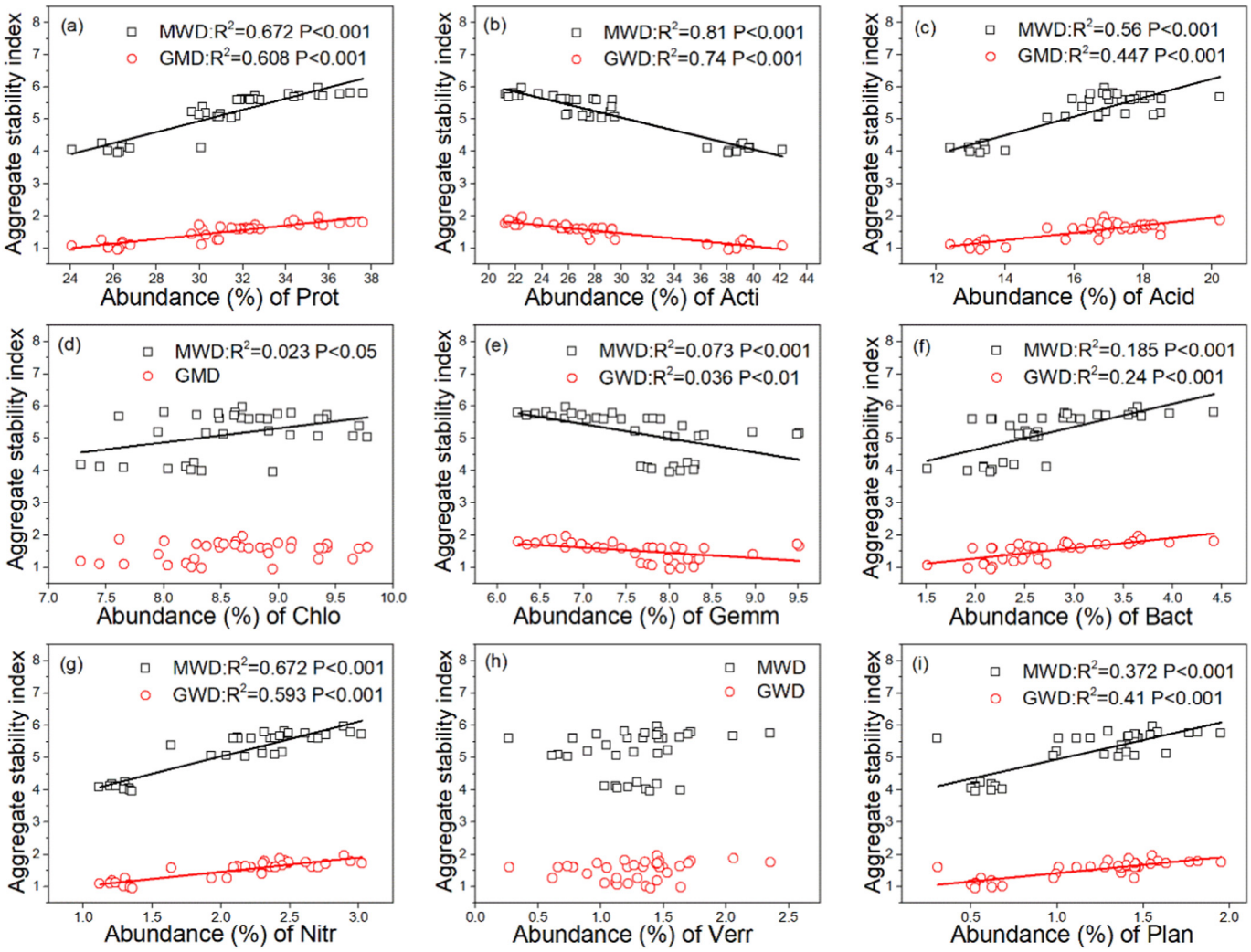

Fig. 7. Relationship between the mean weight diameter (MWD),geometric mean diameter (GMD) and the abundance (% abundance) of Proteobacteria (a), Actinobacteria (b), Acidobacteria (c), Chloroflexi (d), Gemmatimonadetes (e), Bacteroidetes (f), Nitrospirae (g), Verrucomicrobia (h), and Planctomycetes (i) after afforestation.

structure. In our study, afforestation improved soil aggregate stability when compared to the FL plot. However, TOC content and soil aggregate stability indices were lower in the RP27 plot, as compared to those of the RP42 and RP17 plots. This difference could be attributed to microclimatic changes caused by limited light availability, severe competition for water and nutrients, and allelopathy, all of which can decrease soil aggregate stability and TOC content (D.J. Zhang et al., 2014a; H. Zhang et al., 2014b). This result was consistent with a study conducted by C. Zhang et al. (2016a), Y. W. Zhang et al. (2016b) and H. Zhang et al. (2016c) who found that soil water storage decreased with long-term vegetation restoration on the Loess Plateau, affecting soil aggregate stability and resulting in decreased values of measured physical, chemical, and microbiological properties of soil.

4.2. The soil bacterial community is altered by afforestation

Afforestation can affect soil nutrients by changing the nature of litter and root exudates, both of which can alter the growth of soil microbes and ultimately alter soil bacterial diversity (Deng et al., 2016). Our results suggested that the diversity of soil bacteria (as measured by the Shannon Index, H) was higher for older afforested plots (Fig. 3). This increase in diversity could be attributed to higher above-ground biomass in forest soil as compared to that in farmland soil (Tong et al., 2014; Ren et al., 2016a). Above-ground biomass is known to increase bacterial community diversity during afforestation (Kowalchuk et al., 2002; Lozano et al., 2014). Our results are in agreement with those of Ren et al. (2016b), but diverge from those of Zheng et al. (2017). This discrepancy suggests that afforestation may have variable effects on different soil properties such as pH, above-ground plant composition (Kim et al., 2014), above-ground plant composition (Kuramae et al., 2011), and organic input (root exudates and litter) (Faoro et al., 2010), all of which ultimately lead to differences in the diversity of soil bacteria (Chen et al., 2015; Xiao et al., 2015). Additionally, we found *Robinia pseudoacacia* L. succession (RP42, RP27, and RP17) also has a large influence on soil bacterial diversity, and soil bacterial diversity was found to increase sharply in the initial stages of RP succession, then increased gradually at later stages. As the ecosystem matures in the later stages of forest succession, increased competition for nutrients may allow strong competitors to dominate, which may cause a decrease in species richness. This increased competition is likely to contribute to a gradual slowing in the rate of increase in soil bacterial diversity.

While soil bacterial diversity parameters were affected by afforestation of former FL, changes in the bacterial community were detectable by analysis of principal coordinates. The soil bacterial community in the FL plots was different from those in the RP plots, particularly in the RP42 plot (Fig. 4), which indicated that afforestation of former FL can also alter the composition of soil bacteria. Notably,

Acidobacteria were predominant in afforested soil, but not in FL soil (Fig. 5 and Table S1). It is likely that *Acidobacteria* belong to oligotrophic groups and prefer nutrient-poor environments. Changes in bacterial community compositions largely depend on shifts in soil microbial diversity (C. Zhang et al., 2016a; Y. W. Zhang et al., 2016b; H. Zhang et al., 2016c), and bacterial community composition-driven enhancements of soil nutrient cycles are typically associated with high levels of microbial diversity. In this study, the high bacterial diversity in afforested soil can be attributed to changes in the relative abundance of specific bacterial taxa, including the *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, and *Chloroflexi* (Fig. 5). Particularly, *Proteobacteria*, representing the most abundant bacterial phylum, was generally considered to be r-strategists that preferentially utilize easily accessible sources of C (e.g., DOC) (Fierer et al., 2007). A class of *Proteobacteria*, the *Alphaproteobacteria*, are considered to dominate the rhizosphere and can accelerate the accumulation of easily accessible C sources by which they can affect overall soil bacterial diversity. (Lee-Cruz et al., 2013). The bacterial communities in our study generally changed from *Acidobacteria*-dominant to being *Proteobacteria*-dominant over the 42 years of RP succession, which suggested that these belowground communities transitioned from slow-growing oligotrophic groups to fast-growing copiotrophic groups. These specific bacterial taxa are significantly related to soil microbial community structure and function (Zhao et al., 2016), so such changes in the abundance of bacterial phyla after afforestation may further influence SOC dynamics in soil aggregates by affecting the decomposition rate of nutrients (Trivedi et al., 2015).

4.3. The relationship between the soil bacterial community and SOC content in soil aggregates and soil aggregate stability

Changes in plant cover after afforestation induce variations in the soil microbial community structure and activity, which may promote the accrual and physiochemical protection of SOC content within soil aggregates (Garcia-Franco et al., 2015). SOC in soil aggregates is dependent on the relative abundance of certain bacterial taxa. In particular, the abundance of *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Nitrospirae*, and *Planctomycetes* are significantly positively correlated with SOC contents in large macro-aggregates (> 1 mm), small macro-aggregates (0.25–1 mm), micro-aggregate (< 0.25 mm). However, the abundance of *Bacteroidetes* showed no relationship with SOC content in any of in these soil aggregate sizes. (Fig. 6). Our result indicated that soil bacterial abundances increase after afforestation, which could enhance C sequestration by influencing the SOC content in soil aggregates. It is possible that fresh inputs of C after afforestation are a major source of labile organic C for bacterial activity, which promotes the binding of clay and silt-size particles to form micro-aggregates within macro-aggregates, consequently increasing the stability of soil aggregates (Six et al., 2000). Some soil bacteria also mediate nutrient flow from the soil to host plant in exchange for assimilated C and bind soil aggregates or translocate C within soil aggregates, which results in strong positive correlations between the abundance of bacterial taxa that perform such functions and SOC content in soil aggregates (Kruger et al., 2017). Our results are supported by those of previous studies, which report that soil microbial activity has a strong impact on the SOC content in soil aggregates (Garcia-Franco et al., 2015; Nie et al., 2014; Schutter and Dick, 2002). A recent study by Trivedi et al. (2017) also provides evidence to show that soil aggregates support distinct microbial habitats, which in turn support the colonization of different microbial communities. The interaction between bacteria and SOC content in aggregates is necessary for bacterial survival since the SOC content in soil particles affect nutrients and habitat availability for the bacteria (Blaud et al., 2014; Duchicela et al., 2013). *Proteobacteria* target labile C sources in soil aggregates rich in labile C and N. Such soil aggregates originate predominantly from plant residues, which might explain the relationship between *Proteobacteria* and SOC content in soil aggregates.

Changes in soil microbial activity are an important contributor to changes in soil aggregate stability (Duchicela et al., 2012). Higher soil bacterial diversity can cause rapid turnover rates in soil aggregate fractions. Consequently, the availability of different types of nutritional substrates aboveground may also influence the effect of soil bacterial diversity on soil aggregate fractions (Ren et al., 2016a). The soil aggregate stability measurements (MWD, GMD) are closely correlated with soil bacterial abundance (Fig. 7). It has been suggested that improvements to soil structure are mediated by a range of soil bacteria. Our results agree with those of a recent study conducted by Rahman et al. (2017), which reported that MWD was specifically associated with bacteria. This association may exist because bacterial influence on soil aggregate stability after afforestation is dependent on nutrient input and plant root systems (Li et al., 2015). In a previous study we presented evidence that nutrient resources, such as litter and root biomass (Ren et al., 2016a), can provide sufficient levels of nutrition to support bacterial growth that ultimately generates transient binding agents and improves soil structure (Chen et al., 2014; Kara et al., 2008). Plant roots promote aggregation by producing substances that directly stabilize soil particles. These substances also favor bacterial activity in the rhizosphere which, in turn, affects soil structure (Duchicela et al., 2012). Previous studies have demonstrated that afforestation stimulates microbial growth and activity to generate transient binding agents for the aggregation process, and so affects soil aggregate stability (Deng et al., 2016; Singh et al., 2004). Thus, afforestation that enhances restoration of the soil bacterial community may boost soil aggregate stability, which is a key factor for soil conservation, restoration, sustainability of forest ecosystems, and erosion prevention.

Although this research provide the more specific content of interactions between soil aggregate stability and soil bacterial communities, this study only considered the soil information, so it is difficult to make a comprehensive view to illustrate the interaction between above ground and below ground might be a key factor in effective soil conservation, restoration, sustainability of agroecosystems, and erosion prevention. Hence, plant information would be profitable for further research on the Loess Plateau.

5. Conclusion

This study found that soil aggregate stability increases after afforestation. And our results suggested that the diversity of soil bacteria (as measured by the Shannon Index, H) was higher for older afforested plots. In addition, the soil aggregate stability measurements (MWD, GMD) are closely correlated with soil bacterial abundance our results support the importance of soil bacteria as drivers of processes that promote the recovery of aggregate stability in *Robinia pseudoacacia* L. succession forests. The effect of afforestation on the soil bacterial community may enhance soil aggregate stability. Furthermore, our result suggested that the interaction between aggregate sizes and soil microbes might be a key factor for soil conservation, restoration, sustainability of agroecosystems, and prevention of erosion.

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