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Variations in microbial functional potential associated with phosphorus and sulfur cycling in biological soil crusts of different ages at the Tengger Desert, China

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ABSTRACT

Microbial communities play a very important role in soil ecological processes by regulating biogeochemical cycles during biological soil crust (BSC) succession in desert ecosystems. Although the relationships between microbial carbon or nitrogen and the BSC at different successional stages have been a source of great concern, there are few reports regarding the phosphorus (P) and sulfur (S) cycles. In this study, we used a functional gene array (GeoChip 5.0) to analyze the characteristics of microbial communities and their functional genes involved in the P and S cycles along a chronosequence of BSC succession in the Tengger Desert, China. The results showed that the functional genes associated with polyphosphate degradation and sulfite reduction were the major components involved in the P and S cycles, respectively, and the intensities of the functional genes expression involved in the P and S cycles increased significantly in 61-year-old BSCs. Compared with the fungal and archaeal communities, the bacterial community was the major contributor to the P and S cycles, and Proteobacteria (mainly Alphaproteobacteria, Gammaproteobacteria, and Betaproteobacteria) and Actinobacteria were the dominant phyla. A redundancy analysis showed that there was significant synergy between the improvement in soil properties (e.g., soil nutrient content) and the intensities of genes expression related to P and S cycles. These findings indicated that after 61 years, BSC significantly promoted the microbial metabolic potential for P and S cycling, which in turn promoted soil rehabilitation in a desertified dryland.

1. Introduction

Biological soil crusts (BSCs) are complex communities that include cyanobacteria, green algae, fungi, lichens, mosses, and other microorganisms associated with surface soil particles via the cementation of mycelia, rhizoids and secretions. As the ecosystem engineers of the desert landscape, BSCs account for 40–70% of the living cover in drylands (Weber et al., 2016). The formation of BSCs occurs via a gradual successional process that typically shows a progression from cyanobacterial to algal, lichen and moss crusts. BSCs can effectively improve the soil habitat of desert ecosystems, thereby affecting the germination, establishment and reproduction of vascular plants. Hence, BSCs are well studied in semiarid and arid ecosystems from all over the world (Eldridge and Greene, 1994; Li, 2012). However, little is known on functional aspects of such communities in desert regions.

Numerous studies have demonstrated that BSCs play a crucial role in carbon (C) and nitrogen (N) cycling, particularly in desert ecosystems (Baumann et al., 2017; Li, 2012; Zaady et al., 1998). Globally, Elbert et al. (2012) estimated the amount of C (about 3.9 $Pg{\cdot}a^{-1}$) and N (about 49 $Tg{\cdot}a^{-1}$) absorbed by cryptogamic covers, which accounted for about 7% of net primary production of terrestrial vegetation and nearly half of terrestrial biological nitrogen fixation. Due to the high coverage of the living surface and the high light utilization efficiency (e.g., lichens can achieve 0.5–2% light utilization efficiency), well-developed BSCs have a

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greater photosynthetic C-fixing capacity than vascular plants in the same desert habitat (Palmqvist et al., 2000). Microbial communities are involved in the regulation of C and N cycles during BSC succession, and bacteria is the most active group among these communities (Maier et al., 2014). One major function of bacterial community of BSCs is the storage of C and N for desert ecosystem (Liu et al., 2017a). Heterotrophic bacteria (such as *Pseudomonas*, *Klebsiella*, *Shigella*, and *Ideonella*) have the ability to fix N (Pepe-Ranney et al., 2015), and the amount of N fixed annually by microorganisms in BSCs is similar to the annual nitrogen application rate of agricultural systems (Caputa et al., 2013). Compared with bacteria, fungi have the metabolic ability under high temperature and low water potential, which can control almost all N transformation processes in some dry soils. However, although the transfer of mineral nutrients between vascular plant communities and well-developed BSCs is primarily dependent on fungal networks, the role of fungi is less important in the early stages of BSCs (Liu et al., 2018). Previous studies have primarily focused on the C and N biogeochemical cycling in BSCs as well as on the microbial communities involved in these processes. As essential elements of plant nutrition, phosphorus (P) and sulfur (S) also play important roles in the main metabolic processes of plants.

However, P is rarely present in the soil in a soluble form that plants can absorb and utilize directly. Soil microorganisms can convert inorganic and organic phosphorus into plant-available forms through various dissolution and mineralization processes. For example, carbonates and Fe- and Al-bound P can be dissolved by H^+ secreted during respiration or organic acid secretion (Belnap, 2011; Baumann et al., 2017). In addition, due to the multivalent nature of S atoms, S cycle is more complex in biosphere relative to P cycle. Sulfur is subjected to a series of different oxidative and reductive transformation processes that are mediated by bacteria in the soil environment (Kertesz and Frossard, 2015). With the presence of the sulfite reductase gene, bacteria and archaea can grow via the reduction of sulfite, although in some organisms, sulfur oxide might depress their growth (Anantharaman et al., 2018).

In arid and semiarid regions, the widespread occurrence of desertification and the expansion of the area exposed to wind erosion and sand dust have led to a significant increase on the contribution of P and S from desert ecosystems to the global circulation of these elements (Jin et al., 2007). It is particularly important to study the ecological roles and drivers of P and S cycles in desert ecosystems. Previous studies have shown that the biogeochemical cycling of P during natural succession can promote the reconstruction of damaged landscapes (Celi et al., 2013). Furthermore, Glaser et al. (2017) have demonstrated that the richness of BSC organisms is related to the total P content. With regard to sulfur, useful information is primarily obtained from the ocean and sediments (Jørgensen and Kasten, 2006; Zhai et al., 2018), while few studies have reported on the S cycle in desert ecosystems. Although Baumann et al. (2017) have reported that BSC participated in the transformation of inorganic P (Pi) to organic P (Po) compounds in temperate forests, little is known regarding the contribution of microbiome to the P cycles in desert BSCs.

To better understand the microbial functional potential of BSCs associated with phosphorus and sulfur cycling in desert ecosystems, changes in the functional composition of microbial communities and their genes associated with the P and S cycles in BSCs along a revegetation chronosequence in the Tengger Desert were examined. Our study addresses the following questions: (1) how the microbial communities involved in the P and S cycles respond to BSC succession; and (2) whether microbial P and S cycling promotes the succession of BSCs and improve the soil quality of revegetation areas in desert ecosystems. In order to achieve the aforementioned goals, GeoChip 5.0, a microarray tool available for examining the functional capabilities of microbial communities, was employed.

2. Materials and methods

2.1. Site description

The study area was located at the southeast fringe of the Tengger Desert in the Ningxia Hui Autonomous Region of China (37° 32 N, 105° 02 E, at an elevation of 1250 m). According to the records of the local weather station, the annual average temperature is 10.0 °C, and the annual average precipitation is 180 mm. An uneven seasonal distribution of rainfall leads to more than 80% of precipitation being concentrated from May to September. The natural landscape is dominated by mobile and semi-mobile sand dunes, and wind-induced dune migration travels southeastward at a speed of 3–6 m per year (Li et al., 2010).

To protect the Baotou-Lanzhou Railway from sand burial, a nonirrigated revegetation protection system with a length of 16 km and a width of 500 m was initially established in 1956. A series of 1 × 1 m^2 straw checkerboards (with wheat or rice straw) installed on the mobile sand, and xerophytic shrubs such as *Caragana korshinskii*, *Artemisia ordosica* and *Hedysarum scoparium* were planted in the checkerboards (Li et al., 2003). After the sand surface stabilization, in young biocrusts filamentous cyanobacteria and green algae as pioneers excrete sticky extracellular polymer substances that glue the soil particles together. Lichens and mosses and fungi follow in later stages contributing to cementation (Li et al., 2004). The revegetation protection system was expanded in 1964, 1973, 1987 and 2000 using the same methods as in 1956. Currently, after 60 years of stabilization, more than 95% of the soil surface of the sand-binding vegetation areas is covered by BSCs. Within the large treatment area that was expanded over time, the 1956, 1964 and 1973 revegetation areas are covered mainly by moss-dominated BSCs; the 1987 and the 2000 revegetation area dominated by lichen- and moss-dominated BSCs and lichen-dominated BSCs, respectively (Fig. A). Thus, these revegetated areas provide an ideal experimental site to explore the development process of BSCs along a succession chronosequence using the “space-for-time” approach (Li et al., 2007).

2.2. Sample collection and processing

At the end of June 2017, samples of BSC and the underneath soil (0–5 cm) were collected from five revegetated sites established in 1956 (61 years of succession, 61YR), 1964 (53 years of succession, 53YR), 1973 (44 years of succession, 44YR), 1987 (30 years of succession, 30YR), and 2000 (17 years of succession, 17YR). To decrease errors caused by microtopography, samples were collected from each of the four vertices and the diagonal intersection of a large quadrat using a sterile trowel. In order to avoid false replication, five independent large quadrats (10 × 10 m^2) were selected in the areas of each revegetation age, with at least 20 m between two adjacent blocks along the line transect. Thus, a total of 25 BSC samples and 25 soil samples were collected from each revegetation site (5 quadrats × 5 samples) and mixed together to form a composite BSC or soil sample. Then, samples were divided into 3 subsamples and stored in an ice box (Zhao et al., 2020). After transferring to the laboratory, the samples were immediately thoroughly homogenized and sieved (1 mm) to remove large particles and plant roots. The BSC samples were stored at −80 °C for subsequent molecular analysis, and the soil samples were naturally air-dried at room temperature and further used for physical and chemical analyses.

2.3. Analysis of soil physicochemical properties

The soil water content (SWC) was evaluated by drying fresh soil for 24 h at 105 °C (Nanjing Institute of Soil Research, 1980). The clay, silt and sand contents were analyzed by the pipette method (Li et al., 2007). The soil pH was measured in a 1:5 soil: water suspension with a conventional pH meter (Sartorius Professional Meter PP-20, Göttingen,

Germany). The dichromate oxidation method was used to measure the soil organic matter content (Org) (Nelson and Sommers, 1982). Soil total P (TP) and available P (AP) were measured with perchloric acid digestion and extraction with 0.5 M sodium bicarbonate at pH 8.5, respectively (Sommers and Nelson, 1972). Activities of alkaline phosphatase (AKP) and solid sucrase (SC) were determined using the colorimetric method of Guan (1986). All the physiochemical properties are shown in Table A.

2.4. Measurement of functional gene expression

GeoChip 5.0, a functional gene array tool, was used to analyze the functional genes of the microbial communities associated with P and S cycling. The microbial DNA of the BSC samples was extracted using the E.Z.N.A Soil D.NA Kit (Omega, Bio-Tek, Norcross, GA, U.S.) according to the manufacturer's instructions. The purity of the extracted DNA was assessed using a NanoDrop 2000c spectrophotometer (Thermo Fisher Scientific, Waltham, MA, U.S.), and the final product was quantified using the Quant-It Pico.Green Kit (Invitrogen, Carlsbad, CA, U.S.). The primer set used for PCR was according to Liu et al. (2018). A 600 ng sample of purified DNA was labeled with the fluorescent dye Cy3 (GE Healthcare, CA, U.S.) as described previously (Tu et al., 2014). DNA hybridization was performed in a hybridization oven (Agilent Technologies Inc., Santa Clara, CA, USA) at 67 °C for 24 h. After hybridization, the unbound DNA was removed for array scanning (Roche Nimble. Gen, Inc., Madison, WI, U.S.) and image extraction. To avoid false

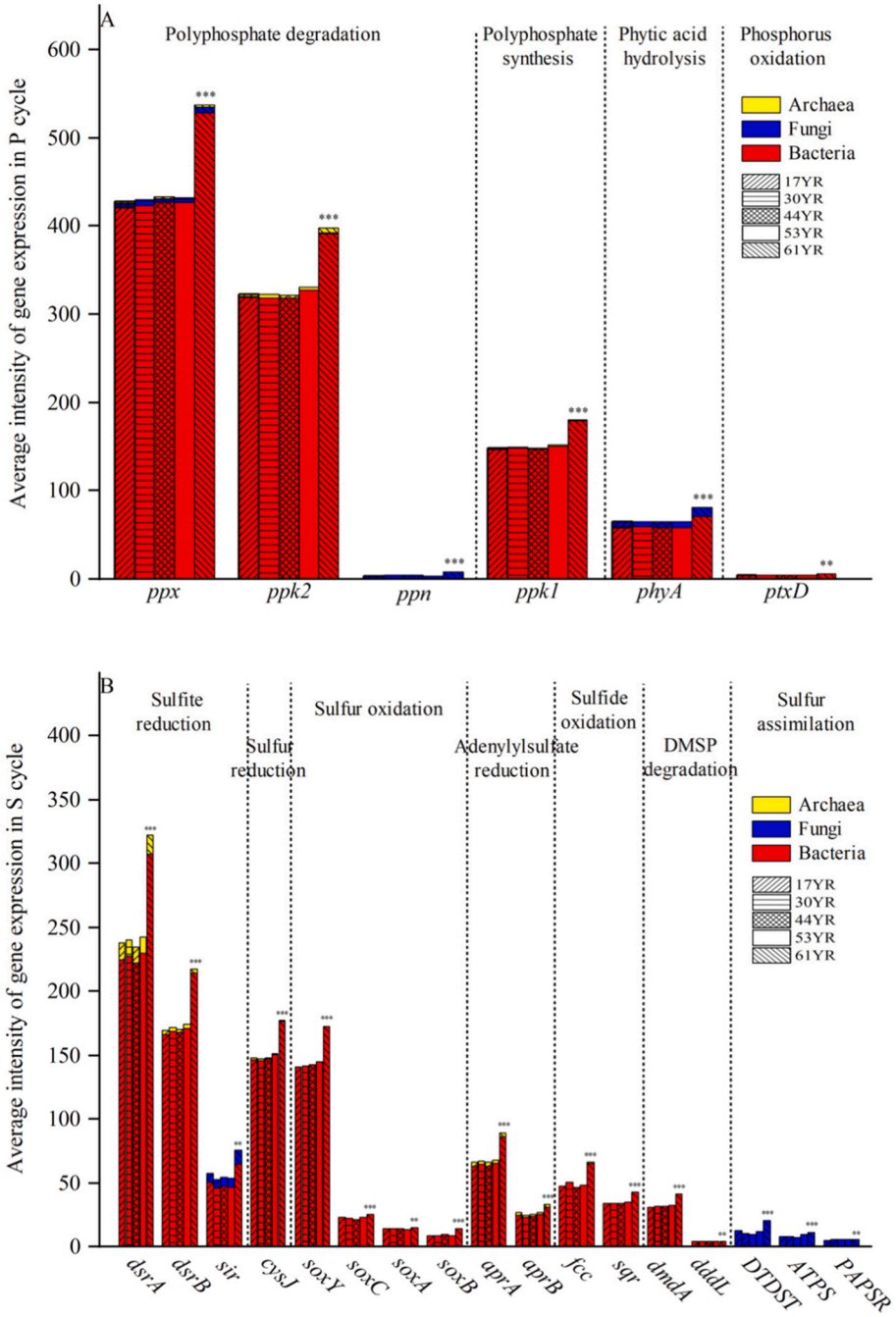

Fig. 1. The average intensity of gene expression involved in different processes of P (A) and S (B) cycles in bacteria, fungi and archaea during BSC succession. 17YR, 30YR, 44YR, 53YR, 61YR represent the revegetation ages. Turkey test was used to assess the significant differences among BSCs of different ages and were denoted by ***P < 0.001, **P < 0.01, *P < 0.05. For explanation of gene abbreviations see Appendix, Table B.

positives, spots with a low signal-to-noise ratio (below 2.0) were removed prior to performing the statistical analysis. The positive signals of all samples were normalized and the species corresponding to the functional gene probes on the chip were annotated. The total abundance of normalized signal intensity of gene expression for each gene category or phyla and classes were calculated by Wang et al. (2014).

2.5. Statistical analysis

SPSS 22.0 (SPSS, Chicago, IL, U.S.) was used for the statistical analysis. ANOVA and Tukey's post hoc test were used to test the differences in the intensity of gene expression among BSC samples of different revegetation ages. The figures were generated using OriginPro 9.0 (OriginLab Corporation, Northampton, MA, U.S.). Redundancy analysis (RDA) was performed using CANOCO 5.0 (Ithaca, NY, U.S.) to assess the relationships between the intensities of the microbial functional genes expression and soil physicochemical properties.

3. Results

3.1. P cycle functional genes at BSC of different successional ages

From five BSC samples, 1319 P cycle probes were obtained and the detected functional genes were related to the processes of polyphosphate degradation, polyphosphate synthesis, phytic acid hydrolysis and phosphorus oxidation (Fig. 1A). The average intensities of all genes expression (6 genes) were significantly higher ($P < 0.01$) in the 61-year-old BSCs than in the BSCs of younger ages. Among the detected genes, the dominant functional genes associated with the P cycle during BSC succession included *ppx*, *ppk2*, *ppk1*, and *phyA* genes (the full name of gene abbreviations see Table B). Polyphosphate degradation was the major process associated with P cycle. Notably, the P-cycling genes were primarily detected in bacteria. However, the *ppn* gene was found only in fungi, the *ppx* and *phyA* genes of low intensity were also detected in fungi. In addition, the *ppx*, *ppk2* and *ppk1* genes of very low intensities were found in archaea.

3.2. S cycle functional genes at BSC of different successional ages

A total of 1792 S cycle probes were obtained across the five different BSC samples, and the functional genes detected participated in the processes of sulfite reduction, sulfur reduction, sulfur oxidation, sulfide oxidation, dimethylsulfoniopropionate (DMSP) degradation, adenylylsulfate reduction and sulfur assimilation (Fig. 1B). Among the detected genes (a total of 27 genes), the dominant functional genes associated with the S cycle during BSC succession included *dsrA*, *dsrB*, *cysJ*, and *soxY* genes. Compared with other S metabolic processes, the highest intensities of gene expression were detected in sulfite reduction process. The intensity of gene expression involved in sulfur oxidation: the *soxY*, *soxC*, *soxA* and *soxB* genes was significantly higher in the 61 YR BSCs as compared with the BSCs of younger successional ages, similarly to the intensities of the *cysJ*, *fcc*, *sqr*, *dmdA*, *dddL*, *aprA*, *aprB*, *DTDST*, *ATPS* and *PAPSR* genes expression. Most of the S-cycling genes detected were from bacteria, whereas the genes involved in sulfur assimilation were all detected in fungi. Moreover, *sir* gene of low intensities were found in fungi, and the *dsrA*, *dsrB*, *aprA* and *aprB* genes of very low intensities were detected in archaea.

3.3. Dominant groups of microorganisms involved in the P and S cycles

The dominant group of microorganisms participated in the P and S cycles belonged to bacteria. BSCs of different ages did not differ on the composition of bacterial phyla involved in P and S metabolic cycles, and Proteobacteria was the dominant group in all metabolic processes (Fig. 2A). Polyphosphate degradation, polyphosphate synthesis, phytic acid hydrolysis, sulfite reduction and sulfur reduction were primarily

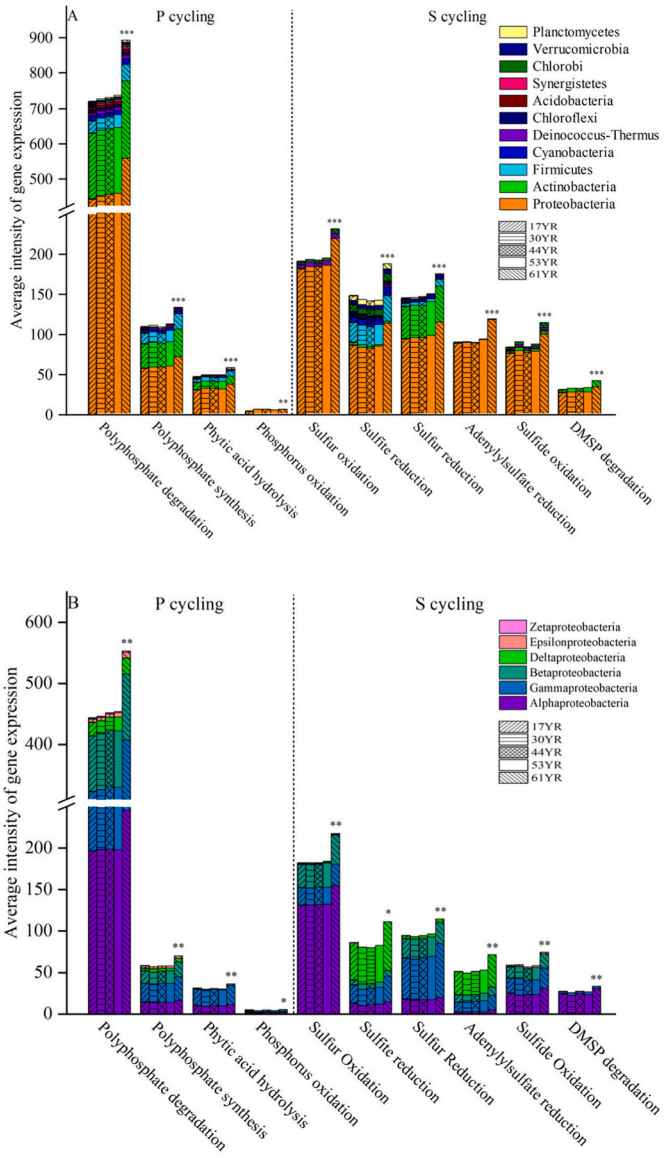

Fig. 2. The average intensity of gene expression involved in different processes of P and S cycles in bacteria at phylum level (A) and in Proteobacteria at class level (B) during BSC succession. 17YR, 30YR, 44YR, 53YR, 61YR represent the revegetation ages. Turkey test was used to assess the significant differences between BSCs of different ages and were denoted by ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

associated with Actinobacteria and Firmicutes, whereas sulfide oxidation and DMSP degradation were only conducted by Actinobacteria. Cyanobacteria, Deinococcus-Thermus, Chloroflexi, Acidobacteria, Synergistetes, Chlorobi, Verrucomicrobia and Planctomycetes also participated in the P and S cycles, although intensities of their genes expression were much lower than those of Proteobacteria, Actinobacteria and Firmicutes. Chloroflexi and Synergistetes were only detected in polyphosphate degradation and sulfite reduction, respectively.

Given the absolute dominance of Proteobacteria in the P and S cycles, a further analysis was performed for Proteobacteria at a lower taxonomic level (Fig. 2B). At the class level, Alphaproteobacteria, Gammaproteobacteria, Betaproteobacteria and Deltaproteobacteria were the dominant functional groups associated with the P and S cycles. Alphaproteobacteria and Gammaproteobacteria essentially participated in all detected processes, while Betaproteobacteria primarily participated in polyphosphate degradation and sulfur oxidation and reduction, and Deltaproteobacteria was the dominant class participated in sulfite

reduction and adenylylsulfate reduction. Zetaproteobacteria and Epsilonproteobacteria were also detected in association with the P and S cycles, although they were not among the dominant classes.

3.4. Relationships between P- and S-cycling microbial genes expression and soil properties

The RDA results showed that the cumulative variation in the intensities of P- and S-cycling functional genes expression explained by four axes (as constrained by the measured soil properties) were 75.1% and 66.0%, respectively, and the first axis explained 71.12% and 65.52% of variations, respectively (Fig. 3). Axis 1 reflects the variability in the expression of functional genes that is associated with gradients in silt and clay contents, nutrient contents (Org, TP, and AP), and enzyme activities (AKP and SC). Of these variables, AKP and SC were associated with the expression of P- and S-cycling genes in highest degree, and the intensity of the expression of genes involved in P- and S-cycling significantly correlated with soil texture, nutrient contents and enzyme activities in the well-developed BSCs (Fig. 3).

4. Discussion

This study assessed the variation in average intensities of genes expression and the composition of dominant microbial taxa involved in the P and S cycles during BSC succession. The major findings showed that the intensities of genes expression involved in the P and S cycles (mainly bacterial) increased with the succession of BSCs and peaked in the 61-year-old BSCs. These functional genes were primarily associated with polyphosphate degradation and sulfite reduction.

4.1. Respond of microbial communities involved in the P and S cycles to BSC succession

One important consideration is how microbial communities involved in the P and S cycles respond to BSC succession. Our analysis showed that microbial communities contribute differentially to both the P and S cycles during BSC succession. In general, the bacterial community demonstrated a more significant role in the P and S cycles than the fungal and archaeal communities during the first 61 years of BSC development. The reason for this difference appears to be a high gene copy abundance (Liu et al., 2018), species diversity (Liu et al., 2017b), and gene intensities expression associated with P and S cycles derived from the bacterial communities (Fig. 1) in comparison with the fungal and archaeal communities. However, fungi were demonstrated as one of the primary assimilators participating in the reduction and incorporation of sulfate to form cysteine (Ravilious and Jez, 2012). Being consistent with previous studies, sulfur assimilation genes were detected only in fungi, suggesting that fungal communities play an indispensable role in the sulfur assimilation process during BSC succession.

In our study, Proteobacteria dominated in all P and S metabolic processes, with Actinobacteria and Firmicutes primarily involved in polyphosphate degradation, polyphosphate synthesis, phytic acid hydrolysis, sulfite reduction and sulfur reduction at different successional stages of BSCs. However, Liu et al. (2017a) studied the compositional changes of bacterial communities in the BSCs of different ages in the Tengger Desert and indicated that the dominant phyla of bacterial communities shifted from Firmicutes to Actinobacteria, and then to Proteobacteria with the development of BSCs. Our results were different from those of the Liu et al. (2017a) findings. The reason for this difference might exist because of microbial communities they studied included not only those associated with P and S cycles, but also those associated with other biogeochemical cycles. Our study revealed that the dominant bacterial phyla in the P- and S-related biogeochemical cycles were consistent at different successional stages of BSCs. This means that the dominant group of functional genes associate with P and S cycles at the phylum level do not change with the succession of BSC. Cyanobacteria are very common and diverse among all BSCs and are the main contributors to C and N fixation in soils during successional processes of BSCs (Belnap and Gardner, 1993). However, our results showed that the intensity of functional gene expression of Cyanobacteria were very low in P and S cycles. This means that Cyanobacteria in the P and S cycles was less important than in the C and N cycles. It also means that different groups of microorganisms have different functions in biogeochemical cycles, in which Cyanobacteria did not substantially participate in the P- and S-cycling processes.

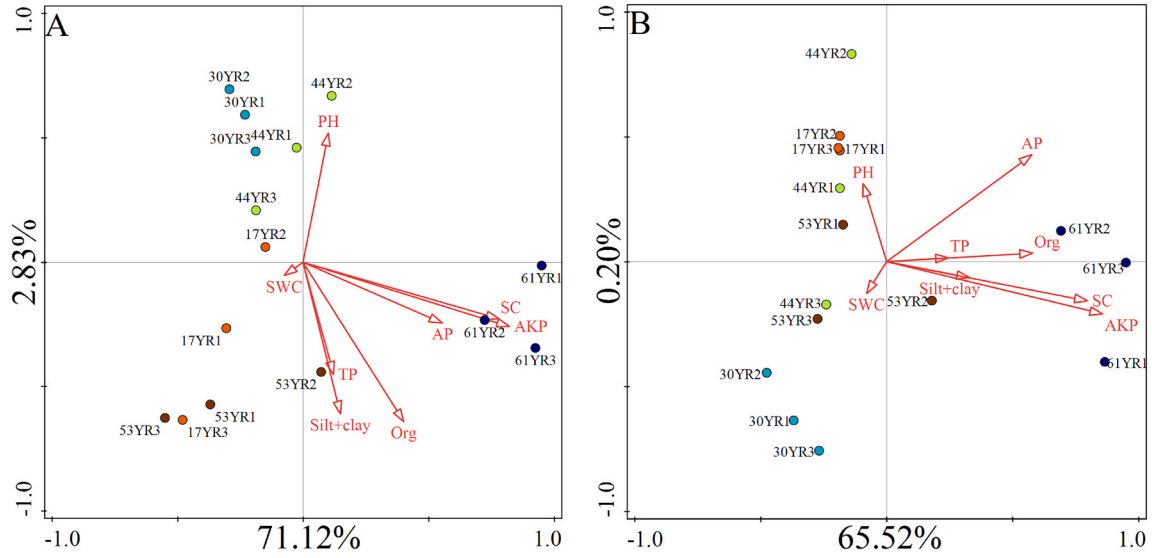

Fig. 3. Redundancy analysis (RDA) showing the relationship between the intensity of microbial functional gene expression involved in the P (A) and S (B) cycles and soil properties during BSC succession. Each circle represents the intensity of microbial gene expression in BSC samples of different ages. Three samples of each age were labeled as 1, 2 and 3. The direction and magnitude of arrows represent the relationship of the intensity of gene expression with soil factors. Abbreviations represent the following soil properties: SC: Soil water content; Silt+ clay: Silt and clay content; Org: Organic matter; TP: Total P; AP: Available P; SC: Solid sucrose; AKP: Alkaline phosphatase.

4.2. Variation in intensity of functional genes expression involved in the P cycles

Our next question was to determine how intensities of gene expression changed involved in the P- and S-cycling processes during the succession of BSC. Phytate is the main component of soil organic P and dominates the P input from land runoff to aquatic systems (George and Richardson, 2008). Phytate can only be hydrolyzed by phytase, and the microbial mineralization of phytate by phytase is a key process for the recovery of P in the biosphere (Lim et al., 2007). However, in our results it showed that the intensity of the *phyA* gene expression was lower than that of the polyphosphate-related genes. This indicated that phosphate input from the external environment to BSC was low, and resulting in lower P transformation and biological effectiveness in BSCs. All BSC organisms take up P in the form of orthophosphate and/or must cleave externally available organic P compounds into an orthophosphate form by phosphatase (Baumann et al., 2018). Our results were consistent with the above research that genes involved in Polyphosphate degradation have high expression intensities compared with other polyphosphate related genes. The restriction of both the P form that can be absorbed by BSC organisms and the reduction of available P through absorption of BSC organisms leads to a high intensity of gene expression related to Polyphosphate degradation in BSCs. The results of our study showed that the average gene intensities related to P metabolism increased significantly in the 61-year-old BSCs. Baumann et al. (2019) studied the biogeochemical P cycling in BSCs during pedogenesis of sandy soil, and found that the concentration of stable P in BSCs greatly decreased, while labile P increased with increasing of mineral weathering. Therefore, it is hypothesized that the intensities of gene expression related to P cycle in BSC increased with the decrease in the size of the sand particle caused by pedogenesis during BSC succession (Duan et al., 2004), and it will need about 61 years to achieve a significant increase in the activity of P cycle related genes in BSC. After this period of development, BSC would greatly influence soil phosphate stability, and have a long-term positive feedback between the P cycle and BSC development, leading to a higher P metabolic potential in the oldest BSCs.

4.3. Variation in intensity of functional genes expression involved in the S cycles

The results of our study showed that most S-cycling genes intensity of their expression changed significantly along the BSC succession were involved in sulfate reduction. This suggests that the sulfate reduction pathway was not the only major process responsible for atmospheric hydrogen sulfide and metal sulfide precipitation (Kaksonen and Puhakka, 2007), but also was a source of sulfur in microbial metabolism during the desert vegetation restoration period. As a result, the emission of sulfide decreased the soil sulfate content, in turn promoted the abundance of sulfate reduction genes. Sulfate reduction and sulfide oxidation were both considered to be mediated by microorganisms (Nübel et al., 2000; Blankenship et al., 1995). In this particular study, the average intensities of gene expression involved in dissimilatory sulfate reduction were found higher than those in any other pathway. It was not because the saturated water content of the soil creates an anoxic environment, but rather because the loss of sulfide and the consumption of oxygen actively promoted the increase of sulfate dissimilatory reduction during the latter stages of BSC development.

4.4. Relationship between microbial P and S cycling and soil physicochemical properties

Another question required to be addressed was whether P and S cycle genes associated with microorganisms promoted the succession of BSCs and the soil quality of revegetation in desert ecosystems. The results of our study showed that soil attributes significantly influenced the expression of microbial functional genes related to P- and S-metabolic processes. Compared with other developmental ages, significant differences in the intensities of genes expression were detected in the 61 YR BSC. This result was visualized by RDA and confirmed that soil silt and clay content, organic matter and enzymatic activity were closely related to microbial functional potential in late stage of BSC development. Caldwell (2005) demonstrated that enzyme activities affect soil fertility by participating in the process of soil nutrient mineralization. As a characterization of soil biological activity, SC is positively correlates with the humic, organic matter and P contents. In addition, AKP is used as an indicator for the direction and intensity of P biotransformation in the soil, and for effective promotion of hydrolysis of organic P compounds (Wang et al., 2005). Our research was consistent with these results and showed that activities of both SC and AKP were significantly correlated with the functional gene potential of the P and S cycles during the succession of BSC (Fig. 3). Our study also found that pH and SWC significantly influenced the intensity of gene expression. Related studies found that the composition and functional potential of microbial communities are closely related to habitat characteristics (Angel et al., 2010), and pH was an important environmental factor affecting the composition of microorganisms, their metabolic activity and surface properties of soil (Rousk et al., 2010). It has been also shown that soil water content strongly affects soil microbial community composition (Drenovsky et al., 2004). The Kern et al. (2019) study devoted to cryptogamic covers in the high Arctic regions showed that there were significant differences in soil organic matter and nutrient content along the moisture gradients. Each of these studies agreed that changes in soil moisture would have an impact on the intensity of microbial gene expression, due to variations of soil nutrients and microbial community compositions resulting from soil water content impacts of the number of microbial species producing functional genes. The appropriate ratio between soil and water improved the soil nutrient content and composition of microbial community structure. It also resulted in the increasing intensity of microbial functional gene expression with the BSC succession, peaked in the 61-year-old BSCs. Both P- and S-cycling microbial potential was improved in the well-developed BSCs, demonstrating noteworthy synergy between these cycles, and soil properties being crucial for shaping the functional potential of microbial community in late stages of BSC development.

5. Conclusions

This study provided data on the microbial functional potential related to the P and S cycles during BSC succession in desert regions, and this potential was significantly enhanced in the 61-year-old BSCs. Overall, the changes in the metabolic potential were primarily related to polyphosphate degradation and sulfite reduction, which were significantly affected by the soil properties. It was also found that a high proportion of functional genes involved in the P and S cycles were detected in the bacterial community; however, even so, fungi communities were shown to play an indispensable role in sulfur assimilation process during BSC succession. This study demonstrated that 61 years of the BSCs development promoted an increase in the microbial functional potential related to the P and S cycles, and this increase is in turn beneficial for the restoration of the desert ecosystem. The results of the study help to better understand the nature of metabolic processes related to the P and S cycles in BSCs.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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