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硅肥与菌剂配施缓解兰州百合连作障碍的关键真菌群落分析

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摘要: 【**目的**】硅与微生物菌剂可缓解连作障碍，研究百合连作土壤中关键微生物群落变化，为微生物菌剂与硅肥在食用百合生产中的应用提供参考。【**方法**】于 2019 年 3 月—2022 年 8 月，进行了为期 3 年的田间试验。供试土壤已连续种植百合 9 年。试验设置 4 个处理：单施硅肥 (SF)，单施微生物菌剂 “Special 8™” (MF)，硅肥与菌剂组合施用 (SMF)，不施硅肥和菌剂的对照 (CK)。在 2020 年、2021 年百合苗期，测定植株地上部分和鳞茎干重、株高和茎粗，并计算其壮苗指数。在 2020 年 7 月 (百合开花期)，每个小区选择 20 株，在距茎基部 10 cm、深 20 cm 处取土壤样品，测定土壤有机质和有效硅含量，采用 ITS 高通量测序测定土壤真菌群落，并分析特有微生物群落。【**结果**】与 CK 处理相比，3 个施肥处理显著促进了百合植株生长，提高了壮苗指数，硅肥与微生物菌剂处理还增加了真菌的相对丰度 (RA) 及多样性，改变了其群落结构。一些微生物群落与壮苗指数或土壤有效硅含量显著相关，真菌属 *Fusarium*、*Dactylonectria*、*Humicola*、*Mortierella*、*Stilbella*，以及种 *Humicola_grisea*，与壮苗指数或土壤有效硅含量呈正相关，另外一些属，如 *Mortierella*、*Stilbella*、*Holtermanniella*，以及种 *Mortierella fatshederae* 与壮苗指数或土壤有效硅含量呈负相关。网络分析结果显示，在相对丰度 (RA)>0.2% 的前 20 个真菌属和前 16 个细菌属中，*Holtermanniella*是唯一与细菌具有相关性的真菌属，该类微生物与细菌属 *Blastococcus*.呈显著负相关，是连接土壤真菌和细菌群落的关键属。微生物功能预测结果显示，与 CK 相比，SF、MF 及 SMF 处理降低了病原真菌数量，增加了益生功能群，如外生菌根真菌、植物腐生菌、叶片腐生菌和丛枝菌根真菌。【**结论**】硅肥与微生物制剂配施可恢复土壤真菌群落多样性，提高植株残体的降解，减少土壤病原微生物数量，优化土壤真菌群落结构，进而缓解兰州百合连作障碍。在该施肥模式下，具有有机物转化功能的益生菌属 *Humicola* 及其种 *H. grisea*，以及具有病原物拮抗功能的益生菌属 *Acremonium*，在改善土壤健康方面发挥着重要作用。

关键词: 兰州百合；土壤真菌多样性；病原菌；腐生菌；硅肥；微生物菌剂

Key fungal communities related to alleviating replanting stress of Lanzhou lily under silicon fertilizer and microbial agents application

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Abstract: 【**Objectives**】Si and microbial application could relieve the crop replanting problems (CRPs). We further studied the change of key microorganisms that are related to the beneficial effects, aiming at provide reference for the manufacture and application of both microbial agents and Si fertilizer in food lily production. 【**Methods**】A field experiment was conducted over a three-year period, from March 2019 to March 2022. The

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experimental field had been continuously cultivated with lily for 9 years. Three treatments were established: silicon fertilizer (SF), microbial agents ("Special 8™" , MF), and combined application of silicon fertilizer and microbial agents (SMF). A control group with blank soil (CK) was also included. At seedling stage of Lanzhou lilies in 2020 and 2021, the shoot and bulb dry weight, and the plant height and stem diameter of Lanzhou lilies were investigated for calculation of seedling index. In July 2020, 20 plants were selected in each plot, and root zone soils were sampled at a depth of 20 cm, 10 cm away from the roots, and then mixed to form a composite sample. The soil available Si and organic matter content were analyzed, and the fungal community structure and some specific microbial groups in soils were determined with high-throughput sequencing of ITS.【**Results**】All the three treatments significantly enhanced the lily plant growth and the seedling index, compared to CK. Besides, SF and MF treatments increased the relative abundances (RA) and diversity of fungal communities, and altered the community structures. The RA of some specific groups were found to be significantly correlated with the seedling index and/or soil available Si. Of them, the RA of the genera *Fusarium*, *Dactylonectria*, *Humicola*, *Stilbella*, and the species *Humicola_grisea* showed a positive correlation, while that of the genera *Mortierella*, *Stilbella*, *Holtermanniella*, *and* the species *Mortierella_fatshederae* showed a negative correlation with seedling index. The genera *Fusarium*, *Stilbella*, the species *Humicola_grisea*, and *Dactylonectria_estremocensis* showed a positive correlation, while the genura *Stilbella,* and the species *Mortierella fatshederae* showed a negative correlation with available Si content. In the co-occurence network of top twenty fungal genera and top sixteen bacterial genera (RA>0.2%), *Holtermanniella* was the only genus that interacted with the bacteria and negatively correlated with bacterial genus *Blastococcus*. *Holtermanniella* was also the most densely connected genera, followed by the genus *Fusarium*, *Didymella* and *Humicola*. In addition, the genus *Holtermanniella* was the key species connecting fungal and bacterial community in soil. Fungal functional prediction revealed that SF, MF and SMF treatments decreased plant pathogens guilds and increased the beneficial guilds *Ectomycorrhizal*, plant saprophyte, leaf saprophyte, and arbuscular mycorrhizal compared to CK.【**Conclusions**】Combined application of silicon fertilizer and microbial agents can alleviate continuous replanting problems of Lanzhou lilies through restoring the fungal community diversity, and promoting plant residue depredation, thus reducing soil born disease incidence. The beneficial genus *Humicola* and its one species *H. grisea* acts as bioconversion, and the genus *Acremonium* acts as plant pathogen inhibitor.

Key words: Lanzhou lily; soil fungi diversity; pathotroph; saprophyte; silicon fertilization; microbial agent

Lanzhou lily (*Lilium davidii* var. *unicolor*), a unique species confined to a limited region in western China[1], stands as the sole sweet lily variety in the country and holds significance as a valuable cash crop in Gansu Province. As asexual and perennial plants, Lanzhou lilies are typically cultivated under conditions necessitating replanting, which unfortunately subjects them to severe consecutive replant problems (CRPs). These issues lead to a decline in quality and a reduction in yield. Hence, there is an urgent need for the development of effective measures to mitigate the CRPs in the Lanzhou lily production system.

Microbial agents have demonstrated plant growth promotion through rhizosphere micro-ecological optimization, as evidenced in diverse crops such as Lanzhou lily[2], cotton (*Gossypium* spp.)[3], eggplant (*Solanum melongena* L.)[4], and watermelon (*Citrullus lanatus*)[5]. Silicon, a beneficial element for both plants and soil microorganisms, positively impacts soil properties, crop growth, and alleviates autotoxicity stress[6–8] . Furthermore, silicon enhances plant resistance to fungal and bacterial pathogens[6, 9] and inhibits plant diseases[9–10]. Our previous research has validated the effectiveness of combining silicon fertilizer with microbial agents in enhancing bulb growth and addressing consecutive replant problems (CRPs)[11].

The causes of consecutive replant problems (CRPs) in Lanzhou lily encompass the accumulation of autotoxic substances secreted by its roots[1, 12], the build-up of pathogenic fungi leading to soil-borne diseases, the deterioration of soil physical and chemical properties, and an imbalance in soil microorganisms[13] . Our previous research has shown that a reduction in soil fungal diversity is associated with the accumulation of specific pathogenic fungi and the occurrence of CRPs in lilies. Furthermore, we have identified several specific fungal pathogens, such as *Fusarium* sp., as causes of soil-borne diseases in lilies[14–15]. Based on this, we hypothesize that the combined application of certain treatments may significantly influence the fungal community in lily replanting soil. However, we currently have limited understanding of the resultant changes in this fungal community. In recent years, microbial agents and bio-organic fertilizers have been extensively utilized to regulate soil microbial communities and enhance soil productivity[11, 16]. However, there have been limited reports on the impact of silicon on soil fungal communities in continuous cropping systems. Therefore, we conducted a two-year field experiment in lily replanting soil to investigate whether the application of silicon fertilizer and microbial agents altered the structure and diversity of soil fungal communities. Additionally, we aimed to identify specific microorganisms that may contribute to the accumulation of beneficial fungi and the depletion of harmful fungi or plant pathogens.

1 Materials and methods

1.1 Field description and experimental design

A field experiment was carried out in Jiangjiashan Village, Lintao County of Gansu Province, located on the Loess Plateau of western China, at an elevation of 2330 m (103°53′12″–103°53′14″ E, 35°49″11″–35°49′13″N). The experimental site experiences arid conditions, and features loessal soil. Lanzhou lily has been cultivated as food in this area for over 140 years. The soil is loessal, characterized by high water-holding capacity, a pH of 7.8, and an organic matter content of 1.3 g/kg.

The field experiment was conducted over a three-year period, from March 2019 to March 2022. The experimental field had been consecutively cultivated with lily for 9 years. The bulb seeds used in the experiment weighed approximately 17 ± 2 grams and were planted at a density of 30 cm × 15 cm per plantlet. The test silicon fertilizer (SiO_2 70% ± 3%) was manufactured by Langfang Wuhe Agricultural Science and Technology Co., LTD, China. The microbial agent was produced by Qingdao Yuanhui Biological Environmental Protection Technology Co., Ltd., China, contained the Special 8™ microbial agent, with a total of 22 isolates comprising 15,000 cfu/g and an organic matter content of ⩾70%. Four treatment groups were designed: silicon fertilizer supplement (SF), microbial agent application (MF), combined application of silicon fertilizer and microbial agent (SMF), and a control group with blank soil (CK). The treatments were randomly arranged with three replicates, and each plot area was 10 m^2 (5 m × 2 m). The remaining fertilization methods and management practices were consistent with those described in the reference[16].

1.2 Plant growth investigation and soil chemical property analysis

On 29 August 2019, and 28 July 2020, five plants in each plot were randomly selected for measuring stem diameter, plant height, biomass of bulbs and shoots. The seedling index was calculated. The root zone soil samples were collected on 28 July 2020, at the flowering stage of Lanzhou lily. In each plot, 4 plants were selected, and root zone soil samples were collected at a depth of 20 cm, and 10 cm away from the roots of each plant, and then mixed to form a composite sample. Each composite soil sample was then divided into two parts: one was stored at −80°C for subsequent DNA extraction, while the other was air-dried for the purpose of soil property analysis.

Soil organic matter was determined by potassium dichromate method, and available Si content by silicomolybdic blue colorimetric method [17].

DNA extraction and PCR amplification followed the procedure described by Yu *et al*[11]. The ITS (Internally Transcribed Spacer) region in this study was chosen for PCR amplification, because it is highly variable and optimal for the shorter reads available with the paired-end Illumina MiSeq. The amplification was generated with the forward primer ITS1-F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and the reverse primer ITS2-R (5′-TGCGTTCTTCATCGATGC-3′). Deep sequencing was performed on the Miseq platform at Allwegene Company (Beijing). After the run, image analysis, base calling, and error estimation was performed using Illumina Analysis Pipeline.

1.3 Data analysis

Data analysis is based on the cloud services of the Beijing Allwegene Company (https://www.allwegene.com, accessed on 25 August 2020). The obtained high-quality sequences were extracted and classified according to the "minimum sample sequence number" before analysis. The effective sequences of the soil samples under different fertilizer treatments were clustered into operational taxonomic units (OTUs) with a similarity degree of 97% using UPARSE[18]. The Venn diagram[18] uses R tools for the statistics and plotting of the OTU clustering results. To determine if the amount of sequencing data from the samples was appropriate and sufficient to reflect the microbial information, rarefaction[19] and Shannon-Wiener[20] and alpha diversity index analysis[21]were calculated with the Mothur software (version 1.45.3). The PCoA (principal co-ordinate analysis) was performed using the R package (version 3.6.0) to examine the statistical significance of the structural similarity among communities in different treatments. The LDA Effect Size analysis[22] was carried out to detect species with significant differences in abundance among fertilizer groups and the threshold was set at 2.5.

The software FUN Guild (https://www.bioincloud.tech/standalone-task-ui/funguild) was used on the fungal function prediction analysis. Using spearman correlation analysis ($P<0.05$, |r|>0 .4) via CYTOSCAPE (version 3.7.0), microorganism co-occurrence network analysis was performed to reveal dormant fungal genera of relative abundance (RA)>0.2% and dominant bacterial genera (RA>0.2%).

1.4 Accession numbers

The sequences obtained in this study were submitted to the NCBI Sequence Read Archive (SRA) under the Bioproject ID PRJNA866339.

2 Results

2.1 Soil available Si and organic matter contents and growth status of Lanzhou lily as affected by Si and microbial agent application

Silicon fertilizer application (SF) increased soil available Si content, while microbial agent application (MF) increased soil organic matter content, and their combined application (SMF) showed the two effects, and resulted in better lily growth indexes (Table 1). In the two-year of experiment, SF and SMF significantly increased the ratio of stem diameter to plant height and the ratio of bulb to shoot biomass, when compared with

表 1 硅肥和菌剂处理对兰州百合植株生长量及土壤有效硅和有机质含量的影响

Table 1 Plant growth of Lanzhou lily and soil available Si and organic matter content under silicon fertilizer and microbial agent treatments

Experimental year	Treatment	Ratio of stem diameter to plant height	Biomass ratio of bulb to shoot	Soil available Si (mg/kg)	Soil organic matter (g/kg)
2019	CK	0.23±0.01 b	1.40±0.02 a	90.51±0.72 c	11.59±0.13 ab
	SF	0.27±0.01 a	1.42±0.02 a	96.23±0.83 ab	11.27±0.10 b
	MF	0.25±0.00 b	1.44±0.03 a	93.27±1.25 bc	12.30±0.46 a
	SMF	0.25±0.00 ab	1.46±0.00 a	98.53±1.19 a	10.24±0.21 c
2020	CK	0.33±0.00 c	2.25±0.01 c	109.34±2.13 c	17.00±0.39 b
	SF	0.34±0.00 b	2.35±0.01 b	121.31±1.02 b	18.02±0.13 b
	MF	0.35±0.00 ab	2.38±0.00 b	118.99±0.79 b	20.07±0.29 a
	SMF	0.35±0.00 a	2.48±0.03 a	128.66±1.75 a	19.30±0.49 a

注：CK、SF、MF、SMF分别代表对照、硅肥、微生物菌剂、硅肥微生物菌剂配施处理。数据后不同小写字母表示处理间差异显著($P<0.05$)。

Note: CK, SF, MF, and SMF represent treatment control, silicon fertilizer, microbial agents, and silicon and microbial agents combined application treatments respectively. Different small letters after data indicate significant differences among treatments ($P<0.05$).

CK. Si application regulated more biomass assignment in the underground parts. In 2020, the ratio of bulb/shoot biomass in SF, MF, and SMF treatments were 13%, 11%, and 28% higher than those in CK, respectively.

2.2 Fungi diversity in root zone soil

A total of 120896 high-quality, chimeric-free reads were carefully screened, and their lengths predominantly fell within the range of 200 to 320 bp in all the soil samples. Specifically, 239271, 199052, 399063, and 364510 sequences were obtained from soil samples subjected to CK, SF, MF, and SMF treatments, respectively. To normalize and standardize the sequencing depth of the reads, all samples were randomly subsampled to a uniform count of 48346 reads. Across all four treated soils, a total of 646 operational taxonomic units (OTUs) were identified. Specifically, 130, 97, 129, and 117 unique OTUs were found in the CK, SF, MF, and SMF treatments, respectively (Fig. 1A). The rarefaction curves (Fig. 1B) and Shannon-Wiener indices (Fig. 1C) both demonstrated that the sequencing data was sufficiently extensive to accurately represent the microbial communities present in the soil samples.

Alpha diversity indices were evaluated using OTUs, revealing significant variations in the Chao1 index among the different treatments (Fig. 2A). Beta diversity analysis, conducted using principal coordinate analysis (PCoA), successfully represented the sample data. Specifically, the three replicate soil samples from each treatment grouped together, with the exception of one sample in the SF treatment (Fig. 2B). The first principal coordinate axis (PCoA1), which accounted for 25.04% of the total variation, and the second principal coordinate axis (PCoA2), which contributed 16.78% to the total variation, collectively explained 41.82% of the total variation observed in the dataset (Fig. 2B).

2.3 Common fungal groups in soils under different treatments

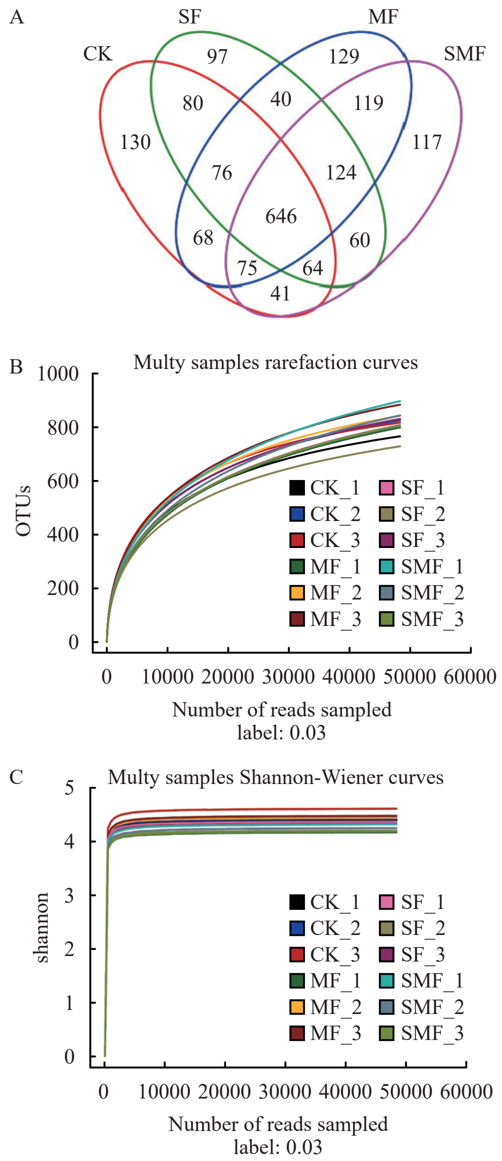

图 1 四个处理下土壤真菌群落的变化 (A，维恩图；B, 土壤样品稀释曲线; C, 香农-威纳指数曲线)

Fig. 1 Venn diagram (A), dilution curve (B), and Shannon-Wiener curve (C) of soil fungal community as affected by silicon fertilizer and microbial agent application

注：CK、MF、SF、SMF 分别代表对照、微生物菌剂、硅肥以及硅肥和微生物菌剂配施处理，处理代号后 1、2、3 代表每个处理的 3 个重复。

Note: CK, SF, MF, and SMF represent treatment control, silicon fertilizer, microbial agents, and silicon and microbial agents combined application treatments respectively, and the number 1, 2, 3 after treatment codes represent the three replicates.

Various fungal groups were identified across different taxonomic levels (Fig. 3). At the phyla level, a total of 36 groups were discerned, and the dominant phyla with relative abundance (RA) > 2% included *Ascomycota, Mortierellomycota,* and *Basidiomycota.* At the class level, the dominant groups (RA>5%) were *Sordariomycetes, Mortierellomycetes, Eurotiomycetes,* and *Pezizomycetes*. At the order level, a total of 96 orders were yielded with the dominant groups (RA>5%) being *Hypocreales, Mortierellales, Pezizales, Sordariales and*

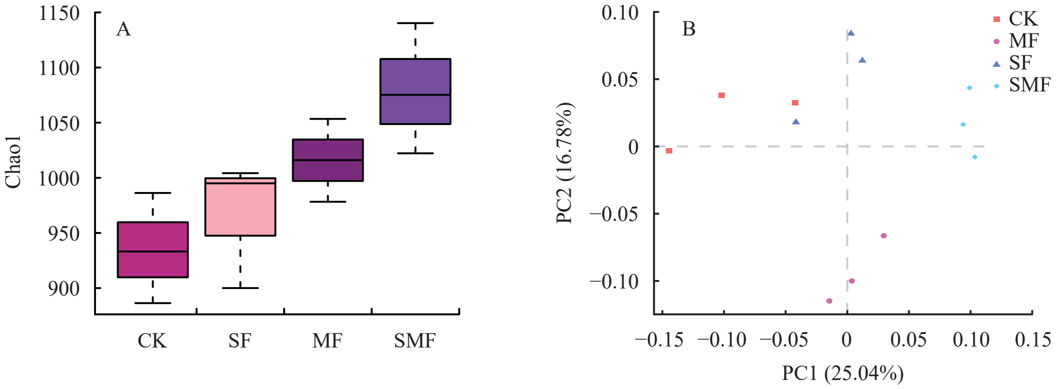

图 2 4 个处理下土壤真菌群落多样性分析

Fig. 2 Diversity analysis of soil fungal community affected by silicon fertilizer and microbial agent application

注：CK、SF、MF、SMF 分别代表对照、硅肥、微生物菌剂、硅肥微生物菌剂配施处理。采用操作分类单元（OTUs）评估了 Alpha 多样性指数，结果显示不同处理组间的 Chao1 指数存在显著差异（图 2A）。通过主坐标分析（PCoA）进行的 Beta 多样性分析，成功表征了样本数据。具体而言，除 SF 处理中的一个样本外，每个处理组的三个重复土壤样本均聚类在一起（图 2B）。第一主坐标轴（PCoA1）解释了总变异的 25.04%，第二主坐标轴（PCoA2）解释了 16.78% 的变异，两者共同解释了数据集中观察到的总变异的 41.82%（图 2B）。

Note: CK, SF, MF, and SMF represent treatment control, silicon fertilizer, microbial agents, and silicon and microbial agents combined application treatments respectively. Alpha diversity indices were evaluated using OTUs, revealing significant variations in the Chao1 index among the different treatments (Fig. 2A). Beta diversity analysis, conducted using principal coordinate analysis (PCoA), successfully represented the sample data. Specifically, the three replicate soil samples from each treatment grouped together, with the exception of one sample in the SF treatment (Fig. 2B). The first principal coordinate axis (PCoA1), which accounted for 25.04% of the total variation, and the second principal coordinate axis (PCoA2), which contributed 16.78% of the variation, collectively explained 41.82% of the total variation observed in the dataset (Fig. 2B).

Onygenales. Moving further to the family level, a total of 205 families were recognized, with the dominant families (RA>5%) being *Mortierellaceae, Nectriaceae, Hypocreales fam Iertae sedis, Pyronemataceae,* and *Onygenales fam Incertae sedis*. Finally, at the genus level, a total of 380 genera were detected, the dominant genera (RA>5%) included *Mortierella, Acremonium, Chrysosporium, Gibberella, Humicola,* and *Aleuria,* among which the most enriched species were *Mortierella alpina, Aoremonium nepalense,* and *Chrysosporium synchronum*.

2.4 The specific fungal groups in soils under different treatments

LEfSe analysis illuminated the disparities in the soil fungal community among the treatments at various taxonomic levels (Fig. 4). Notably, several key or dominant fungal groups exhibited significant differences across the treatments. The figure's panels B, C, and D depict the significantly altered genera between pairs of treatments, respectively.

Further analysis delved into the correlation between fungal genera and species (with relative abundance > 0.2%) and both the seedling index and soil available silicon (SF) content. The results revealed that five genera and three species were significantly correlated with either the seedling index or the available Si content, and intriguingly, five of these were found to be associated with both indices (Table 2).

2.5 Prediction of fungal function

The FUN Guild categorizes fungal communities into four fundamental trophic types: symbiotrophs, saprotrophs, pathotrophs, and others. When compared to the CK, the pathotroph fungi, which are known to damage host cells, decreased in the SF, MF, and SMF treatments. Additionally, the saprotroph fungi decreased in the SF, MF, and SMF treatments (Fig. 5A).

We further identified 19 guilds that belonging to these four basic trophic types. Among them, three were classified as putatively beneficial groups, and one as a harmful group. The beneficial groups, which included Ectomycorrhizal fungi, plant saprophytes, and leaf saprophytes, exhibited an increase in abundance in the SF, MF, and SMF treatments compared to the CK. Conversely, the plant pathogens decreased in abundance compared to the CK. Furthermore, arbuscular mycorrhizal fungi were found to be increased in abundance in the MF treatment compared to the CK (Fig. 5B).

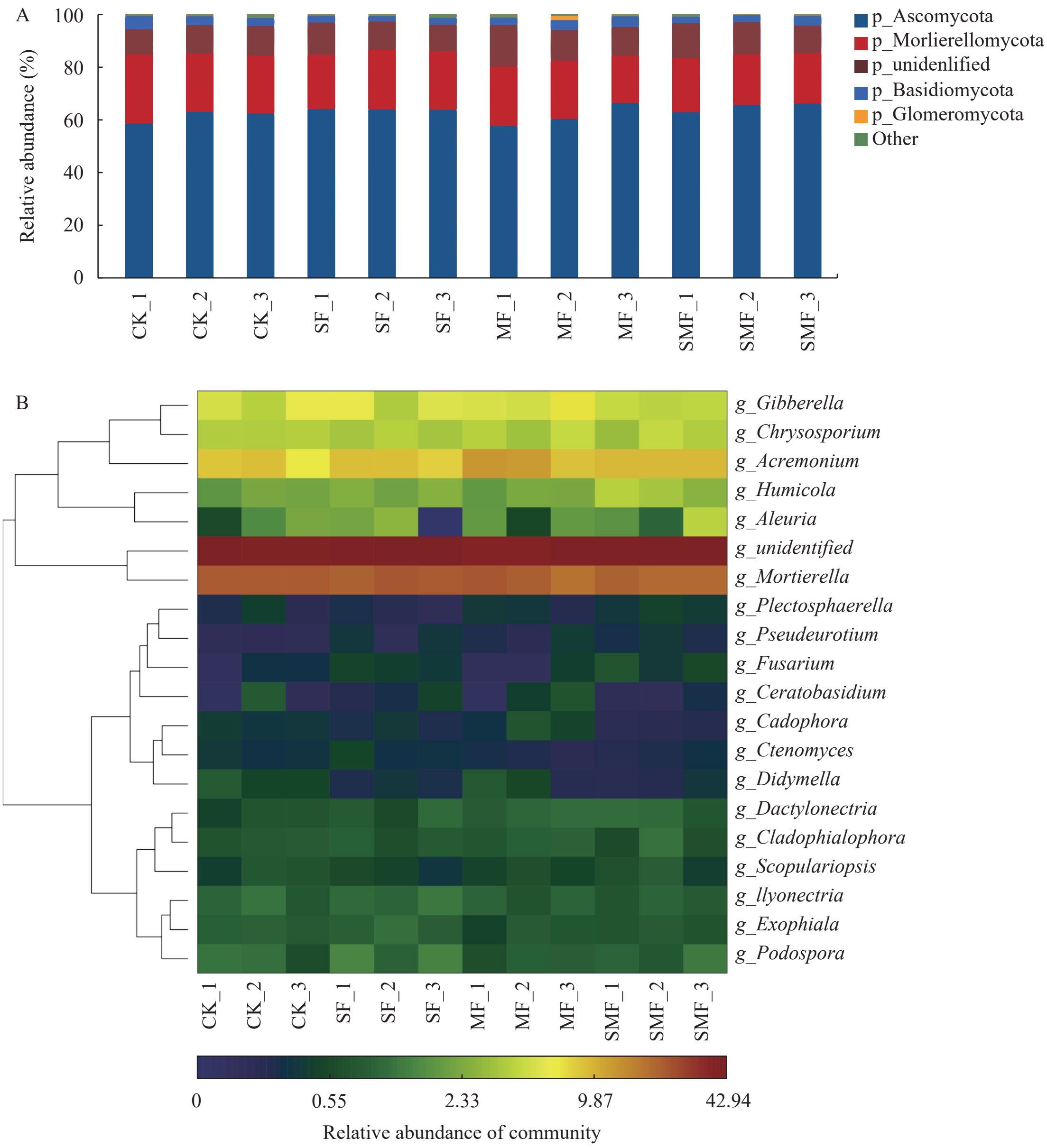

图 3 土壤样品真菌群落门水平柱状图 (A) 属水平热图 (B)

Fig. 3 Barplot of soil fungal community at the phylum level (A) and heat map at the genus level (B) in each soil sample

注：CK、SF、MF、SMF 分别代表对照、硅肥、微生物菌剂以及硅肥和微生物菌剂配施处理，处理代号后的 1、2、3 代表每个处理的 3 个重复。

Note: CK, SF, MF, and SMF represent treatment control, silicon fertilizer, microbial agents, and silicon and microbial agents combined application treatments respectively, and the number 1, 2, 3 after treatment codes represent the three replicates.

2.6 Co-occurrence network of fungal and bacterial groups as affected by silicon fertilizer and microbial agent application

We performed network analysis to reveal the interaction within fungal and the sixteen bacterial communities[23] at the genus level (Fig. 6). Among the bacterial genera, RB41 was the the most densely genus, and positively correlated to the other 10 bacterial genera. And *Holtermanniella* was the only fungal genus interacting with the bacteria, it was negatively correlated with bacterial genus *Blastococcus* (P<0.05).

3 Discussion

3.1 Fungal diversity and functional guilds related to soil health under application of silicon fertilizer and microbial agents

Microorganism diversity is an important part of soil biodiversity. In nature, soil biodiversity has a positive

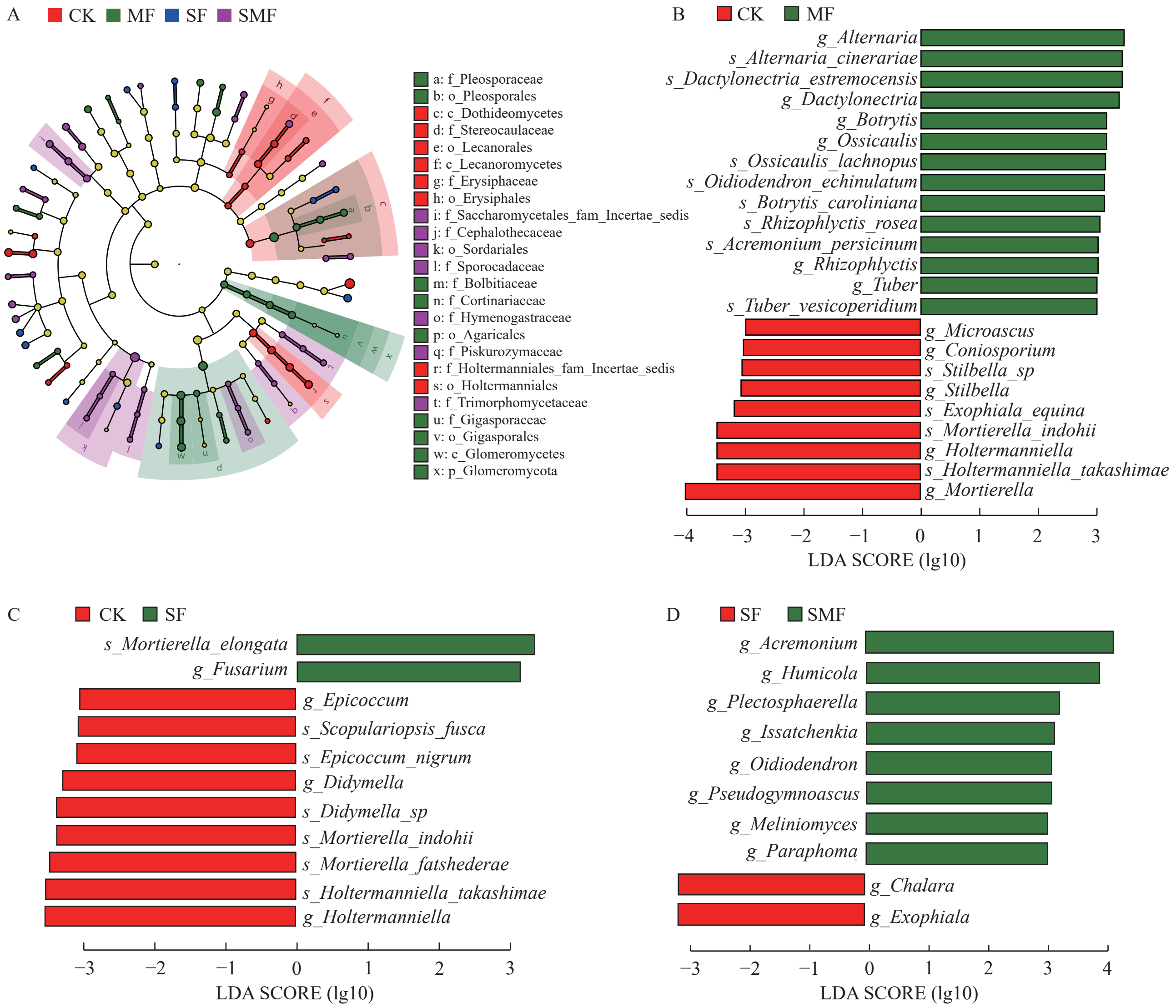

图 4 不同处理土壤样品的土壤真菌群落的 LEfSe 分析

Fig. 4 LEfSe analysis of soil fungal community as affected by silicon fertilizer and microbial agent application

注：CK、MF、SF、SMF 分别代表不施加对照、微生物菌剂、硅肥以及硅肥和微生物菌剂配施处理。图 A 为 4 个处理下门、纲、目、科水平的支系图；图 B、C、D 分别为 CK 与 MF、CK 与 SF、SF 与 SFM 之间属水平的 LDA 图。

Note: CK, MF, SF, and SMF represent treatment control, microbial agents, silicon fertilizer, and silicon and microbial agents combined application treatments, respectively. Fig. A is the cladogram among four treatments at the phylum, class, family and order levels; Fig. B, C, D are LDA diagrams between CK and MF, CK and SF, and SF and SFM at the genus levels, respectively.

correlation with the productivity and sustainability of a system[24] . Previous research showed the loss and simplification of soil fungal community composition in the Lanzhou lily replanting system, which was thought as one reason for soil degradation in this replanting system. In this study, the fungal richness in the Lanzhou lily root zoon soil were significantly increased by the Si and microbial agent application, and the effect of the treatments were as elevated in order of CK<SF<MF<SMF (Fig. 2A), both PCoA and LEfSe analysis (Fig. 2B, and Fig. 4) also showed significant changes of soil fungal communities structures caused by application of silicon fertilizer, microbial agent, or both together.

To our excitement, this study unveiled that SF, FM, and SFM treatments significantly reduced the relative abundance of certain pathotroph fungi, particularly those belonging to the plant pathogen guild, which are notorious for destroying host plant cells and precipitating plant diseases (Fig. 5A, B). Numerous studies have documented silicon’s capacity in soil to bolster plant resistance, curb plant diseases[10], and elicit a defensive mechanism in plants against autotoxicity stress, while

表 2　优势真菌 (RA>0.2%) 与土壤有效硅含量和幼苗指数的相关性

Table 2　The dominant fungal groups (RA>0.2%) correlated significantly with soil available Si content or the seedling index

Fungus taxa	Available Si (*r*)	Seedling index (*r*)	Relative abundance (RA, %)
g__*Fusarium*	0.62*	0.51	0.40
g__*Dactylonectria*	0.49	0.63*	0.82
g__*Humicola*	0.65*	0.63*	2.54
g__*Mortierella*	−0.49	−0.68*	20.88
g__*Stilbella*	−0.78**	−0.88**	0.25
g__*Holtermanniella*	−0.85**	−0.80**	0.25
s__*Mortierella_fatshederae*	−0.68*	−0.58*	0.61
s__*Humicola_grisea*	0.65*	0.63*	2.54
s__*Dactylonectria_estremocensis*	0.48	0.63*	0.82

注：共检测到 23 属 29 种 (RA>0.2%)；*—*P*<0.05，**—*P*<0.01；幼苗指数=(幼苗直径/株高 + 地下部分干生物量/地上部分干生物量)×植株干重， 数据来自2020年各处理。

Note: A total of 23 genera and 29 species (RA>0.2%) were detected; *—*P*<0.05; **—*P*<0.01; Seedling index = (shoot diameter/plant height + dry biomass ratio of underground part/aboveground part) × plant dry weight. The data are from each treatment in 2020.

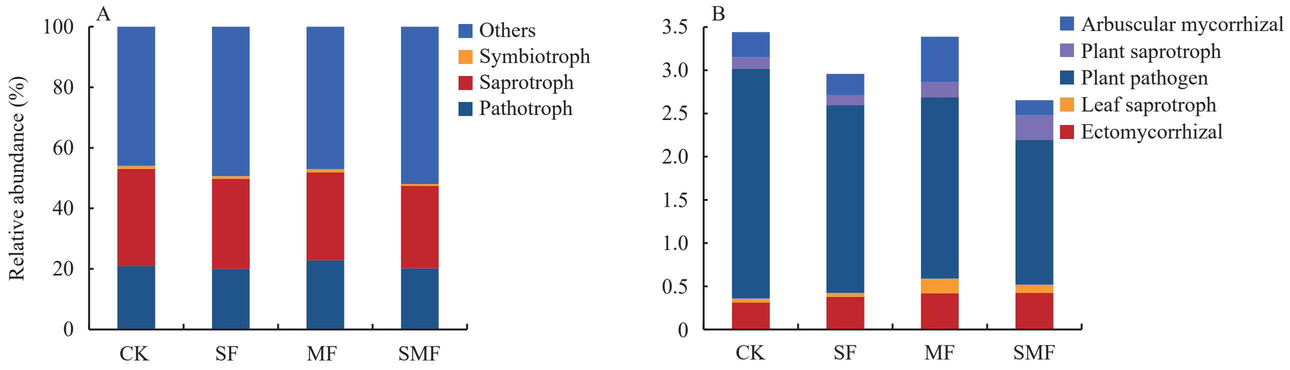

图 5　不同处理 4 类营养型真菌种群的相对丰度 (A) 及进一步细分的 19 种真菌类型 (B)

Fig. 5　The relative abundance of four trophic types of fungal groups in different treatments (A) and the 19 guilds obtained by further classification (B)

注：CK、SF、MF、SMF 代表空白对照、硅肥、微生物菌剂以及硅肥和微生物菌剂配合处理。图 A 中, 腐生型真菌相对丰度在 4 个处理间差异显著 (*P*<0.05)。

Note:CK, SF, MF, and SMF represent treatment control, silicon fertilizer, microbial agents, and silicon and microbial agents combined application treatments, respectively. In Fig. A, the relative abundance of saprotroph fungi is significantly different among treatments (*P*<0.05).

also mitigating environmental stressors[6, 10] . Our research further substantiated silicon’s impact on fungal community structures. Specifically, all SF, MF, and SMF treatments decreased the relative abundance (RA) of aprotroph fungi in soil while enhancing the RA of three beneficial guilds: Ectomycorrhizal, plant saprophyte, and leaf saprophyte. Notably, the MF treatment also markedly increased the RA of arbuscular mycorrhizal fungi (AMF) (Fig. 5A, B). These beneficial guilds derive nutrition from decomposing plant residues, thereby contributing to the enhancement of soil organic matter (Table 1).

Our prior research indicated that soil properties exert a profound influence on fungal communities. As the replanting period elongates, soil nutrient levels decline and become unbalanced, leading to a reduction in total lily fungal abundance and diversity. These changes changes are intimately linked to the presence of continuous replanting problems (CRPs) in lilies[15] . Organic matter has been reported to significantly impact the microbial community in potato rhizosphere soil across different monoculture durations[25] . Furthermore, organic matter content positively correlates with fungal community abundance in potato rhizosphere soil[26]. Our findings revealed that the organic matter content increased

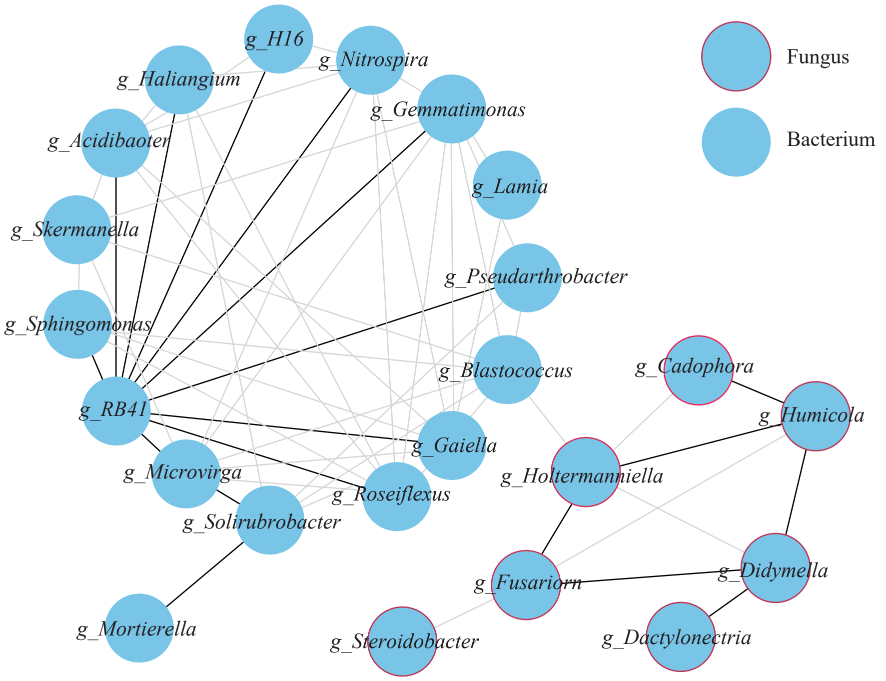

图 6 土壤样品中主要真菌属和细菌属 (相对丰度>0.2%) 的网络分析

Fig. 6 Network analysis of the major fungal and bacteria genera (relative abundance >0.2%) in soil samples

注：16 个细菌属来自已发表的网络分析结果[25]。黑线和灰线分别代表负相关和正相关。

Note: 16 bacteria genera were from the published network analysis results[25]. Black and gray lines represent negative and positive correlation, respectively.

significantly in MF and SMF treatments when compared to CK and SF treatments[2]. In summary, under the combined application of silicon fertilizer and microbial agents, fungal diversity was partially recovered, and soil nutrition levels were improved. These improvements are beneficial to mitigating the incidence of soil-borne diseases.

3.2 Application of silicon fertilizer and microbial agents brought into soil with special fungal members related to soil health

The phylum Ascomycota, comprising predominantly saprotrophic fungi, plays a pivotal role in decomposing soil organic matter and plant-animal residues, maintaining ecological dominance in soil microbial communities[27]. Cao *et al*[6] and Abuduaini *et al*[26] reported it as the predominant saprophytic fungi in replanting soils treated with microbial agents. Similarly, in our research, Ascomycota emerged as the top phylum (with an average relative abundance (RA) exceeding 60%) (Fig. 3), highlighting its crucial role in decomposing soil organic matter.

Intriguingly, we discovered a dominant genus, *Humicola*, and a species, *Humicola grisea*, both belonging to the Ascomycota phylum. Their RA in the SMF treatment was significantly higher than in the SF treatment (Fig. 4). Furthermore, they were positively correlated with the seedling index and available silicon (Table 2). Numerous studies have explored fungi of the *Humicola* genus, revealing that many species exhibit hydrolytic activities in soil[28] . Specifically, *H. grisea var. thermoidea* is recognized as a robust cellulase producer[29]. Scientists have demonstrated its potential as an industrial microorganism, particularly for the bioconversion of sugar cane bagasse, which can yield valuable by-products such as components for animal feed and plant fertilizers .

Our previous study demonstrated that the accumulation of fungal genera *Acremonium, Fusarium, Gibberella, Alternaria, Cryptococcus, Phoma*, and *Ilyonectria*, together with the depletion of beneficial genus *Penicillium* occurred in soils planted Lanzhou lilies consecutively for 0 to 9 years[15] . The saprophytic genus *Acremonium* is reported having inhibitory effect on pathogenic fungi[30] . In this study, *Acremonium* was significantly accumulated in MF treatment (Fig. 3), and therefore was putatively beneficial to soil heath.

The genus *Fusarium* in the lily root zone soil was fund positively ($P<0.05$) correlated with soil available silicon content, but not correlated with the seedling index (fig. 4B, Table 2). Among the five dominant subset species of *Fusarium*, three species (*F. solani.*, *F. oxysporum*, and *F. tricinctum) were* reported as the lily wilt disease pathogen[14], and the RA of all these five species were not significantly different among the four treatments. We previously reported that the accumulation of the genus *Fusarium* in lily rhizosphere soil was closely correlated to lily CRPs[15] , while this research detected several fungal groups correlated with soil available Si content or seedling index (Table 2). In addition, the network analysis demonstrated the interaction between fungal and bacterial communities, in particular, fungal genus *Holtermanniella* seemed act as hub in linking fungal and bacterial information network (Fig. 6). Moreover, a large number of sequences were still unidentified in this study, therefore, more researches are necessary to identify these above mentioned sequences and the related specific microorganism, aiming to explore the function of special microorganisms in the future.

4 Conclusion

The application of silicon and microbial agents, either individually or in combination, has the potential to restore fungal diversity, enhance soil organic matter content, and improve the growth index of lily seedlings in replanted soil. And under this fertilization mode, the beneficial genus *Humicola* and its one species *H. grisea* acted as bioconversion, and the genus *Acremonium* acted as plant pathogen inhibitor, both playing important role in improving soil health.

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