



# 摩西斗管囊霉改善连作花生根际土壤的微环境

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**摘要** 花生(*Arachis hypogaea*)长期连作导致土壤环境恶化, 严重影响产量和品质。丛枝菌根真菌(AMF)作为有益真菌能够与80%的陆生植物根系形成共生关系, 这种共生体能够改善植物根系微环境, 提高植物对营养物质的吸收和对逆境胁迫的抗性。为了探究AMF对花生连作土壤微环境的影响, 该研究通过对花生连作土壤接种和未接种摩西斗管囊霉(*Funneliformis mosseae*)试验, 在花生不同生长期检测根际土壤的酶活性、土壤矿物质含量、土壤微生物群落结构和多度的变化情况, 以及对连作花生产量和品质的影响。研究结果表明: 1)摩西斗管囊霉能够显著提高花生根际土壤蔗糖酶、脲酶、碱性磷酸酶和硝酸还原酶的活性; 2)摩西斗管囊霉显著增加花生连作土壤中全氮、全磷、全钾、速效磷和速效钾的含量; 3)摩西斗管囊霉显著降低土壤中有害真菌曲霉属(*Aspergillus*)的多度, 减少镰刀菌属(*Fusarium*)和赤霉菌属(*Gibberella*)的多度, 但是没有达到显著水平, 显著增加有益细菌放线菌(*Gaiella*)属的多度; 4)摩西斗管囊霉显著提高连作花生的产量, 增加籽仁中蛋白质、油酸和亚油酸的含量。因此, 摩西斗管囊霉能够改善连作花生根际土壤微生态环境, 增强连作土壤对致病菌的抵抗能力, 从而缓解连作障碍对花生根系的危害。

**关键词** 花生; 连作; 丛枝菌根真菌; 根际微生态; 微生物

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## Improvement of continuous microbial environment in peanut rhizosphere soil by *Funneliformis mosseae*

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### Abstract

**Aims** Long-time continuing cropping of peanut (*Arachis hypogaea*) would result in soil deterioration, which would seriously affect the productivity and the quality of peanut. Arbuscular mycorrhizal fungi (AMF) have been used as a fertilizer that may improve root microenvironment, increase nutrient uptake and stress resistance of the plants. This study investigated the effects of *Funneliformis mosseae* on peanut rhizosphere microenvironment under continuing peanut cropping.

**Methods** We conducted an experiment to examine soil properties, peanut productivity and quality between the treatments of: (1) peanut seedlings inoculated with *F. mosseae* in continuous cropping soil, and (2) peanut seedlings without the inoculation.

**Important findings** We observed that *F. mosseae* significantly enhanced the activity of sucrase, urease, alkaline phosphatase and nitrate reductase in soil, significantly increased the soil contents of total nitrogen, total phosphorus, total potassium, available phosphorus and available potassium. Meanwhile, the abundances of *Aspergillus*, *Fusarium* and *Gibberella* in the rhizosphere soil of continuous cropping were decreased, while the abundances of

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*Gaiella* was significantly increased comparing to the treatment without *F. mosseae* inoculation. In addition, *F. mosseae* significantly increased the peanut yield and quality, including protein, oleic acid and linoleic acid content. Our results suggested that *F. mosseae* improve the peanut rhizosphere environment, alleviate the obstacles of continuous cropping.

**Key words** peanut; continuous cropping; arbuscular mycorrhizal fungi; rhizosphere microecology; microorganism

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花生(*Arachis hypogaea*)是我国重要的油料作物,在保障我国食用植物油安全等方面具有举足轻重的地位。近年来花生主产区相对集中,加上种植土壤和种植面积受限,在花生主产区连作现象十分严重(万书波等, 2007)。连作花生植株表现为根系活力降低、形态矮小、光合作用减弱、病虫害几率增加、产量降低、品质下降等连作障碍现象(封海胜等, 1999; 李孝刚等, 2015; 滕应等, 2015)。研究表明,花生长期连作导致土壤中各种酶活性降低(李忠等, 2018)。孙秀山等(2001)研究发现,随着连作年限的增加,土壤中蔗糖酶、脲酶和磷酸酶的活性呈下降趋势。土壤酶活性的降低造成了土壤中磷、钾、钙、硼、铁等元素匮乏,导致植株不能从土壤中吸收所需的营养元素,从而影响其正常生长发育(封海胜等, 1999; 滕应等, 2015)。另外,长期花生连作严重影响土壤微生物平衡,土壤真菌中病原性真菌数量明显增加,而有益真菌多样性和数量则相应减少(Chen *et al.*, 2012; Li *et al.*, 2014)。土壤中的有益细菌也被连作障碍定向选择,土壤微生物从细菌型向真菌型转变(Chen *et al.*, 2014)。土壤微生物菌落结构失衡是连作花生病虫害加剧,产量和品质下降的一个重要原因。

大量的研究表明,丛枝菌根真菌(AMF)作为有益菌在农业生产中发挥着重要的作用,在农业可持续发展及生态保护等方面具有重要意义(屈明华等, 2019)。AMF属于球囊菌亚门,能与80%的陆生植物形成丛枝菌根(AM)。研究表明,AMF侵染植株根系后,通过一系列分子信号作用,诱导根系发生改变,从而与其建立共生体,为寄主植物提供养分和水分(Rouphael *et al.*, 2015),增加植株产量,提高果实品质(Jakobsen *et al.*, 2001; 韩冰等, 2012)。另外,AMF的菌丝体产生糖蛋白保护根系免受土壤病原菌的侵袭,对植物的土传病害有抑制作用(Azcón-Aguilar & Barea, 1997; 周宝利等, 2015); AM改变植物根系

的激素含量和其他次生物质含量,从而调节寄主生长发育(Pozo *et al.*, 2015); AM还能够与根际的其他微生物发生相互作用,如与根瘤菌、放线菌等发生相互作用,改善植物根际的微生物环境(Bagyaraj *et al.*, 1979)。上述研究表明,AMF在土壤改良和植物生长发育方面发挥着重要的作用。

我们前期的研究发现,接种摩西斗管囊霉(*Funneliformis mosseae*)能够促进连作条件下的花生植株生长(Cui *et al.*, 2019);但是,摩西斗管囊霉如何改善连作花生土壤微环境还有待于进一步研究。本研究通过对接种和未接种摩西斗管囊霉连作花生根际土壤酶活性、矿物质含量、土壤真菌和细菌群落结构和多度等进行比较分析,明确摩西斗管囊霉对连作花生土壤的改良效果,探讨摩西斗管囊霉在土壤退化中的应用潜力,为进一步深入研究AMF在农业生产中的应用提供实践和理论依据。

## 1 材料和方法

### 1.1 供试材料

取连作5年花生的土壤0–20 cm的耕土层,经钴60辐照灭菌后室温放置5天。采用盆栽试验,盆口直径为39 cm,高30 cm,每盆装土18 kg。花生品种为‘花育22’,种子经消毒后放入黑暗培养箱,待根长至3–5 cm时移入灭菌花生连作土壤中。每盆3穴,每穴2粒。AMF来自北京农林科学院植物营养与资源研究所,编号为BGCHLJ02,种名为摩西斗管囊霉。试验处理分为:(1)接种摩西斗管囊霉(花生播种时种子周围均匀撒入含有摩西斗管囊霉孢子的菌土), (2)未接种摩西斗管囊霉(播种时种子周围均匀撒入等量的经高温高压灭菌的菌土作为对照,CK)。所有处理均施等量基肥,折合每kg土共施氮( $\text{CO}(\text{NH}_2)_2$ ) 0.521 g、磷( $\text{P}_2\text{O}_5$ ) 0.172 g、钾( $\text{K}_2\text{O}$ ) 0.285 g。摩西斗管囊霉按每穴400个孢子(10 g含有摩西斗管囊霉孢子的沙土)在播种时撒入种子周围的土壤中。出苗

后每穴保留长势一致的1株健康苗。每个试验处理120盆花生植株, 试验设6次重复。为了减少外界环境对试验的影响, 整个试验在旱棚中进行。

## 1.2 研究方法

根际土壤样品采集分别于出苗后30天(苗期)、60天(盛花期)、90天(荚果膨大期)、120天(收获期)取花生根际土样。取样方法: 将花生根系从土壤中挖出, 抖落与根系松散结合的土壤, 然后用刷子将与根系紧密结合的土壤刷下来作为根际土壤, 各处理均取3次重复, 进行下一步试验。

土壤酶活性测定参照关松荫(1986)的方法: 蔗糖酶的测定采用3,5-二硝基水杨酸比色法, 脲酶的测定采用苯酚-次氯酸钠比色法, 碱性磷酸酶的测定采用磷酸苯二钠法, 硝酸还原酶活性测定采用 $\alpha$ -萘胺比色法。

土壤养分含量检测参考鲍士旦(1999)的方法: 全氮含量采用凯氏定氮法检测, 全磷含量采用酸溶-钼锑抗比色法测定, 全钾含量采用氢氧化钠熔融-火焰分光光度法测定, 碱解氮含量采用碱解-扩散法测定, 速效磷含量采用碳酸氢钠-钼锑抗比色法测定, 速效钾含量用醋酸铵提取-火焰分光光度法测定。每个指标均重复3次。

连作花生根际土壤真菌和细菌测序: 在花生盛花期和收获期取根际土壤经液氮快速冷冻后放入 $-80^{\circ}\text{C}$ 超低温冰箱, 每个处理重复3次; 然后提取花生根际土壤的DNA, 经质量检测合格后送上海美吉生物医药科技有限公司进行PCR扩增和测序, 扩增真菌的引物为ITS1和ITS2, 序列为: ITS1F 5'-CTTGGTCATTTAGAGGAAGTAA-3', ITS2R 5'-GCTGCGTTCTTCATCGATGC-3'; 扩增细菌的引物为16S rRNA, 序列为: 338F 5'-ACTCCTACGGGAGGAGCAG-3', 806R 5'-GGAAGTACHVGGGTWCTAAT-3'。测序平台为PE300。原始测序数据经过优化统计和去杂之后进行抽平, 然后以97%的相似性为标准将有效序列聚类成操作分类单元(OTU), 分别在域、界、门、纲、目、科、属、种各个分类水平上统计各样本的群落组成, 并分析不同处理对真菌和细菌属水平的影响。

花生产量测定: 花生收获时每个处理随机选取20株, 自然晒干测定单株产量, 考察单株结果数和单株果实质量, 计算总产量。

荚果品质测定: 利用多功能谷物近红外分析仪

(DA7250 Perten, Hågersten, Sweden)对各处理籽仁的蛋白质、总氨基酸、油酸和亚油酸含量等进行测定。

## 1.3 数据处理

采用Excel处理试验数据, SPSS 16.0数据处理系统进行显著性分析, 采用Student's *t*-test检测法进行显著性比较, 显著性水平设为 $p < 0.05$ 和 $p < 0.01$ 两个水平。

## 2 结果

### 2.1 AM共生体对连作花生根际土壤酶活性的影响

由图1所示, 接种摩西斗管囊霉的连作花生土壤蔗糖酶活性在花生连作苗期、盛花期、荚果膨大期和收获期都要高于对照, 而且在收获期达到显著水平( $p < 0.05$ )。接种摩西斗管囊霉的连作花生土壤的脲酶活性在花生各个生长时期都高于未接种的土壤, 并在苗期和收获期达到显著水平( $p < 0.05$ )。与对照相比, 接种摩西斗管囊霉的花生连作土壤碱性磷酸酶活性在花生各个生长时期都显著提高( $p < 0.05$ )。另外, 未接种摩西斗管囊霉的土壤硝酸还原酶活性在花生盛花期之后开始下降, 而接种土壤则开始上升, 而且显著高于未接种的土壤( $p < 0.05$ ) (图1)。

### 2.2 AM共生体对连作花生根际土壤矿物质养分的影响

由表1可知, 与未接种的相比, 接种摩西斗管囊霉的连作花生土壤全氮和全磷含量在盛花期和收获期都有显著提高( $p < 0.05$ ), 而全钾含量只有在收获期显著增加( $p < 0.05$ ), 盛花期土壤全钾含量的增加没有达到显著水平( $p > 0.05$ ) (表1)。另外, 摩西斗管囊霉提高了土壤中碱解氮含量, 但是没有达到显著水平( $p > 0.05$ ), 这与土壤中的全氮含量显著提高结果不一致。而接种摩西斗管囊霉的花生连作土壤显著提高了速效磷的含量( $p < 0.05$ ), 其与土壤中全磷的含量变化一致。速效钾含量与土壤中的全钾含量变化趋势一致, 也表现为收获期的速效钾含量显著增加( $p < 0.05$ ) (表2)。

### 2.3 AM共生体对连作花生根际微生物的影响

#### 2.3.1 接种摩西斗管囊霉对连作花生土壤真菌的影响

真菌抽平之后的序列数为65 818, 对其进行OTU分析, 共获得1 115个OTU。未接种摩西斗管囊霉的连作花生在盛花期和收获期的OTU数目分

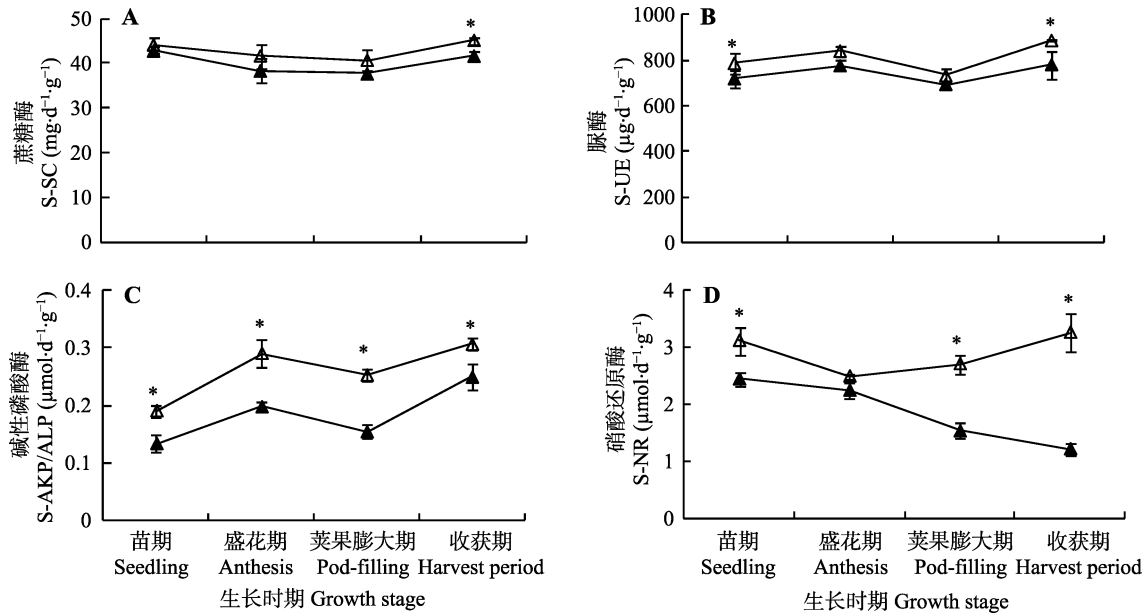


图1 接种摩西斗管囊霉对连作花生不同生长时期的根际土壤蔗糖酶(A)、脲酶(B)、碱性磷酸酶(C)和硝酸还原酶(D)活力的影响(平均值±标准误差)。\*表示不同处理之间差异显著( $p < 0.05$ )。▲, 未接种摩西斗管囊霉; △, 接种摩西斗管囊霉。

**Fig. 1** Effects of inoculation with *Funneliformis mosseae* on enzyme activities of solid-sucrase (S-SC)(A), solid-urease (S-UE)(B), solid alkaline-phosphatase (S-AKP/ALP)(C) and solid-nitrate reductase (S-NR)(D) in rhizosphere soil of continuing cropping peanut at different growth stages (mean ± SE). \* indicates significant difference between the two treatments ( $p < 0.05$ ). ▲, without *F. mosseae* inoculation; △, *F. mosseae* inoculation.

表1 接种和未接种摩西斗管囊霉的连作花生根际土壤全氮、全磷和全钾含量比较(平均值±标准误差,  $n = 3$ )

**Table 1** Comparison of soil contents of total nitrogen, total phosphorus and total potassium between the treatments with and without *Funneliformis mosseae* inoculation under continuing cropping of peanuts (mean ± SE,  $n = 3$ )

处理 Treatment	全氮 Total N (g·kg <sup>-1</sup> )				全磷 Total P (g·kg <sup>-1</sup> )				全钾 Total K (mg·g <sup>-1</sup> )			
	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period
-AMF	1.23 ± 0.06	0.74 ± 0.02	0.59 ± 0.06	0.37 ± 0.04	6.67 ± 0.22	3.57 ± 0.67						
+AMF	1.44 ± 0.06*	0.82 ± 0.03*	0.70 ± 0.03*	0.47 ± 0.07*	7.41 ± 0.57	5.39 ± 0.73*						

\*表示差异显著( $p < 0.05$ )。-AMF, 未接种摩西斗管囊霉; +AMF, 接种摩西斗管囊霉。

\* indicates significant difference ( $p < 0.05$ ). -AMF, without *F. mosseae* inoculation; +AMF, *F. mosseae* inoculation.

表2 接种摩西斗管囊霉对连作花生根际土壤碱解氮、速效磷和速效钾含量的影响(平均值±标准误差,  $n = 3$ )

**Table 2** Effects of *Funneliformis mosseae* inoculation on the soil contents of alkaline nitrogen, available phosphorus and available potassium (mean ± SE,  $n = 3$ )

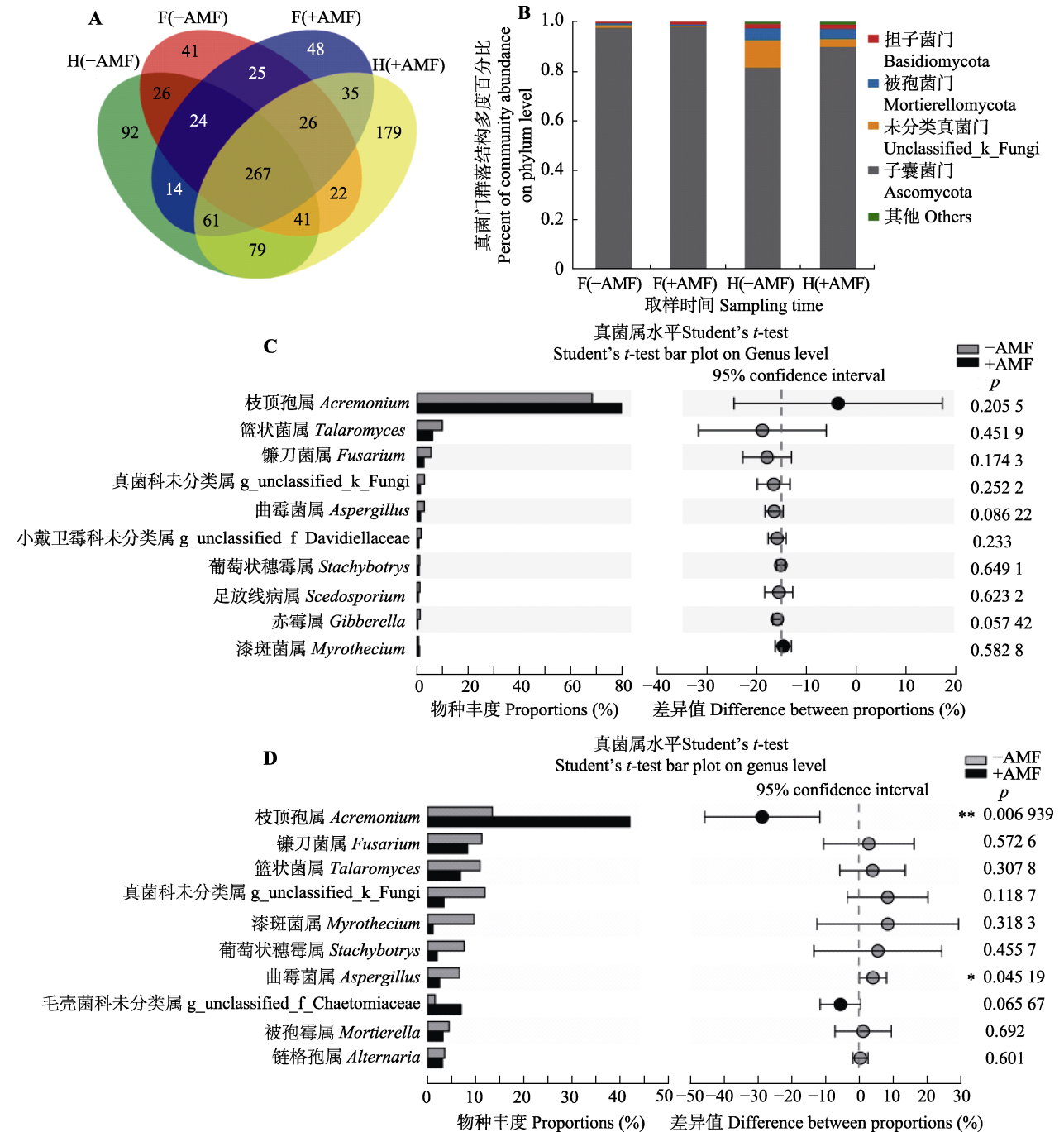
处理 Treatment	碱解氮 Alkaline N (mg·kg <sup>-1</sup> )				速效磷 Effective P (g·kg <sup>-1</sup> )				速效钾 Effective K (mg·kg <sup>-1</sup> )			
	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period	盛花期 Anthesis	收获期 Harvest period
-AMF	73.39 ± 3.66	75.77 ± 3.66	0.18 ± 0.01	0.15 ± 0.01	15.40 ± 0.56	11.03 ± 0.64						
+AMF	74.86 ± 5.54	81.67 ± 7.00	0.21 ± 0.02*	0.18 ± 0.00*	16.17 ± 0.47	13.20 ± 0.66*						

表中数据为3次试验的平均值; \*,  $p < 0.05$ 。-AMF, 未接种摩西斗管囊霉; +AMF, 接种摩西斗管囊霉。

Sample size  $n = 3$ ; \*,  $p < 0.05$ . -AMF, without *F. mosseae* inoculation; +AMF, *F. mosseae* inoculation.

别为471和594, 而接种摩西斗管囊霉增加了连作花生盛花期和收获期土壤中真菌的OTU丰度, 其OTU数目分别为504和705; 其中267个OTU为接种和未接种摩西斗管囊霉在盛花期和收获期共同所有(图2A)。进一步对真菌门水平分析发现, 接种和未接种摩西斗管囊霉的连作花生土壤中优势真菌为子囊菌门。在盛花期和收获期, 接种和未接种摩西斗管囊

霉的连作花生土壤子囊菌门占整个真菌门的比例分别为98%、97%、89%和81%。其他的真菌门相对较少, 它们分别是被孢菌门、担子菌门和未分类菌门(图2B)。通过对真菌属水平进一步分析发现, 接种摩西斗管囊霉的土壤中枝顶孢属(*Acremonium*)多度比未接种的有所增加(图2C), 特别在收获期达到了极显著水平( $p < 0.01$ )(图2D)。在盛花期, 篮状菌属



**图2** 接种和未接种摩西斗管囊霉对花生连作土壤真菌群落结构及多度的影响。**A**, 不同时期不同处理间真菌分类操作单元丰度的韦恩图。**B**, 接种摩西斗管囊霉改变花生连作土壤真菌门的丰度。**C**, 接种摩西斗管囊霉对盛花期花生根际土壤真菌属影响不显著(平均值±标准误差,  $n = 3$ )。**D**, 接种摩西斗管囊霉对收获期花生根际土壤真菌属影响显著(平均值±标准误差,  $n = 3$ )。-AMF, 未接种摩西斗管囊霉; +AMF, 接种摩西斗管囊霉。F(-AMF), 未接种摩西斗管囊霉的盛花期花生根际土壤; F(+AMF), 接种摩西斗管囊霉的盛花期花生根际土壤; H(-AMF), 未接种摩西斗管囊霉的收获期花生根际土壤; H(+AMF), 接种摩西斗管囊霉的收获期花生根际土壤。\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ 。

**Fig. 2** Effects of with and without *Funneliformis mosseae* inoculation on the structure and abundance of soil fungi community under continuing cropping of peanut. **A**, The Venn figure shows the number of fungal operational taxonomic units in different treatments. **B**, Abundance of soil fungi in continuing cropping of peanut was changed by *F. mosseae*. **C**, Abundance of fungal genera were not significantly different between with and without *F. mosseae* inoculation in the flowering period of continuing cropping peanuts (mean ± SE,  $n = 3$ ). **D**, Abundance of some fungal genera were significantly different between with and without *F. mosseae* inoculation at harvest period (mean ± SE,  $n = 3$ ). -AMF, without *F. mosseae* inoculation; +AMF, *F. mosseae* inoculation. F(-AMF), peanut rhizosphere soil without *F. mosseae* inoculation during the flowering period; F(+AMF), rhizosphere soil of peanut with *F. mosseae* inoculation; H(-AMF), peanut rhizosphere soil without *F. mosseae* inoculation during the harvest period; H(+AMF), peanut rhizosphere soil with *F. mosseae* inoculation during the harvest period. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ .

(*Talaromyces*)、镰刀菌属(*Fusarium*)、曲霉菌属(*Aspergillus*)、葡萄状穗霉属(*Stachybotrys*)、足放线病属(*Scedosporium*)和赤霉菌(*Gibberella*)的多度在接种摩西斗管囊霉的花生连作土壤中都有所减少, 但是没有达到显著水平( $p > 0.05$ )(图2C)。而在收获期, 与未接种的相比, 接种摩西斗管囊霉显著降低了花生连作土壤中曲霉菌属(*Aspergillus*)的多度( $p < 0.05$ )(图2D)。

### 2.3.2 接种摩西斗管囊霉对连作花生土壤细菌的影响

细菌抽平之后的序列数共有34 590个, 通过有效聚类共获得4 529个细菌OTU。其中, 未接种摩西斗管囊霉盛花期的OTU数为3 947, 接种的为3 893; 与盛花期相比, 接种和未接种摩西斗管囊霉的收获期OTU数都有所减少, 分别为3 913和3 837个; 无论是盛花期还是收获期都表现为接种摩西斗管囊霉减少了OUT的丰度(图3A)。对细菌门水平分析表明, 接种和未接种摩西斗管囊霉的花生连作土壤中优势细菌依次为放线菌门、变形菌门、绿弯菌门、酸杆菌门和厚壁菌门(图3B)。未接种摩西斗管囊霉的连作花生根际土壤在盛花期的放线菌门多度是25%, 而接种的为27%, 提高了2%。同样, 摩西斗管囊霉也提高了连作花生收获期土壤中放线菌门的多度, 提高幅度约为3%。然而, 与放线菌的增加趋势相反, 接种摩西斗管囊霉的连作花生土壤中绿弯菌门的多度有所减少, 与未接种的相比, 在盛花期和收获期分别减少了5%和2%。同时, 摩西斗管囊霉也提高了芽单胞菌门和硝化螺旋菌门的相对比例(图3B)。进一步分析盛花期连作花生根际土壤细菌属的变化情况, 结果发现, 摩西斗管囊霉显著提高了盛花期土壤中JG30-KF-CM45目未知菌属(*g\_norank\_o\_JG30-KF-CM45*)和芽单胞菌科未知属(*g\_norank\_f\_Gemmatimonadaceae*)的多度, 而微球菌科未分类属(*g\_unclassified\_f\_Micrococcaceae*)的多度显著减少( $p < 0.05$ )(图3C)。而在收获期则表现为, 摩西斗管囊霉显著增加了Gaiellales目未知属(*g\_norank\_o\_Gaiellales*)和*Gaiella*的多度( $p < 0.05$ )(图3D)。另外, 摩西斗管囊霉增加了花生连作土壤中硝化螺旋菌属(*Nitrospira*)的多度, 但是没有达到显著水平( $p > 0.05$ )。

### 2.4 AM共生体对连作花生产量和品质的影响

由表3可知, 与对照相比, 接种摩西斗管囊霉的连作花生单株结果数、单株果质量和饱果率分别提

高了12%、20%和10%, 显著增加了连作花生的产量( $p < 0.05$ )。进一步对接种和未接种摩西斗管囊霉的连作花生籽仁的品质进行检测, 结果表明, 摩西斗管囊霉显著提高了连作花生籽仁蛋白质、总氨基酸、油酸和亚油酸的百分比( $p < 0.05$ ), 分别为3.55%、3.01%、4.92%和3.08%。

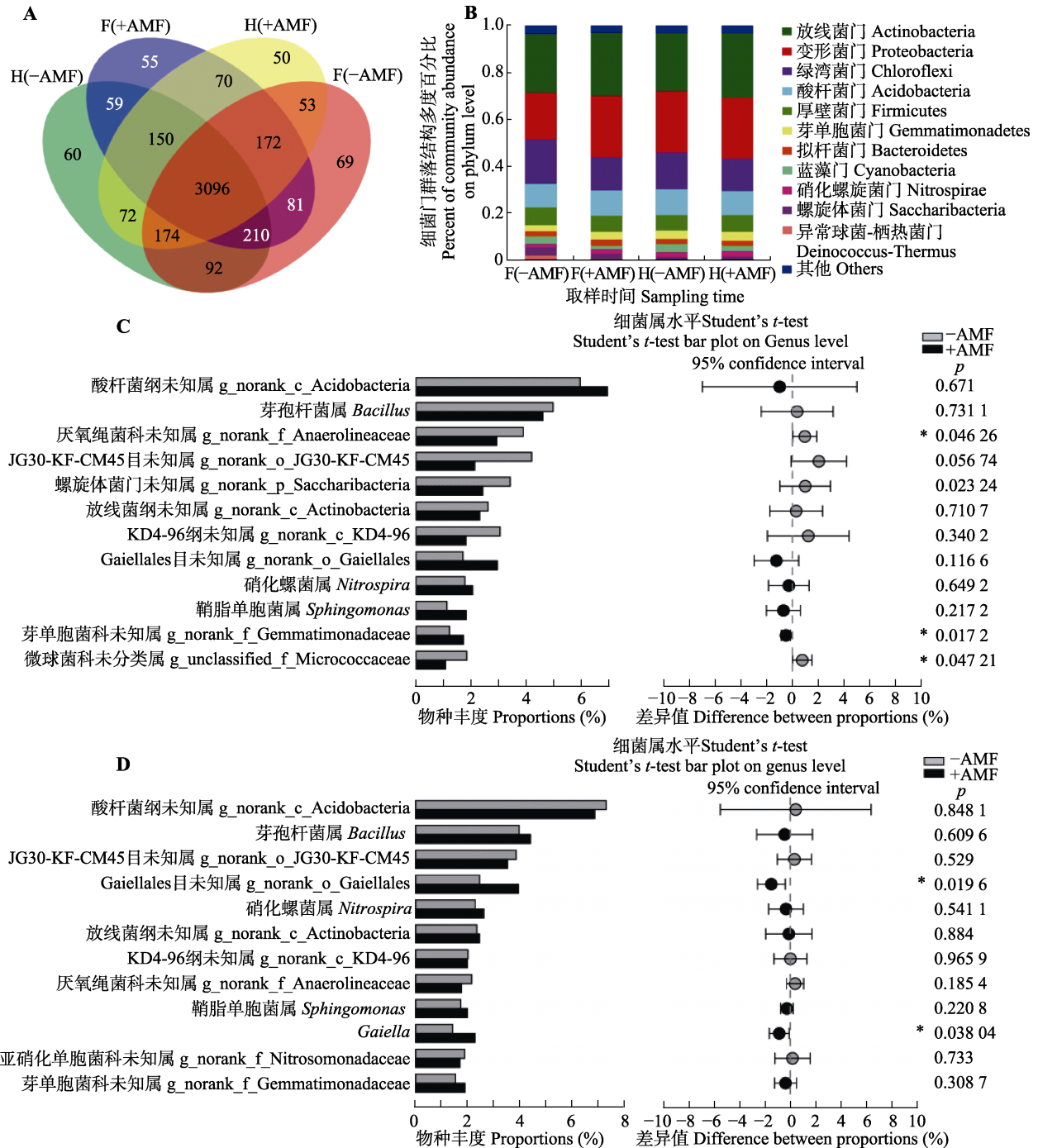
## 3 讨论

### 3.1 AM共生体提高连作花生根际土壤酶的活性

花生是我国重要的油料作物和经济作物, 由于种植面积受限, 连作现象非常严重。长时间的花生连作易对土壤微生态造成严重破坏, 土壤微环境失去平衡, 土壤酶活性降低。土壤酶是土壤微生态系统中重要的调节者, 参与土壤矿物质元素的转化, 与土壤肥力密切相关。土壤蔗糖酶、脲酶、磷酸酶常作为土壤微生物活性指标(孙瑞莲等, 2008)。研究表明, AMF能够提高土壤蔗糖酶、脲酶和磷酸酶的活性, 从而促进土壤中矿物质元素的转化速率(王瑾等, 2014; 雷卉等, 2019)。随着花生连作年限的增加, 土壤碱性磷酸酶、蔗糖酶和脲酶活性逐渐降低(孙秀山等, 2001)。本研究结果发现, 摩西斗管囊霉增加了连作花生土壤蔗糖酶、脲酶、磷酸酶的活性, 这可能是因为摩西斗管囊霉提高了土壤中放线菌的数量引起的, 因为土壤放线菌能够促进碱性磷酸酶和脲酶的活性(王瑾等, 2014)。另外, 接种摩西斗管囊霉的花生连作土壤硝酸还原酶活性在花生生长发育过程中是呈现升高的趋势, 而未接种摩西斗管囊霉的则呈降低的趋势, 这可能是摩西斗管囊霉提高了土壤中氮含量的原因(高萍等, 2017)。

### 3.2 AM共生体促进连作花生根系对矿物质养分的吸收

伴随着花生连作年限的增加, 土壤酶活性逐渐降低, 土壤中有效养分含量减少, 从而导致植物根系对养分吸收降低(滕应等, 2015)。封海胜等(1999)对中等肥力的花生连作土壤研究表明, 土壤中速效磷和速效钾的含量随着连作年限的增加而减少, 而碱解氮含量变化不大。AMF能够活化土壤中矿物质营养, 增加植物对氮、锌、铜、钾、钙、铁等矿质营养元素的吸收(Lehmann & Rilling, 2015)。本研究结果表明, 摩西斗管囊霉提高花生连作土壤中全氮的含量, 这是摩西斗管囊霉提高土壤中脲酶、硝酸还原酶活性和土壤硝化螺旋菌属多度的结果, 因为



**图3** 接种摩西斗管囊霉对花生连作土壤细菌群落结构及丰度的影响。**A**, 不同时期不同处理间细菌操作分类单元丰度的韦恩图。**B**, 接种摩西斗管囊霉改变细菌门多度。**C**, 接种摩西斗管囊霉显著改变盛花期花生根际土壤细菌属的多度(平均值±标准误差,  $n = 3$ )。**D**, 接种摩西斗管囊霉显著改变收获期花生根际土壤细菌属的多度(平均值±标准误差,  $n = 3$ )。-AMF, 未接种摩西斗管囊霉; +AMF, 接种摩西斗管囊霉。F(-AMF), 未接种摩西斗管囊霉的盛花期花生根际土壤; F(+AMF), 接种摩西斗管囊霉的盛花期花生根际土壤; H(-AMF), 未接种摩西斗管囊霉的收获期花生根际土壤; H(+AMF), 接种摩西斗管囊霉的收获期花生根际土壤。\*,  $p < 0.05$ 。

**Fig. 3** Effects of *Funneliformis mosseae* on the structure and abundance of soil bacterial community in rhizosphere soil of peanut under continuing cropping. **A**, The Venn figure shows the number of bacterial operational taxonomic units in the two treatments. **B**, Abundance of soil bacteria in continuous cropping of peanut changed in the *F. mosseae* inoculation treatment. **C**, Abundance of bacterial genera were significantly different between with and without *F. mosseae* inoculation in the flowering period of continuous cropping peanuts (mean  $\pm$  SE,  $n = 3$ ). **D**, Abundance of bacterial genera were significantly different between with and without *F. mosseae* inoculation in the harvesting period of continuous cropping peanuts (mean  $\pm$  SE,  $n = 3$ ). -AMF, without *F. mosseae* inoculation; +AMF, *F. mosseae* inoculation. F(-AMF), peanut rhizosphere soil without *F. mosseae* inoculation during the flowering period; F(+AMF), rhizosphere soil of peanut with *F. mosseae* inoculation; H(-AMF), peanut rhizosphere soil without *F. mosseae* inoculation during the harvest period; H(+AMF), peanut rhizosphere soil with *F. mosseae* inoculation during the harvest period. \*,  $p < 0.05$ .

表3 接种摩西斗管囊霉对连作花生产量和品质的影响

Table 3 Effects of *Funnelformis mosseae* inoculation on the yield and quality of continuous cropping peanut

处理 Treatment	单株结果数 Pod number per plant	单株果质量 Pod mass per plant (g)	饱果率 Full fruit rate (%)	蛋白质 Protein (%)	总氨基酸 Total amino acid (%)	油酸 Oleic (%)	亚油酸 Linoleic (%)
-AMF	34.67 ± 2.08	41.85 ± 2.87	60.82 ± 0.02	18.34 ± 0.17	18.29 ± 1.68	52.46 ± 1.16	24.12 ± 1.37
+AMF	39.33 ± 0.58*	52.05 ± 0.79*	70.33 ± 0.04*	21.89 ± 0.22*	21.30 ± 0.97*	57.38 ± 1.32*	27.20 ± 1.19*

表中数据为3次试验的平均值; \*,  $p < 0.05$ 。-AMF, 未接种摩西斗管囊霉; +AMF, 接种摩西斗管囊霉。

Sample size  $n = 3$ ; \*,  $p < 0.05$ 。-AMF, without *F. mosseae* inoculation; +AMF, *F. mosseae* inoculation.

这三者在土壤氮循环中起到重要的作用。同时, 摩西斗管囊霉提高了连作花生根际土壤中磷的含量, 这与AMF促进植物对难溶性元素磷的吸收结果一致(Smith *et al.*, 2015; Li *et al.*, 2016), 其原因可能是AMF提高土壤中磷酸酶的活性和诱导植物根系中磷转运基因的表达(Adolfsson *et al.*, 2017)。另外, 摩西斗管囊霉提高了连作花生土壤中钾的含量, 而土壤中钾增加可能是土壤酶活性提高的结果, 这也是AMF提高植物吸收 $K^+$ 原因(Garcia *et al.*, 2017)。

### 3.3 AM共生体改善连作花生根际微生物群落结构

长期花生连作严重影响土壤微生物群落结构平衡, 真菌中病原性真菌数量明显增加, 如尖孢镰孢菌和曲霉菌属中的一些致病菌种, 而有益真菌多样性和数量则相应减少, 如木霉属, 被孢霉属, 球囊霉属等(Chen *et al.*, 2012; Li *et al.*, 2014)。镰刀菌属中大部分是致病性镰刀菌, 有的致病性镰刀菌能够侵染植物, 导致植物腐烂、枯萎, 从而导致作物产量和品质降低, 甚至绝产(LeBlanc *et al.*, 2017)。赤霉属常作为镰刀菌属真菌的有性阶段, 许多赤霉属可以引起具有破坏性的植物病害, 而且其产生的特定毒素或活性代谢物对人和动物具有毒害作用(Desjardins, 2003)。另外, 土壤是花生曲霉菌的主要来源, 曲霉菌属中有的种类能够产生高致癌性和高毒性的次级代谢产物黄曲霉素(张初署, 2013)。前人研究表明, AMF能够减轻花生的茎腐病、黄瓜立枯病、烟草青枯病(贺忠群等, 2010; Ozgonen *et al.*, 2010; 刘先良等, 2014)。在本研究中, 摩西斗管囊霉减少了连作花生根际土壤中镰刀菌属、赤霉属和曲霉菌属的多度, 这可能因为AM共生体引起了植物根系细胞膜透性、分泌物和渗出物等发生改变, 形成了独特微生物区系保护层, 从而使根际真菌病原菌减少(Dehne *et al.*, 1978; Marschner *et al.*, 2001; 高萍等, 2017)。这说明摩西斗管囊霉可以减少连作花生土壤有害真菌的相对含量, 降低花生被病原真菌侵染的几率。

花生长期连作有利于土壤中病原真菌的增加,

抑制了有益细菌的生长, 造成连作花生土传病害大幅上升(姚小东等, 2019)。AMF可通过菌根分泌物改变土壤微环境, 促进土壤中细菌的繁殖(付晓峰等, 2016)。放线菌门是植物内生菌的重要组成部分, 其可以通过多种促生机制促进植物生长(申枚灵等, 2018)。随着花生连作年限的增加, 土壤中放线菌门的含量明显减少(黄玉茜等, 2011)。本研究发现, 摩西斗管囊霉增加连作花生土壤中放线菌门的多度, 并且随着放线菌门多度的增加, 其下面的两个属Gaiellales未知属和Gaiella的多度也显著增加, 这可能是AMF提高寄主植物对病原菌抵抗能力的主要原因(黄玉茜等, 2011)。因为, 放线菌门中有很多属能够产生活性物质来帮助植物免受病原菌的侵染, 减少了植物的感病几率(封晔, 2017)。也有研究表明, 放线菌门不但可以帮助植物抵御病原菌的侵害、加强寄主对逆境的抗性, 还能够增加植物对养分的吸收(宁楚涵等, 2019), 这也是本研究推测摩西斗管囊霉缓解花生连作障碍是通过增加花生连作土壤中放线菌门相对含量来实现的原因。

花生属于豆科植物, 其根瘤具有固氮功能, 因此对氮的吸收较少, 而对磷、钾、硼、铁等元素的吸收较多(滕应等, 2015)。花生长期连作势必会使土壤酶活性及微生物区系平衡受到破坏, 导致矿物质元素的匮乏, 从而严重影响花生的产量和品质(Kunoh, 2002)。AMF通过提高寄主植物对营养元素的吸收和对逆境胁迫的抗性来增加植物的产量, 改善品质(孙秀秀等, 2017; Luo *et al.*, 2019)。本研究结果表明, 接种摩西斗管囊霉的连作花生产量和品质都有所提高, 这与摩西斗管囊霉增加土壤酶活性、提高土壤中矿物质含量、减少土壤中有害真菌镰刀菌属和曲霉菌属的多度、增加有益细菌放线菌门的多度有密切关系。

## 4 结论

总之, 本研究表明摩西斗管囊霉能够提高连作花生根际土壤酶活性, 增加土壤中氮、磷、钾矿物

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质元素的含量,降低根际有害真菌曲霉属、镰刀菌属和赤霉属的多度,增加土壤中有益细菌放线菌门的多度,从而改善连作花生根际周围的微环境,促进连作花生地上部分生长,增加连作花生的产量和品质。

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