



添加毛叶苕子对红壤旱地土壤真菌群落的影响

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摘要:【目的】长期高强度的连作及大量化肥施用导致红壤旱地退化和土传植物病原菌累积。真菌是农业生态系统中与土壤健康密切相关的微生物。本文通过研究土壤真菌群落的变化, 探究施用毛叶苕子对红壤旱地农业生态系统的影响。【方法】采用定量聚合酶链式反应和高通量测序技术, 研究红壤旱地真菌群落对单施矿质肥(mineral nitrogen, phosphorus and potassium fertilization, NPK)与矿质肥配施毛叶苕子(mineral nitrogen, phosphorus and potassium fertilization with hairy vetch, NPKG) 2种施肥措施的响应。【结果】与对照 NPK 相比, NPKG 显著提高土壤肥力、花生产量和土壤真菌丰度, 降低土壤 pH 和土壤真菌多样性。不同处理显著改变土壤真菌群落组成。与对照 NPK 相比, NPKG 处理土壤腐生营养型真菌相对丰度显著提高 37.42%, 花生尾孢菌(*Cercospora arachidicola*)和可可毛色二孢菌(*Lasiodiplodia theobromae*) 2种花生病原菌相对丰度分别降低 89.11%和 88.10%。【结论】施用毛叶苕子显著提高了红壤旱地肥力, 降低了花生土传病害风险, 提高了花生作物产量。因此, 施用毛叶苕子有利于我国南方红壤旱地的可持续发展。

关键词: 绿肥; 农业生态系统; 真菌群落; 植物病原菌; 红壤旱地

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Application of hairy vetch (*Vicia villosa* Roth L.) affects fungal community in upland red soil

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Abstract: [Objective] The long-term intense continuous cropping and abuse of mineral fertilizers result in the degradation of upland red soil and the accumulation of soil-borne plant pathogens. Fungi are the microorganisms closely related to soil health in agroecosystems. We investigated the changes of soil fungal community to explore the effects of hairy vetch (*Vicia villosa* Roth L.) application on the agroecosystem with upland red soil. [Methods] We employed quantitative polymerase chain reaction (qPCR) and high-throughput sequencing (Illumina MiSeq) to investigate the responses of fungal communities to mineral fertilizer (hereinafter referred to as NPK) alone and mineral fertilizer combined with hairy vetch (hereinafter referred to as NPKG) in upland red soil. [Results] Compared with NPK, NPKG increased the soil fertility, peanut yield, and fungal abundance and decreased soil pH and soil fungal diversity. Different treatments significantly altered the soil fungal community composition. Compared with NPK, NPKG increased the relative abundance of saprophytic fungi by 37.42% and decreased the relative abundance of *Cercospora arachidicola* and *Lasiodiplodia theobromae* by 89.11% and 88.10%, respectively. [Conclusion] The application of hairy vetch significantly increased soil fertility, reduced the risk of peanut exposure to soil-borne diseases, and increased peanut yield in the upland red soil. Therefore, the application of hairy vetch was conducive to the sustainable development of upland red soil in southern China.

Keywords: green manure; agroecosystem; fungal communities; plant pathogen; upland red soil

在土壤微生物群落中,真菌具有重要的生态学意义。真菌作为土壤中重要的分解者,在土壤养分循环中发挥着重要作用^[1]。在植物有机体分解的早期阶段,真菌比细菌和放线菌更为活跃^[2]。真菌不仅可以改良土壤结构、提高土壤肥力,还与植物的生长发育关系密切,可以为植物提供营养物质^[3]、促进植物生长、保护植物免受生物(病原菌)和非生物(干旱等)的胁迫^[4-5]。另外存在部分真菌是重要的植物病原菌,如常见的禾旋孢腔

菌(*Cochliobolus sativus*)、尖孢镰刀菌(*Fusarium oxysporum*)等,这些病原菌会引起作物生长发育异常,导致作物产量和品质严重下降^[6]。

施肥被认为是导致土壤微生物群落改变的主要驱动因子^[7]。近几十年,为了提高作物产量,农业生态系统投入大量的化肥。然而,化肥的过度施用对土壤质量和生态环境造成严重的负面影响^[8]。长期施用化肥不仅会导致土壤酸化、土壤板结等问题^[9],并且会降低土壤真

菌多样性、改变真菌的群落结构^[10], 增加农业病虫害的风险^[11]。研究表明施用有机肥料会增加土壤有机质含量、稳定土壤结构^[12]。在有机肥源中, 种植并翻压豆科绿肥所取得的环境和社会效益最佳^[13]。豆科绿肥配施化肥可以减少农业生态系统对化肥的过度依赖、保持土壤有机质含量、提高土壤肥力^[14]。然而, 目前种植翻压豆科绿肥在水田中应用比较广泛, 种植翻压豆科绿肥对红壤旱地土壤肥力、土壤真菌群落和作物产量的影响研究值得深入探讨^[15]。

红壤作为我国南方重要的土壤类型, 广泛分布于长江流域及其以南地区, 涉及 15 个省区, 面积达 218 万 km², 占全国耕地面积的 27.8%^[16]。然而红壤含铁、铝成分较多, 有机质少、酸性强、土质黏重^[17], 另外长期施用矿质肥料等不合理的开发利用, 导致土壤微生物多样性降低, 水土流失严重, 土壤肥力持续下降^[18]。红壤已经成为我国南方低产土壤, 红壤旱地的退化更为突出。花生是我国南方红壤旱地重要的经济作物, 长期单一的种植模式导致红壤旱地花生连作障碍较为普遍, 致使土壤中病原微生物富集严重, 土传病害加剧, 花生产量受到很大影响^[19]。如何培肥改良红壤、充分发挥其生产潜力, 提高花生产量是我国南方红壤旱地农业可持续发展亟需解决的问题。

目前关于施用豆科绿肥毛叶苕子对红壤旱地花生产量和真菌群落的影响鲜有报道。本研究利用盆栽试验通过施矿质肥料并配施毛叶苕子, 采用定量聚合酶链式反应(quantitative polymerase chain reaction, qPCR)和高通量测序(Illumina MiSeq)技术, 从土壤真菌多样性、群落结构和功能等方面探讨施用毛叶苕子对红壤旱地生态系统的影响, 以期改善我国红壤旱地质量、提高花生作物产量、促进农业可持续发展提供理论依据和技术保障。

1 材料与方 法

1.1 试验区概况

试验在江西省抚州市东乡区红壤综合试验站露天网室中进行(28°10'59"N, 106°35'11"E; 海拔 50 m), 年平均气温为 18 °C, 属于典型的亚热带气候。总降水量为 1 189.6 mm。试验地土壤类型为第四纪红黏土母质发育而来的红壤。原始土壤性质为: pH 5.11, 总氮(total nitrogen, TN) 1.01 g/kg, 土壤有机碳(soil organic carbon, SOC) 8.31 g/kg, 碱解氮(alkaline hydrolyzable nitrogen, AN) 82.2 mg/kg, 有效磷(available phosphorus, AP) 14.4 mg/kg。

1.2 试验设计

试验为花生盆栽试验, 每盆盆栽用土 5 kg。花生品种选用粤油 256, 于四月中下旬播种, 八月下旬收获。试验共设置 2 个处理, 分别为: (1) 矿质肥(NPK); (2) 矿质肥+毛叶苕子(NPKG), 每个处理 9 次重复, 共 18 盆; 其中矿质肥施用量为: 尿素(含 N 46%) 1.30 g/pot, 钙镁磷肥(含 P₂O₅ 12%) 3.00 g/pot, 氯化钾(含 K₂O 60%) 1.00 g/pot, 为当地田间花生施肥量(N 135 kg/hm², P₂O₅ 81 kg/hm², K₂O 135 kg/hm²)的 2 倍^[20], 全部基施。毛叶苕子鲜体施用量为: 40 g/pot, 相当于大田毛叶苕子翻压量 2 250 kg/hm², 与土壤拌匀施用。毛叶苕子含水量为 88.71%, 干基养分含量为: 含 N 2.57%, 含 P 0.27%, 含 K 2.58%。试验中水分管理等措施尽量与田间种植保持一致。

1.3 土壤取样

于 2020 年 7 月花生花针期采集土壤。取 0–20 cm 土壤, 用细土钻沿作物不同方向分别取 3 次土样, 混合为一个样品。去除杂质混合均匀后过 2 mm 土筛, 将所得土壤样品分 2 个部分保存, 一部分风干后用于测定土壤理化性质; 另一部分放入冰箱–20 °C 保存, 用于土壤微生物高通量测序。

1.4 花生产量和土壤理化性质的测定

取每一盆花生植株全部结实荚果,在 65 °C 烘箱中烘干至恒重后测定其干重,计算花生产量;土壤 pH 值采用雷兹互感器(上海)有限公司 pH 计测定;SOC 采用重铬酸钾容量法-外加热法测定;土壤全氮用凯氏定氮法测定;土壤全磷用碱熔-钼锑抗比色法,使用紫外分光光度计测定;土壤碱解氮用碱解扩散法测定;土壤速效磷用 0.5 mol/L NaHCO₃ 浸提法萃取-钼抗比色法测定。

1.5 土壤 DNA 提取及测序

使用 FastDNA[®] SPIN 试剂盒提取土壤 DNA。将提取的 DNA 溶解在 60 μL 的 TE 缓冲液中,并在 -20 °C 保存。使用 ITS1F (5'-CTTGGT CATTAGAGGAAGTAA-3')和 ITS2R (5'-GCT GCGTTCTTCATCGATGC-3')扩增真菌 ITS 基因区域^[21]。PCR 反应体系为 50 μL 的反应混合物,即: 25 μL DNA 聚合酶(SYBR[®] Premix Ex Taq, Takara Bio); 1 μL DNA 模板, 0.5 μL 正向引物, 0.5 μL 反向引物, 23 μL ddH₂O。PCR 扩增程序: 95 °C 5 min; 94 °C 45 s, 55 °C 45 s, 72 °C 45 s, 共 35 个循环; 72 °C 延长 10 min。扩增产物经 2% 琼脂糖凝胶电泳检测,将扩增合格的 PCR 产物送往上海美吉生物公司测序。

测序完成后采用 QIIME 1.9.0^[22]对原始数据进行优化和数据质控处理,去除所有的单体和嵌合体,用 UCLUST 通过 97% 相似度进行聚类获得操作分类单元(operational taxonomic units, OTUs),采用 RDP 数据库(Ribosomal Database Project, RDP)与真菌数据库(Release 7.2, <http://unite.ut.ee/index.php>)进行物种注释分析,获得每个 OTU 的分类学信息。

1.6 数据分析

利用 SPSS 20.0 独立样本 *t* 检验比较花生产量、土壤理化性质、真菌丰度、OTU richness、

Shannon index 及真菌优势门、优势属相对丰度的差异;采用非参检验比较花生尾孢菌和可可毛色二孢菌的相对丰度差异。使用 Pearson 相关分析检验土壤理化性质与土壤真菌丰度、OTU richness、Shannon index 的相关性。使用 R 软件(version 4.1.3)的 vegan 包进行非度量多维度分析(non-metric multidimensional scaling, NMDS)和相似性分析(ANOSIM; permutations=999)并作图^[23]。利用 Mantel test 检验土壤理化性质和距离矩阵的相关性程度。采用线性判别分析(line discriminant analysis effect size, LDA effect size)确定不同处理土壤真菌标志物^[24]。使用 R 软件中 labdsv 分析包进行指示属分析。利用 FUNGuild 软件(version 1.0)对 OTUs 进行功能预测^[25]。利用 R 软件中的 dplyr、igraph 和 Hmisc 分析包构建土壤真菌共现网络,并用 Gephi 软件(version 0.9.2)进行可视化^[26]。采用 Pearson 相关性分析研究土壤理化性质与真菌共现网络拓扑特征之间的相关关系。

2 结果与分析

2.1 土壤理化性质和花生产量

土壤理化性质测定结果如表 1 所示,施加毛

表 1 不同处理下土壤的理化性质

Table 1 Physical and chemical characteristics of soil in different treatments

Soil properties	NPK	NPKG
pH	5.35±0.20a	4.74±0.17b
SOC (g/kg)	7.78±0.37b	10.50±0.32a
TN (g/kg)	0.96±0.05b	1.19±0.04a
TP (g/kg)	0.75±0.05a	0.73±0.03a
AN (mg/kg)	90.20±2.67b	121.70±16.30a
AP (mg/kg)	15.90±2.65b	22.53±2.38a

Mean count±standard deviation (*n*=9). Different lowercase letters indicate significant differences between groups (*P*<0.05); The same lowercase letters indicate no significant differences between groups.

叶苕子后土壤 pH 值下降 0.61, 说明施用毛叶苕子后引起土壤酸化; 相比 NPK 处理, NPKG 处理中土壤有机碳(SOC)、总氮(TN)、碱解氮(AN)和有效磷(AP)含量分别提高 35.27%、24.56%、34.84%和 41.55%, 说明添加毛叶苕子能有效提高土壤养分含量。

NPKG 处理显著提高了花生产量, 比 NPK 处理增产 16.81%。花生产量与土壤有机碳(SOC,

$P<0.001$)、总氮(TN, $P<0.001$)和土壤有效磷(AP, $P<0.001$)含量均呈显著正相关关系(图 1)。

2.2 土壤真菌丰度和 α 多样性

采用定量 PCR 技术研究土壤真菌丰度, 结果显示, 相比于 NPK 组, NPKG 处理组真菌的丰度显著增加 910%。在所有土壤样品中共获得 864 243 条真菌高质量序列, 每个样本的序列从 31 823 到 66 124 不等。由图 2 可知, 相比于 NPK

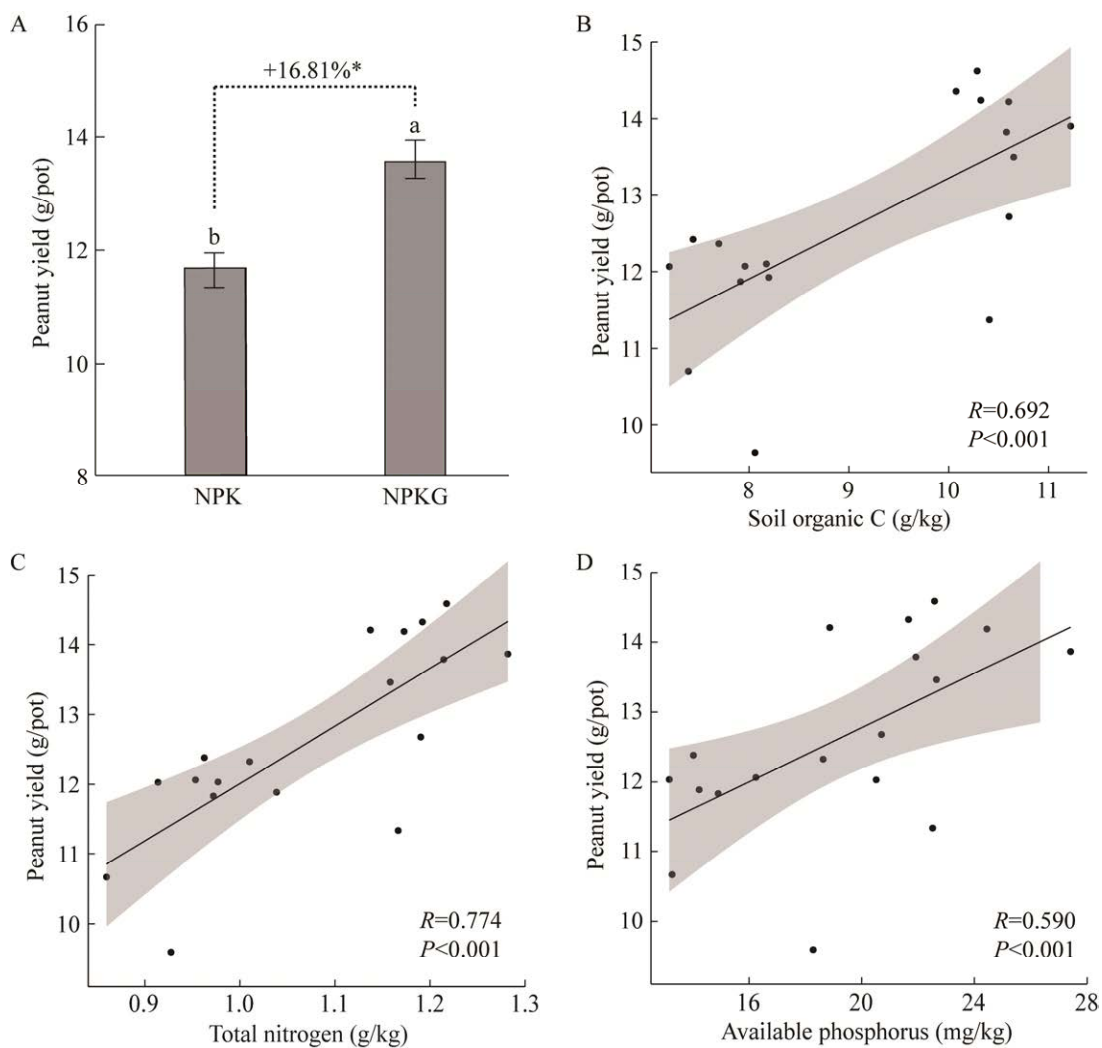


图 1 不同处理花生产量(A)和土壤理化性质与花生产量相关性(B-D)

Figure 1 Peanut yield of different treatments (A) and correlation between soil physicochemical properties and peanut yield (B-D). B: Correlation between soil organic carbon and peanut yield. C: Correlation between soil total nitrogen and peanut yield. D: Correlation between soil available phosphorus and peanut yield. Different letters above bar plots indicate significant differences at 0.05 level. *: $P<0.05$.

组, OTU richness 和 Shannon index 在 NPKG 处理组中分别降低 13.52% 和 10.12%。使用 Pearson 相关性分析检验土壤理化性质与土壤真菌丰度、OTU richness、Shannon index 的相关性。结果表明, 土壤真菌丰度与土壤 pH 值呈显著负相关, 与土壤 SOC、TN、AN 和 AP 含量呈显著正相关($P < 0.01$)。土壤真菌群落多样性指数 OTU richness、Shannon index 与土壤 pH 值呈显著正相关($P < 0.05$), 与土壤 SOC、TN、AN 和 AP 含量呈显著负相关($P < 0.05$) (表 2), 通过对以上结果的分析, 本研究认为施用毛叶苕子后土壤有机质含量的上升导致土壤真菌丰

度显著增加, 而土壤 pH 下降导致真菌多样性显著降低。

2.3 土壤真菌群落组成

采用非度量多维度(NMDS)分析和相似性分析(ANOSIM: permutations=999)研究土壤真菌群落特征, 结果显示土壤真菌群落组成在不同处理下存在显著差异($P = 0.001$; 图 3)。采用 Mantel test 分析土壤真菌群落组成与土壤理化性质间的关系。由表 3 可知, 土壤 pH ($R = 0.616$, $P = 0.001$)、SOC ($R = 0.575$, $P = 0.001$)、AN ($R = 0.538$, $P = 0.001$)、TN ($R = 0.553$, $P = 0.001$)是影响土壤真菌群落组成改变的主要因素。

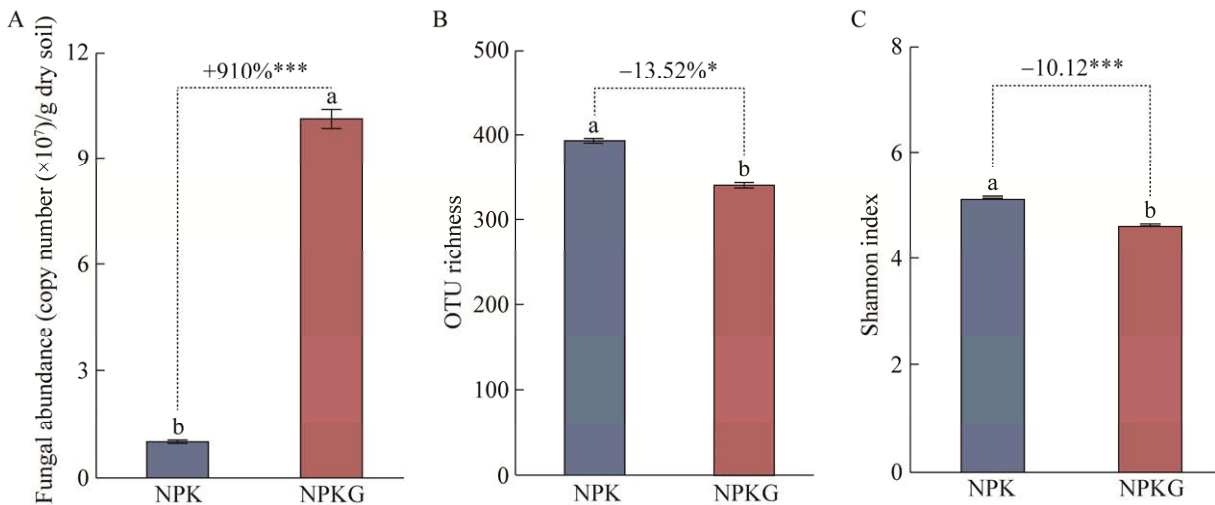


图 2 不同处理土壤真菌丰度(A)和 α 多样性(B、C)的比较

Figure 2 Fungal abundance in different soil treatments (A) and comparison of fungal alpha diversity (B and C). Different letters above bar plots indicate significant differences at 0.05 level. *: $P < 0.05$; ***: $P < 0.001$.

表 2 土壤真菌多样性与土壤理化性质之间的 Pearson 相关性分析

Table 2 Pearson correlations between soil fungal alpha diversity and soil physical and chemical properties

Soil physical and chemical properties	Fungal abundance		OTU richness		Shannon index	
	R	P	R	P	R	P
pH	-0.852	0.000	0.635	0.005	0.861	0.000
SOC (g/kg)	0.970	0.000	-0.489	0.040	-0.814	0.000
TN (g/kg)	0.934	0.000	-0.491	0.038	-0.768	0.000
TP (g/kg)	-0.144	0.569	-0.083	0.742	0.025	0.923
AN (mg/kg)	0.798	0.000	-0.638	0.004	-0.866	0.000
AP (mg/kg)	0.818	0.000	-0.532	0.023	-0.744	0.000

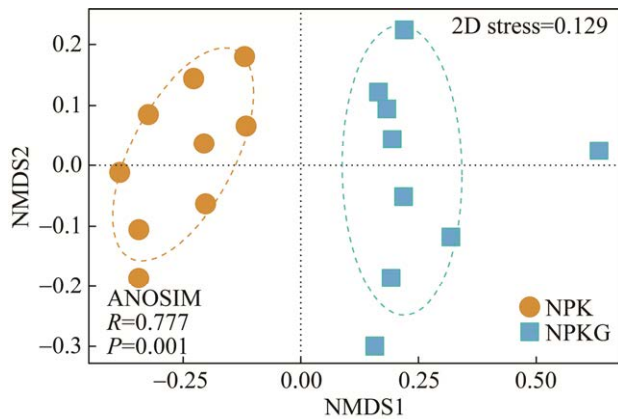


图 3 非度量多维度分析揭示不同处理真菌群落组成的差异

Figure 3 Fungal community structure indicated by non-metric multi-dimensional scaling (NMDS). 2D stress: The difference between the distance of a point in 2-dimensional space and the distance of a point in multidimensional space. Stress<0.2 indicate significant differences in soil fungal community composition of different treatments.

表 3 真菌群落组成与土壤理化性质的 Mantel 分析
Table 3 Mantel test of the correlation between fungal beta diversity and soil properties

Soil properties	R	P
pH	0.616	0.001
SOC (g/kg)	0.575	0.001
TN (g/kg)	0.538	0.001
TP (g/kg)	0.077	0.237
AN (mg/kg)	0.553	0.001
AP (mg/kg)	0.395	0.002
Yield (g/pot)	0.325	0.001

土壤真菌的主要优势门类为子囊菌门 (*Ascomycota*, 80.5%)、接合菌门 (*Zygomycota*, 8.2%)、担子菌门 (*Basidiomycota*, 7.5%)、聚合菌门 (*Glomeromycota*, 0.6%)。相比于 NPK, NPKG 处理担子菌门的相对丰度显著增加 78.63%, 接合菌门相对丰度显著降低 34.18%, 而不同处理之间子囊菌门和聚合菌门的相对丰度无显著性差异(图 4)。

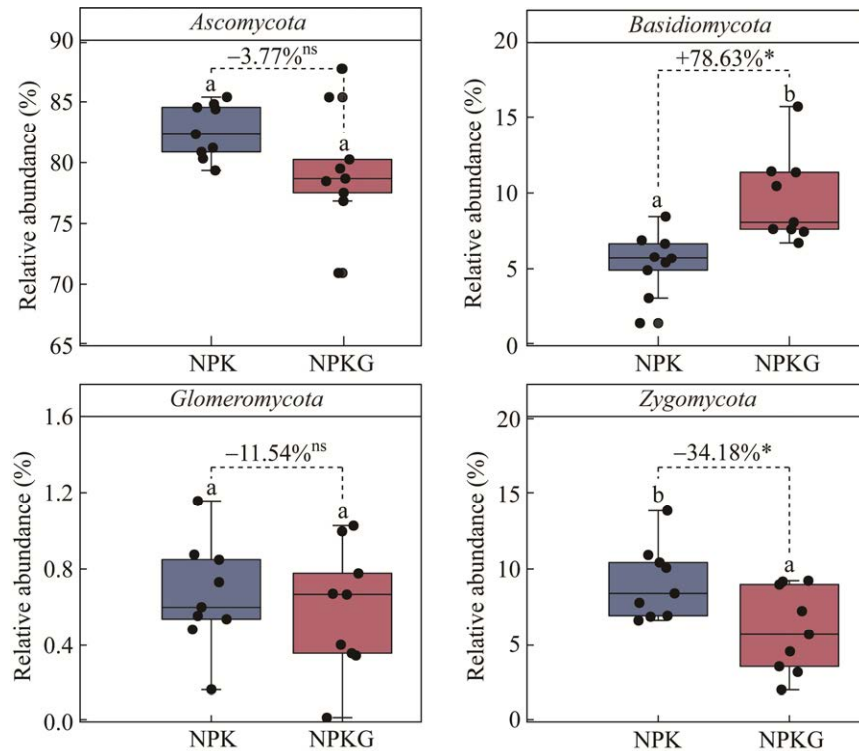


图 4 不同处理对土壤真菌优势门类相对丰度的影响

Figure 4 Relative abundance of soil fungal communities in different treatments at phyla level. Different letters above bar plots indicate significant differences at 0.05 level. ns: $P>0.05$; *: $P<0.05$.

利用 LDA Effect Size (LEfSe)分析评估不同处理间显著富集的生物标识物(图 5), 其中在 NPK 处理组显著富集的真菌有 4 个纲[圆盘菌纲 (*Orbiliomycetes*)、盘菌纲(*Pezizomycetes*)、伞菌

纲(*Agaricomycetes*)、座囊菌纲(*Dothideomycetes*)] 和 12 个目[葡萄座腔菌目(*Botryosphaeriales*)、刺球壳目(*Chaetosphaeriales*)、红菇目(*Russulales*)、格孢腔菌目(*Pleosporales*)等]; 在 NPKG 处理组显

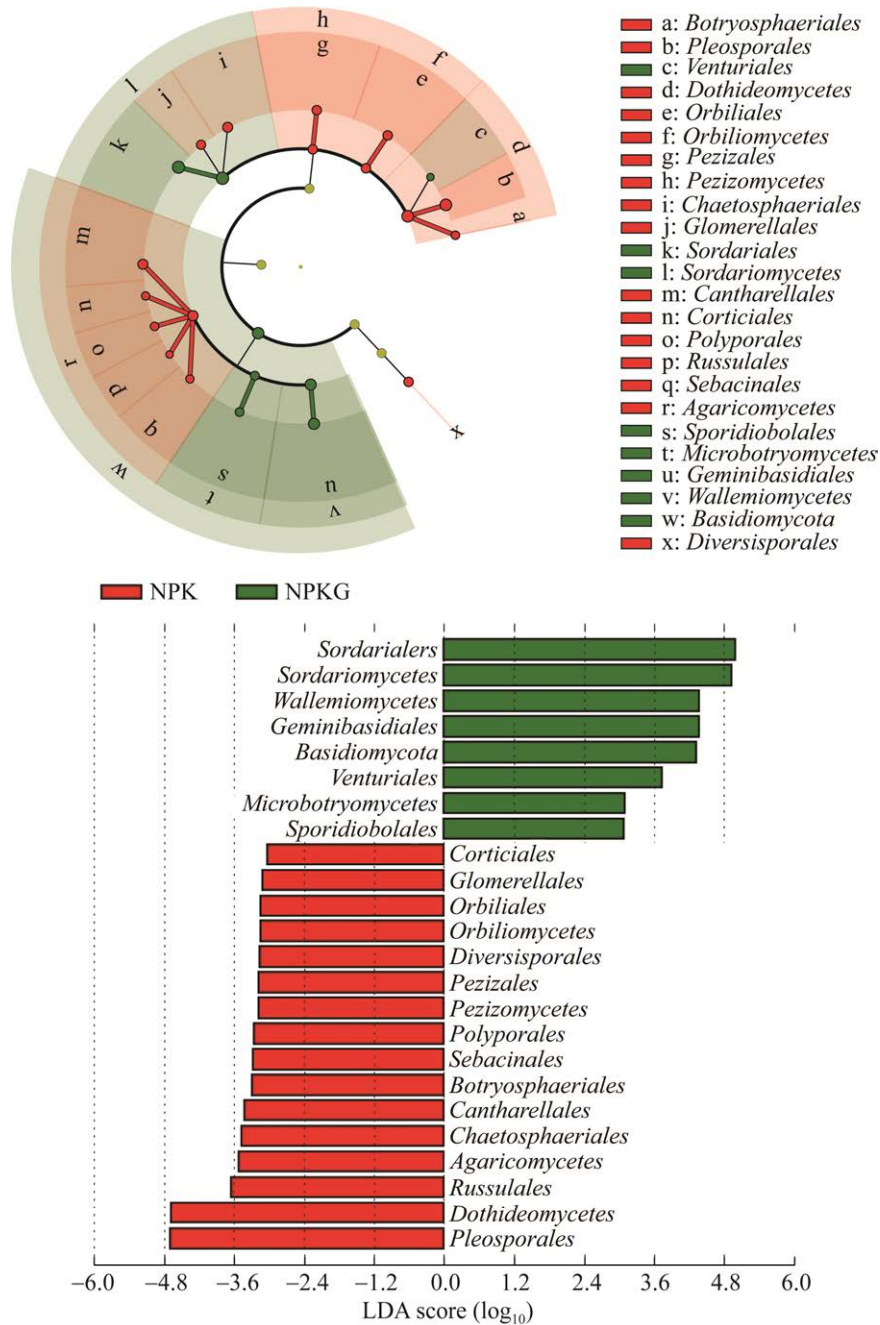


图 5 不同处理土壤真菌 LEfSe 分析(效应大小>2, α 值<0.05)

Figure 5 LefSe analysis of soil fungi in different treatments (the effect size>2 and the alpha value<0.05).

著富集的真菌有 1 个门[担子菌门(*Basidiomycota*)]、3 个纲[粪壳菌纲(*Sordariomycetes*)、节担菌纲(*Wallemiomycetes*)、微球黑粉菌纲(*Microbotryomycetes*)]和 4 个目[粪壳菌目(*Sordariales*)、双担菌目(*Geminibasidiales*)、黑星菌目(*Venturiales*)、锁掷酵母目(*Sporidiobolales*)]。指示物种分析用于鉴别不同处理土壤真菌的指示属, 结果表明 NPK 处理显著富集的真菌属主要有曲霉菌属(*Aspergillus*)、镰刀菌属(*Fusarium*)、蓝状菌属(*Talaromyces*)等 11 种; NPKG 处理中显著富集的真菌属主要为双担菌属(*Geminibasidium*)、腐质霉属(*Humicola*)等 6 种(表 4)。

2.4 土壤真菌共现网络

探究不同施肥处理对红壤旱地土壤真菌群落之间互作关系的影响, 构建土壤真菌群落共现网络(图 6A), 并计算网络的拓扑特性(表 5)。

表 4 不同处理土壤真菌的指示属

Table 4 Indicator genera of soil fungi in different treatments

Treatment	Taxonomy	<i>P</i>	Relative abundance (%)
NPK	g_ <i>Acrocalymma</i>	0.001	0.006
	g_ <i>Aspergillus</i>	0.013	0.096
	g_ <i>Talaromyces</i>	0.003	0.021
	g_ <i>Chloridium</i>	0.036	0.008
	g_ <i>Clonostachys</i>	0.001	0.013
	g_ <i>Acremonium</i>	0.002	0.004
	g_ <i>Fusarium</i>	0.002	0.063
	g_ <i>Gibellulopsis</i>	0.037	0.006
	g_ <i>Schizothecium</i>	0.003	0.008
	g_ <i>Ceratobasidium</i>	0.027	0.003
	g_ <i>Entrophospora</i>	0.003	0.003
NPKG	g_ <i>Sarcinomyces</i>	0.003	0.007
	g_ <i>Acidomelania</i>	0.011	0.004
	g_ <i>Pseudogymnoascus</i>	0.004	0.003
	g_ <i>Scedosporium</i>	0.008	0.002
	g_ <i>Humicola</i>	0.001	0.050
	g_ <i>Geminibasidium</i>	0.001	0.058

网络中一个节点代表一个 OTU, 边代表物种间的联系, 网络中节点、边和度能够代表网络的复杂度。结果表明, NPKG 处理相较于 NPK 网络节点数、边数、平均连通度、平均聚类系数及图密度均明显增加。以自然连通度评价网络稳定性(图 6B), 结果表明施加毛叶苕子后网络稳定性更高。

2.5 土壤真菌功能预测分析

对 NPK 及 NPKG 土壤真菌群落 OTUs 进行营养类型功能注释分析(图 7A), 共检测出 7 种营养类型, 分别是病原-腐生营养型(pathotroph-saprotroph)、病原-腐生-共生营养型(pathotroph-saprotroph-symbiotroph)、病原营养型(pathotroph)、共生营养型(symbiotroph)、腐生营养型(saprotroph)、腐生-共生营养型(saprotroph-symbiotroph)和病原-共生营养型(pathotroph-symbiotroph)。添加毛叶苕子后病原-腐生营养型和腐生-共生营养型真菌丰度分别降低 63.46%和 34.21%, 腐生营养型真菌相对丰度显著提高 37.42%, 而其他营养类型的相对丰度在不同处理之间差异不显著。对病原真菌进一步研究发现, 添加毛叶苕子后, 土壤中花生尾孢菌(*Cercospora arachidicola*)和可可毛色二孢菌(*Lasiodiplodia theobromae*)的相对丰度分别下降 89.11%和 88.1% (图 7B), 这说明添加毛叶苕子可能会降低花生致病菌的相对丰度。

3 讨论

3.1 添加毛叶苕子对红壤旱地土壤养分含量的影响

本研究发现相比于仅施用矿质肥的传统农业种植方式, 配施毛叶苕子显著增加土壤有机碳、总氮、碱解氮和有效磷的含量及作物产量(表 1, 图 1), 这与牛雅琼等^[27]和张久东等^[14]的研究结果一致。土壤中有有机碳、氮和磷含量都是土壤肥力的重要指标^[28], 施用毛叶苕子不

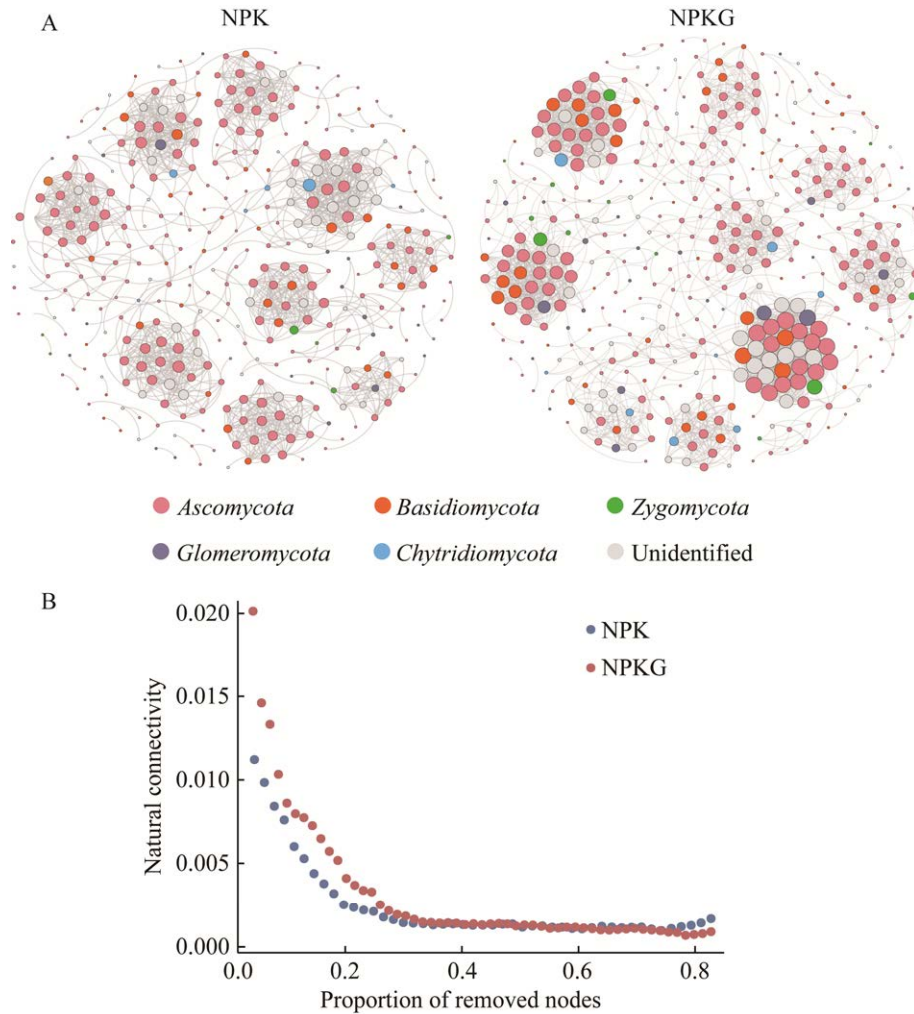


图 6 不同处理下土壤真菌门阶元分类水平共现网络结构(A)和自由连通度(B)

Figure 6 The co-occurrence network structure of phylum level of intestinal fungal (A) and natural connectivity (B) at different developmental stages.

表 5 不同处理下土壤真菌分子网络拓扑特性
Table 5 Topological properties of soil fungal interaction networks in different treatments

Property	NPK	NPKG
Nodes	368	428
Edges	1 574	2 338
Diameter	17	33
Average degree	8.554	10.925
Average path length	5.704	11.314
Average clustering coefficient	0.698	0.719
Modules	0.883	0.847
Density	0.023	0.026

仅可以提高土壤有机碳含量, 还可以提高土壤氮素供应及磷素生物有效性^[29-30], 从而改善土壤肥力, 提高作物产量。然而本研究发现施用毛叶苕子降低土壤 pH, 导致土壤酸化。前人研究也发现施用豆科绿肥会造成土壤酸化^[31]。豆科绿肥含有大量有机氮, 氮硝化过程产生氢离子, 导致土壤酸化^[32]。另外有研究表明豆科植物生长阶段从土壤中吸收的阳离子可能多于阴离子, 它们的根则需分泌质子来维持电荷平衡^[33], 进而引起土壤酸化。虽然施用豆科绿肥毛叶苕子显

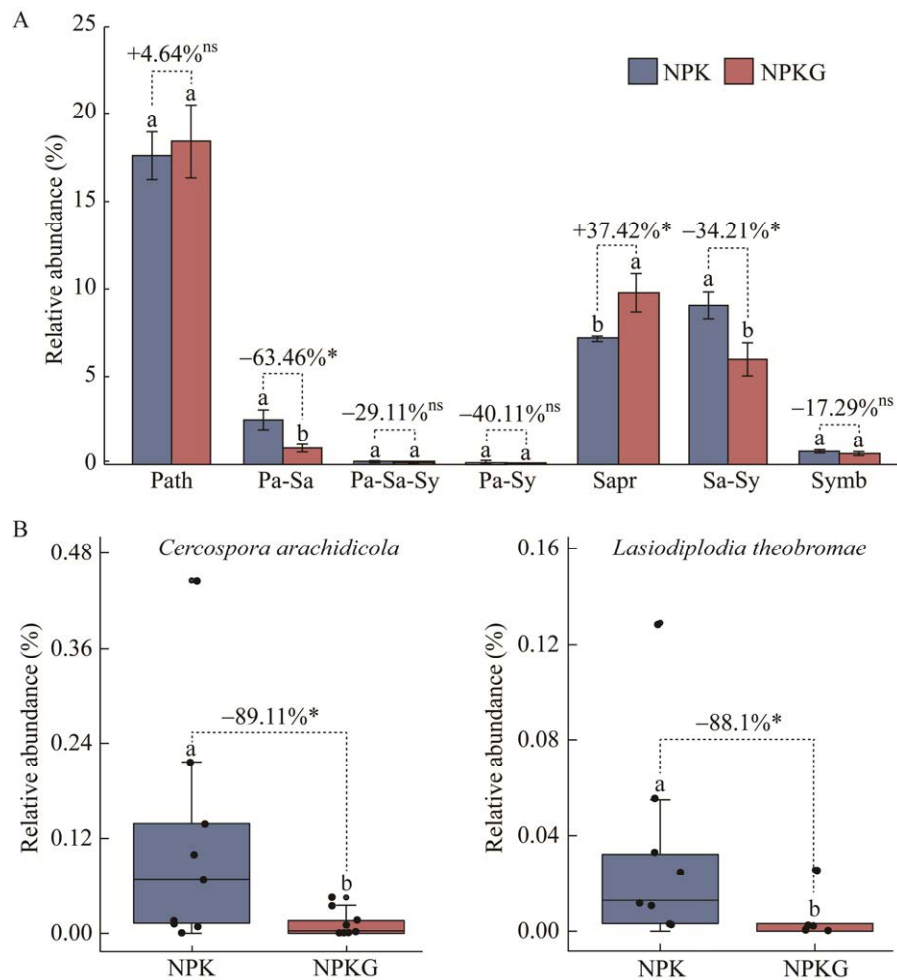


图7 土壤真菌群落主要营养型(A)和土壤花生病原型真菌相对丰度(B)

Figure 7 Soil fungi trophic mode (A) and relative abundance of prototype fungi for soil flower disease (B). Path: Pathotroph; Pa-Sa: Pathotroph-saprotroph; Pa-Sa-Sy: Pathotroph-saprotroph-symbiotroph; Pa-Sy: Pathotroph-symbiotroph; Sapr: Saprotroph; Sa-Sy: Saprotroph-symbiotroph; Symb: Symbiotroph. Different letters above bar plots indicate significant differences at 0.05 level. ns: $P>0.05$; *: $P<0.05$.

著增加土壤养分, 但是其造成的土壤酸化现象也需要格外关注。

3.2 添加毛叶苕子对土壤真菌多样性及群落结构的影响

土壤 pH 是影响土壤真菌群落的重要因素^[34]。本研究发现施用毛叶苕子后土壤 pH 下降, 进而改变土壤真菌的生长环境。真菌对土壤 pH 比较敏感, 土壤 pH 下降导致部分真菌不能适应酸化环境, 生长受到抑制或逐渐消亡, 进而降低土

壤真菌的多样性, 改变真菌的群落组成^[35]。同时, 施用毛叶苕子增加土壤有机质含量, 提高土壤真菌底物水平。在土壤 pH 下降后适应酸化环境的土壤真菌在大量有机质供应下快速繁殖^[36-37], 显著增加土壤真菌的丰度。

虽然本研究发现施用毛叶苕子降低土壤真菌多样性, 但是总体来看, 多样性下降的幅度较小。由于微生物存在功能冗余现象, 土壤酸化导致真菌多样性的轻微减少并不会使真菌生

态功能降低^[38-39]。先前有研究表明土壤多功能性的主要驱动因素是微生物丰度,并非生物多样性^[39-41]。此外,本研究施用毛叶苕子后土壤真菌网络更为复杂,网络稳定性增强(图 6)。具有复杂微生物网络的生态系统对环境扰动变化表现更加稳定,并支持更高的生态多功能性^[42]。因此,施用毛叶苕子增加土壤真菌丰度,促进真菌生态多功能性,对红壤旱地具有积极作用。

3.3 添加毛叶苕子对红壤旱地土壤有益真菌类群的影响

不同的施肥方式改变土壤的优势菌群。本研究发现配施毛叶苕子后,土壤中担子菌门(*Basidiomycota*)、粪壳菌目(*Sordariales*)、双担菌属(*Geminibasidium*)和腐质霉属(*Humicola*)显著富集(图 4,表 4,图 5)。真菌功能预测分析也表明随着毛叶苕子的施加,土壤中腐生营养型真菌显著富集(图 7A)。担子菌门与土壤中外源有机质的降解有关^[43-45],在植物残体降解过程中发挥着重要作用^[44-46];粪壳菌目具有较强的分解木质素和纤维素的能力^[47];双担菌属具有分解和释放土壤矿质营养的能力^[48];腐质霉属^[49-50]可降解纤维素等大分子物质。这类有益菌均可通过降解有机质来提高土壤养分水平^[46-51]。添加毛叶苕子为土壤提供大量外源有机质,有利的生存环境使这类有益菌群逐渐增加^[52],进而提高土壤养分。因此,施用毛叶苕子引起红壤旱地养分和有益真菌的正反馈作用,有利于作物生长。

3.4 添加毛叶苕子对红壤旱地土壤潜在致病菌的影响

本研究发现土壤中葡萄座腔菌目(*Botryosphaeriales*)、格孢腔菌目(*Pleosporales*)、角担菌属(*Ceratobasidium*)以及镰刀菌属(*Fusarium*)的相对丰度在 NPKG 处理中显著降

低(表 4,图 5)。葡萄座腔菌目包含大量植物病原菌^[53];格孢腔菌目是导致土壤中连作障碍的植物病原菌,主要引起烟草黑星病、小麦根腐病、甜菜叶斑病等病害^[54];角担菌属是西瓜根腐病的病原^[55];镰刀菌属的大多数真菌物种都是植物病原菌,可侵染多种经济作物,引起植物的根腐、茎腐、花腐和穗腐等多种病害^[56-57]。本研究重点关注影响花生生长的病原菌。研究发现施用毛叶苕子后,土壤中花生尾孢菌(*Cercospora arachidicola*)和可可毛色二孢菌(*Lasiodiplodia theobromae*)相对丰度显著降低(图 7B)。花生尾孢菌主要危害花生叶片,导致花生发生褐斑病,严重时可侵害花生植株的叶柄、托叶和茎秆等^[58];可可毛色二孢菌是一种广泛存在的土传病原真菌^[59],可导致花生发生茎腐病、烂果病^[60]。施加毛叶苕子显著提高了土壤真菌丰度,改变土壤微生物组成^[61],进而可能与病原菌形成竞争和拮抗效应^[62],导致土壤中病原真菌下降。

4 结论

本研究探究了红壤花生旱地施用毛叶苕子对土壤真菌群落结构和功能的影响。与常规矿质施肥相比,配施毛叶苕子显著提高土壤养分含量、真菌丰度和作物产量,并显著改变土壤真菌群落结构。配施毛叶苕子增加土壤中担子菌门、粪壳菌目、双担菌属和腐质霉属等有益菌群的相对丰度,加速土壤有机质的降解,提高土壤肥力;降低葡萄座腔菌目、格孢腔菌目、角担菌属、镰刀菌属、花生尾孢菌和可可毛色二孢菌等植物病原菌的相对丰度,减少病害的发生。本研究详细探讨施用豆科绿肥对红壤旱地生态系统的影响,研究结果对指导实施农业可持续发展具有一定的理论和实践意义。

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