ENVIRONMENTAL SCIENCE

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黄河下游谷子花生间作农田土壤细菌群落结构与功能 预测

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摘要:通过明确谷子花生 4: 4间作对黄河下游农田土壤细菌群落结构及其多样性的影响,探索农田土壤肥力对谷子花生间作模式响应的微生态变化特性,为促进黄河下游农田生态修复和耕地质量提升提供参考依据. 采用 Illumina MiSeq 高通量测序技术与 QIIME 2 平台,分析单作谷子(SM)、单作花生(SP)、间作谷子(IM)、间作花生(IP)和谷子花生间作(MP)这 5 种土壤的细菌群落组成差异及其影响因素,并预测其生态功能. 结果表明,间作土壤细菌群落 α 多样性与单作存在差异,但不显著, β 多样性则具有显著差异(P<0.05);所有土壤样品共获得7081 ASV,划分为34 门、109 纲、256 目、396 科、710 属和1409 种,其中共有的 ASV 为727 个,在 5 种土壤中占 24.5%~27.8%;谷子花生间作及其单作土壤细菌群落的菌门组成相似,但相对丰度各异;5 种土壤均以放线菌门、变形菌门、酸杆菌门和绿弯菌门为主,相对丰度可达 79.40%~81.33%;土壤有机碳和碱解氮分别是引起 5 种土壤细菌群落结构门、属水平产生差异的最主要因子;通过 PICRUSt 功能预测发现,初级功能新陈代谢的相对丰度最大(78.9%~79.3%),次级功能外源生物降解与代谢的相对丰度波动最大(CV = 3.782%);在 BugBase 表型方面,间作谷子或花生土壤较相应单作的氧化胁迫耐受细菌相对丰度增加,且间作谷子土壤较单作谷子显著增加(P<0.05);氧化胁迫耐受、革兰氏阳性及需氧三类表型细菌间两两极显著正相关(P<0.01),且三者均与潜在致病性、革兰氏阴性及厌氧呈极显著负相关(P<0.01),由此可见,谷子花生间作改变了土壤细菌群落多样性、丰富度和代谢功能,存在降低潜在土壤病害发生的可能性,可用于调控土壤微生态环境,以推动黄河下游农田生态修复和农业可持续发展.

关键词:黄河下游; 间作; 土壤细菌; 群落结构; BugBase 表型

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Soil Bacterial Community Structure and Function Prediction of Millet/Peanut Intercropping Farmland in the Lower Yellow River

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Abstract: The objective of this study was to explore the microecological variability in farmland soil fertility in response to millet-peanut intercropping patterns by clarifying the effects of millet-peanut 4:4 intercropping on soil bacterial community structure and its diversity, as well as to provide a reference basis for promoting ecological restoration and arable land quality improvement in the lower Yellow River farmland. The Illumina MiSeq high-throughput sequencing technology and QIIME 2 platform were used to analyze the differences in bacterial community composition and their influencing factors in five soils [sole millet (SM), sole peanut (SP), intercropping millet (IM), intercropping peanut (IP), and millet-peanut intercropping (MP)] and to predict their ecological functions. The results showed that the α-diversity of intercropping soil bacterial communities differed from that of monocropping, though not significantly, whereas the β -diversity was significantly different (P < 0.05). A total of 7081 ASVs were obtained from all soil samples, classified into 34 phyla, 109 orders, 256 class, 396 families, 710 genera, and 1409 species, of which 727 ASVs were shared, accounting for 24.5% to 27.8% in five soil species. The bacterial communities of millet-peanut intercropping and its monocropping soils were similar in phylum composition but varied in relative abundance. All five soils were dominated by the Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi, with a relative abundance of 79.40%-81.33%. Soil organic carbon and alkaline nitrogen were the most important factors causing differences in the structures of the five soil bacterial communities at the phylum and genus levels, respectively. The PICRUSt functional prediction revealed that the relative abundance of primary functional metabolism was the largest (78.9%-79.3%), and the relative abundance of secondary functional exogenous biodegradation and metabolism fluctuated the most (CV = 3.782%). In terms of the BugBase phenotype, the relative abundance of oxidative stress-tolerant bacteria increased in intercropping millet or peanut soils compared to that in the corresponding monocultures and significantly increased in intercropping millet soils compared to that in sole millet (P < 0.05). Oxidative stress-tolerant, Gram-positive, and aerobic phenotypes were highly significantly positively correlated with each other (P<0.01), and all three showed highly significant negative correlations with potential pathogenicity and Gram-negative and anaerobic phenotypes (P<0.01). This showed that millet-peanut intercropping resulted in differences in soil bacterial community diversity, abundance, and metabolic functions and the possibility of reducing the occurrence of potential soil diseases. It can be used to regulate the soil microbiological environment to promote ecological restoration and sustainable development of farmland in the lower Yellow River.

Key words: lower Yellow River; intercropping; soil bacterial; community structure; BugBase phenotype

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土壤微牛物是土壤牛态系统的重要组成部分, 主导土壤生态系统养分循环和能量流动,对维持系 统的稳定性和可持续性具有重要作用[1,2]. 土壤细 菌生物量占土壤微生物总量的70%~90%,其生理 类群对腐殖质形成、有机质分解、土壤养分循环和 转化发挥着关键的作用[2,3]. 已有研究发现,不同土 地利用方式、耕作制度、物料还田和植被类型等均 会对土壤细菌种类和数量产生影响,进而影响土壤 细菌群落结构和空间分布[3~7]. 此外,农田管理措施 如施肥、浇水和除草等也会改变土壤细菌的群落组 成及多样性[8,9]. 细菌群落结构及其多样性与土壤 可持续利用紧密相关,可作为反映农田生态特征、 评价土壤质量的生物指标[1]. 土壤细菌多样性的研 究方法很多,Illumina MiSeq 高通量测序技术日趋成 熟,目前已经广泛应用于土壤微生物群落结构多样 性的研究.

间作是指在同一生长季,两种或多种作物分行 或分带相间种植在同一田块上的种植制度. 作为我 国传统农业的精髓,间作具有增产增效、提高光热 资源利用率[10,11]、增加农田生物多样性和持续控制。 病虫草害的优势,还可以改善农田生态环境,促进生 态平衡[11~13]. 间作也可以改变土壤微生物群落多样 性[13],增加作物对养分的吸收[11]. 花生是我国重要 的油料作物,谷子是华北地区重要的杂粮作物,谷子 花生间作是一种典型的高矮秆作物配置体系,可以 发挥作物空间的互补作用,在黄淮地区已有较大面 积的种植. 研究表明, 禾本科与花生间作可以显著增 加土壤细菌数量[14,15];间作系统中,根际相互作用 对于改善土壤微生态环境,增加土壤细菌丰富度和 多样性具有重要意义[16]. 然而,谷子花生间作对土 壤细菌群落结构及其多样性影响的研究还未见报 道,明确谷子与花生间作农田土壤细菌群落结构特 征,是揭示土壤细菌群落结构对不同种植模式土壤 肥力变化响应的必要环节. 因此,本文通过位于黄河 下游的大田研究,明确土壤细菌群落结构对谷子、 花生单作及其间作的响应差异,阐明谷子花生间作 影响农田土壤肥力的微生态特性,以期为黄河下游 农田土壤微生态环境调控和农业可持续发展提供参 考依据.

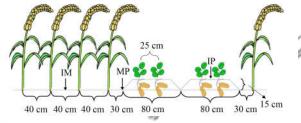
1 材料与方法

1.1 试验概况

本试验位于黄河下游山东省肥城市(116.78° E,35.98° N),属暖温带大陆性季风气候区,四季分明,光照充足,气候温暖.年日照时数2607 h,年均气温12.9℃,无霜期约200 d,年均降水量660 mm.

供试土壤为棕壤,耕层 0~20 cm 土壤 ω [有机质 (TOM)]为 11.6 g·kg⁻¹、 ω [全氮 (TN)]为 1.0 g·kg⁻¹、 ω [碱解氮 (AN)]为 75.9 mg·kg⁻¹、 ω [有效磷 (AP)]为 28.0 mg·kg⁻¹和 ω [速效钾 (AK)]为 168.6 mg·kg⁻¹,pH 为 7.0.

2019年5~9月以谷子(SM)和花生(SP)单作种植为对照,设置谷子花生4:4间作(MP,图1)种植模式,幅宽3.4 m. 其中,间作谷子株距2 cm,单作谷子4 cm,行距相同;单作花生种植规格与间作相同,穴距10 cm,单粒精播.每个种植模式田间面积约0.45 hm²,分别划分为3个自然重复.2019年5月7日播种,9月12日采集单作谷子(SM)、单作花生(SP)、间作谷子(IM)、间作花生(IP)和谷子花生间作(MP,间作谷子花生交汇处,图1)这5种土壤样品.谷子供试品种为济谷20,花生为花育36;播前基施氮磷钾复合肥(15-15-15)750 kg·hm²,其他田间管理措施基本一致.



IM、IP 和 MP 分别为间作谷子、间作花生和谷子 花生间作土壤的取样位点

图 1 谷子花生 4:4间作田间示意

Fig. 1 Field schematic diagrams of the millet/peanut 4:4 intercropping

1.2 样品采集

于2019年8月25日,5种土壤每个重复"S"形采集30点0~20cm土层样品,均匀混合为1个样本,共计15个样本,用干冰保存并迅速带回实验室.剔去沙石、根系等杂质后,部分鲜土样品转入无菌冻存管中,储存于-80℃冰箱,用于分析土壤细菌群落结构;剩余样品自然风干后过0.25cm和1mm筛测定土壤理化性状.

1.3 测定方法

土壤基础理化性质测定参考《土壤农化分析》[17],土壤 TN 采用凯氏定氮法,土壤 AN 采用碱解扩散法,土壤 AP 采用碳酸氢钠-钼锑抗分光光度法,土壤 AK 采用醋酸铵-原子吸收火焰分光光度计法,土壤有机碳(TOC)采用重铬酸钾氧化-外加热法,pH 采用电位法(水土比 2.5:1).

参照 OMEGA Soil DNA Kit 试剂盒(USA)说明书提取土壤 DNA,用1%的琼脂糖凝胶电泳进行检

测,使用核酸定量仪(Nano Drop ND-2000)检测提取 DNA 的浓度和纯度.选择细菌 V3-V4 区的 16S rRNA序列进行 PCR 扩增,扩增引物为 338F(5'-ACTCCTACGGGAGGCAGCAG-3') 和 806R (5'-GGACTACHVGGGTWTCTAAT-3').

PCR 扩增采用 TransGen AP221-02: TransStart FastPfu DNA Polymerase, 20 μL 反应体系: FastPfu Buffer 4 μL 循环 5 次, 2.5 mmol·L⁻¹ dNTPs 2 μL, 5 μmol·L⁻¹ Forward Primer 0.8 μL, 5 μmol·L⁻¹ Reverse Primer 0.8 μL, FastPfu Polymerase 0.4 μL, BSA 0.2 μL, Template DNA 10 ng, ddH₂O 补至 20 mL. PCR 反应参数为:95℃持续 3 min, 27 次循环 (95℃持续 30 s,55℃ 退火 30 s,72℃持续 45 s),72℃ 延伸 10 min, 10℃ 至停机 (PCR 仪: ABI GeneAmp-9700 型).

使用 2% 琼脂糖凝胶电泳检测 PCR 产物,依照 AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, USA) 说明书进行纯化,再用 QuantiFluor™-ST (Promega, USA)进行定量.通过Illumina MiSeq 平台构建 Paired-end 测序,由上海美吉生物医药科技有限公司提供技术支持.

2 000 1 800 1 600 1 400 1 200 W 1 000 W 800 600 400 400 - - SM - SP - MP - IM

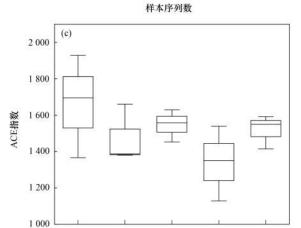
200

4 000

SM

SP

8 000



MP

IM

12 000 16 000

1.4 数据处理

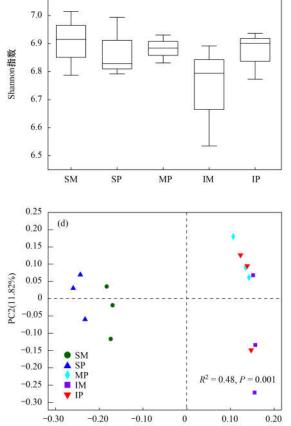
基于 QIIME 2(v2020.2)流程^[18]进行质控、拼接和降噪,聚类为 ASV(amplicon sequence variants), 置信度阈值为 0.7,比对 silva 138/16s 数据库,并按最小样本序列数抽平. 利用 Mothur 软件进行土壤细菌群落 α 多样性分析; 利用基于 bray-curtis 距离的 PCoA 分析揭示土壤细菌群落的 β 多样性,并通过Adonis 分析进行组间差异检验; 利用冗余分析(RDA)反映菌群与环境因子之间的关系; 利用PICRUSt2 对细菌群落进行功能预测,利用 BugBase进行表型预测.通过 R 语言作图,使用 SPSS 26.0 进行单因素方差分析(one-way analysis)和多重比较(LSD).

2 结果与分析

7.1 - (b)

2.1 土壤细菌群落多样性比较

将15个样本按最小样本序列数抽平1次,每个样本得到24769条有效序列,且ASV稀释曲线均趋于平缓[图2(a)],表明本研究的测序深度已基本覆盖到样品中所有物种,序列信息可以充分反映土壤细菌群落的真实信息.尽管5种农田土壤细菌群



PC1(25.09%)

图 2 土壤细菌群落多样性

IP

IP

24 000

20 000

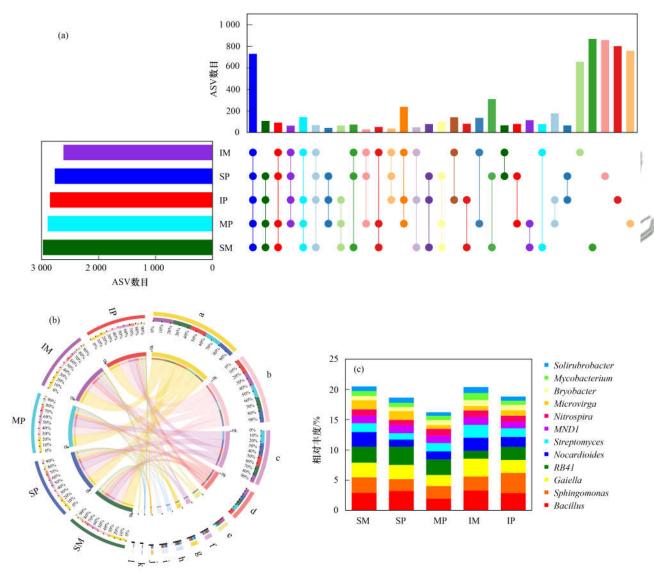
Fig. 2 Diversity of soil bacterial community

落的 Shannon [图 2(b)]和 ACE [图 2(c)]指数无显著性差异,但在单作或间作条件下细菌群落的 α 多样性产生了变化. 应用基于 bray-curtis 距离算法的 PCoA 分析比较 5 种土壤细菌群落的 β 多样性 [图 2(d)]. 结果表明,主成分 PC1 和 PC2 分别解释 25.09%和11.82%群落组成差异. IM、IP 和 MP 这 3 种土壤样品在 PC1 轴上距离接近或存在重合,表明 3 种土壤样品物种组成相似;结合 Adonis 分析表明,谷子花生间作和单作土壤细菌群落的 β 多样性差异显著 (P = 0.001, R^2 = 0.39).

2.2 土壤细菌群落结构组成

15 个土壤样本共获得有效序列371 535条,基于97%的相似度进行聚类,获得7081 ASV,划分为34门、109 纲、256 目、396 科、710 属和1 409种.通过UpSet Venn 分析[图 3(a)],5 种土壤样本中共有的ASV 为727 个,在5 种土壤中占24.5%~27.8%; SM、SP、MP、IM 和 IP 独有的ASV 分别为865、854、755、653 和798 个,占各自土壤细菌ASV 总数的29.1%、30.9%、26.1%、25.0%和28.0%.

SM、SP、MP、IM 和 IP 土壤细菌门水平的群落



(a) 横排柱状图表示每个模式土壤样本 ASV 的数量;竖排柱状图表示不同模式土壤样本取交集后 ASV 的数量;点和点之间的连线表示不同模式土壤样本中共有的 ASV,单个点表示某个模式土壤样本中特有的 ASV;(b) 左半圆表示土壤细菌群落中门的组成情况,外层彩带的颜色表示的是不同种类土壤,内层彩带的颜色表示细菌门,长度表示该物种在对应土壤样本中的相对丰度;右半圆表示门水平下物种在不同种类土壤样本中的分布比例情况,外层彩带表示细菌门,内层彩带颜色表示不同种类土壤,长度表示该土壤样本在某一门中的分布比例,字母 a~1分别表示放线菌门(Actinobacteria)、变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)、绿弯菌门(Chloroflexi)、厚壁菌门(Firmicutes)、芽单 胞 菌 门(Gemmatimonadetes)、其 他(合 并 相 对 丰 度 小 于 0.01)、拟 杆 菌 门(Bacteroidetes)、Myxococcota、Methylomirabilota、硝化螺旋菌门(Nitrospirota)和未被分类细菌;(c) 在任一土壤样本中相对丰度大于 1% 的已知细菌属,其中未标记或未命名的物种未列人

图 3 土壤细菌群落组成

Fig. 3 Composition of soil bacterial community

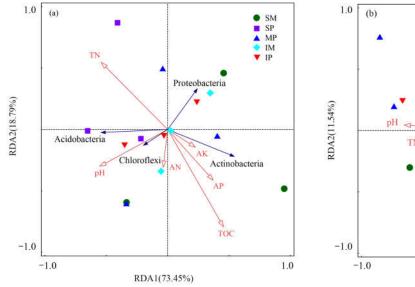
结构组成相似,但细菌门相对丰度各有差异[图 3 (b)].5 种土壤中相对丰度大于 0.01 的已知细菌包含 10 门,相对丰度小于 0.01 的其他细菌在 2.01%~3.62%之间.放线菌门(Actinobacteria)、变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)和绿弯菌门(Chloroflexi)在 5 种土壤中占 79.40%~81.33%;这4门细菌的相对丰度明显高于厚壁菌门(Firmicutes)、芽单胞菌门(Gemmatimonadetes)、拟杆菌门(Bacteroidetes)、Myxococcota、Methylomirabilota和硝化螺旋菌门(Nitrospirota).放线菌门在 SM 和 IM 中的相对丰度明显高于 SP、IP和 MP,酸杆菌门在 5 种土壤中相对丰度的高低则与放线菌门相反.

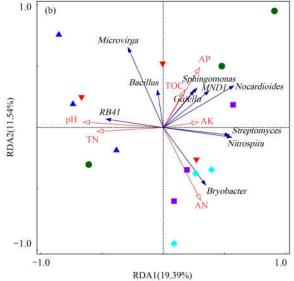
在SM、SP、MP、IM和IP任一土壤样本中相对 丰度大于 1.0%的已分类细菌属共 12 类[图 3 (c)]. 这些细菌属在 SM和 IM中相对丰度合计分别为 20.51%和 20.41%,在 SP和 IP中则分别为 18.66%和 18.84%;在 MP中仅 16.23%,较 SM、SP、IM和IP降低了 13.05%~20.86%,表明 MP增加了其他土壤细菌属的相对丰度. 芽孢杆菌属 (Bacillus)、鞘氨醇单胞菌属 (Sphingomonas)、Gaiella和 RB41,这4类细菌属在5种土壤中平均相对丰度大于 2.0%;类诺卡氏菌属(Nocardioides)仅

在 SM 和 IM 中相对丰度大于 2.0%, 链霉菌属 (Streptomyces) 仅在 IM 中相对丰度大于 2.0%; MND1、硝化螺菌属(Nitrospira)、微枝形杆菌属 (Microvirga)、 Bryobacter、 分 枝 杆 菌 属 (Mycobacterium)和 Solirubrobacter 则均小于 2.0%.

2.3 土壤细菌群落与环境因子的关系

为研究造成谷子花生间作或单作后土壤细菌群 落产生差异的关键环境因子,对5种土壤细菌群落 组成与土壤理化性质进行冗余分析(图4).在门水 平上「图 4(a)], RDA1 和 RDA2 可以累计解释土壤 细菌群落 92.24% 的变异量, TOC、TN 和 pH 是影响 细菌群落门组成结构的重要因子; 在属水平上[图 4(b)], RDA1 和 RDA2 可以累计解释 30.93% 的变 异量,AN、pH、AP和TN是影响细菌群落属组成结 构的重要因子. 图 4 (a) 可以看出, 放线菌门 (Actinobacteria)与TN和pH呈正相关,与TOC、 AP、AK 和 AN 呈负相关;变形菌门(Proteobacteria) 与TN和AK呈正相关,与pH、TOC、AP和AN呈负 相关;酸杆菌门(Acidobacteria)与TN、pH和AN呈 正相关,与 TOC、AP 和 AK 呈负相关;绿弯菌门 (Chloroflexi)与 TOC、TN、pH 和 AN 呈正相关,与 AP 和 AK 呈负相关. 图 4(b) 可以看出, 不同细菌属 与 TOC、TN、AN、AP 和 AK 相关性也不尽相同.





红色箭头表示环境因子,箭头长度表示环境因子与细菌群落结构相关性的强弱;蓝色箭头表示细菌类型,箭头指向与环境因子箭头同向表示高度正相关;TOC表示有机碳,TN表示全氮,AN表示碱解氮,AP表示有效磷,AK表示速效钾

图 4 土壤细菌群落与环境因子的 RDA 分析

Fig. 4 RDA analysis of soil bacterial community and environmental factors

2.4 土壤细菌群落功能与表型预测

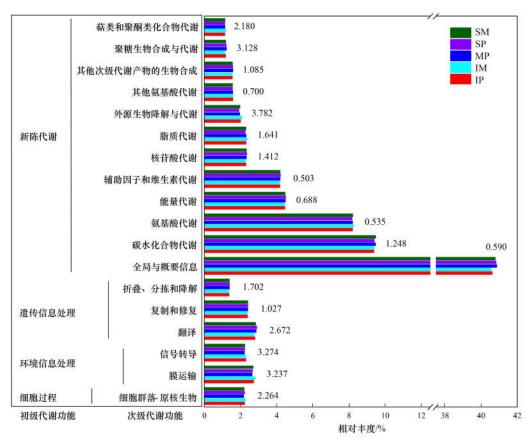
将高通量测序信息与 KEGG 数据库(Kyoto encyclopedia of genes and genomes)比对,利用 PICRUSt 对 5 种土壤的细菌群落进行功能预测,结果注释到初级功能代谢通路 6 条,次级功能代

谢通路 46 条,三级功能代谢通路 404 条. 在初级功能代谢通路中,新陈代谢在 5 种土壤中相对丰度达 78.9%~79.3%,明显高于环境信息处理、遗传信息处理、细胞过程、人类疾病和有机系统;在次级功能代谢通路中,相对丰度大于

1.0%的通路包含18条,其中全局与概要信息的相对丰度高达40.6%~40.9%(图5).从图5可以看出,在5种土壤中,外源生物降解与代谢的变异系数最高达3.782%,聚糖生物合成与代谢、信号转导和膜运输的变异系数在3.128%~3.274%之间,这4条次级功能代谢通路的相对丰度波动相对较大.

利用 BugBase 工具对 15 个土壤样本进行表型预测,结果包含生物膜形成[图 6(a)]、革兰氏阳性[图 6(b)]、革兰氏阴性[图 6(c)]、氧化胁迫耐受[图 6(d)]、移动元件[图 6(e)]、致病性[图 6(f)]和氧需求七类,氧需求又分为需氧[图 6(g)]、厌氧[图 6(h)]和兼性厌氧[图 6(i)].由于一个物种可

能属于多种表型,因此可能会重复计算表型丰度,导致每种土壤中的总表型丰度通常高于 100%. 在 7 类表型中,生物膜形成占比最高达 21.6%~22.3%,其次是革兰氏阴性;在氧需求中,需氧占比最高达 13.4%~14.6%. 在 5 种土壤中,MP 和 IM 的革兰氏阳性、革兰氏阴性及致病性的相对丰度存在显著差异(P<0.05),IM 氧化胁迫耐受的相对丰度也显著高于 SP 和 MP(P<0.05). 比较 5 种土壤中细菌 BugBase 表型间的相关性(表 1),结果表明氧化胁迫耐受、革兰氏阳性和需氧这 3 类表型细菌间两两极显著正相关,潜在致病性、革兰氏阴性和厌氧这 3 类间两两极显著正相关;而这两组表型细菌间均具极显著负相关.



柱状图数值表示变异系数(CV),单位为%

图 5 土壤细菌群落的 KEGG 功能

Fig. 5 KEGG function of soil bacterial community

表 1 土壤细菌群落 BugBase 表型间的相关性 $^{1)}$

Table 1 Correlation between Bugbase phenotypes of soil bacterial communities

•	需氧	厌氧	兼性厌氧	移动元件	生物膜形成	革兰氏阴性	革兰氏阳性	潜在致病性	氧化胁迫耐受
需氧	- 1								
厌氧	-0.566*	1							
兼性厌氧	0. 231	- 0. 816 **	1						
移动元件	0.358	- 0. 783 **	0. 597 *	1					
生物膜形成	0. 101	0. 576 *	-0. 856 **	-0.328	1				
革兰氏阴性	-0.661 **	0. 651 **	-0.408	-0.319	0. 187	1			
革兰氏阳性	0. 661 **	-0.651 **	0.408	0.319	-0.187	- 1. 000 **	1		
潜在致病性	-0.726 **	0. 712 **	-0.494	- 0. 346	0. 223	0. 919 **	-0.919**	1	
氧化胁迫耐受	0. 809 **	- 0. 785 **	0.46	0. 567 *	-0.169	- 0. 878 **	0. 878 **	-0.912**	1

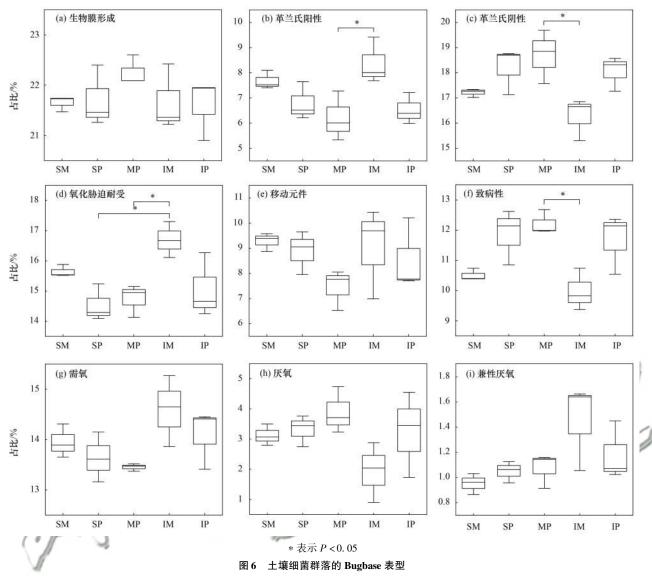


Fig. 6 Bugbase phenotype of soil bacterial community

3 讨论

3.1 间作对农田土壤细菌群落多样性的影响

土壤微生物群落是土壤耕地质量和生态系统稳定的重要量化指标,对植被敏感的同时,又能强烈影响土壤养分转化和作物生长^[2,19];而土壤养分转化和作物生长又会反作用于土壤微生物群落,使其群落多样性发生改变.本研究发现,间作土壤细菌群落α多样性的 Shannon 指数和 ACE 指数与单作存在差异,β多样性的 PCoA 分析则具有显著差异(P=0.001),说明谷子花生间作可以改变单作谷子或花生土壤的细菌群落多样性.这可能是因为,与单作相比,间作使农田作物覆被发生变化,使作物根系在土壤中的分布更复杂,导致土壤细菌与作物根系分泌物互动更频繁,从而改变了土壤细菌的代谢活性,促使间作土壤细菌群落多样性与单作土壤产生差异^[13,15].另外,一是谷子花生间作或单作后使土壤

中有效养分发生变化,二是豆科花生的固氮体系可以增加土壤氮素,这两方面也可能是影响土壤细菌群落多样性变化的原因. 这与前人研究的玉米豆科^[16]、甘蔗大豆^[20]、木薯花生^[21]和甘蔗花生^[22]等间作模式通过改变土壤养分含量,进而改变土壤微生物群落多样性的研究结果基本一致.

3.2 间作对农田土壤细菌群落结构的影响

禾本科豆科间作系统不仅可以改变土壤细菌的多样性和丰富度,对土壤细菌群落组成结构和优势菌群类别也具有一定影响^[14,15].本研究发现的放线菌门(Actinobacteriota)、变形菌门(Proteobacteria)、酸杆菌门(Acidobacteriota)和绿弯菌门(Chloroflexi),在其他土壤样本的研究中也经常观察到^[7,23,24].说明不同种植模式下土壤细菌群落具有适应性和调节功能,这4类相对丰度较高的土壤细菌门可能有助于维持根系养分吸收和微环境的平衡,以改善土壤环境^[25].5种土壤中,相对丰度大于

1.0% 的细菌门或属的丰度高低排序均发生明显变 化,这可能与种植模式及作物种类有关[24,26]. O'Donnell等[27]研究发现地上作物类型通过影响土 壤环境,而影响土壤微生物群落结构.不同的植被类 型决定着各自的土壤微生物群落组成和分布,表现 为土壤微生物群落有明显的差异[7,28]. 土壤细菌属 水平中,谷子花生间作(MP)使相对丰度小于1.0% 的细菌属增加,这也可能与作物类型及其根系分泌 物有关,因为该位点土壤处于两种作物根系交汇区 域. 已有研究发现,由于作物种内或种间相互作用关 系的变化,导致作物的根系分泌特性相应改变,继而 调节土壤微生态环境,使土壤中微生物活动力度改 变,反过来影响细菌群落结构[29,30]. 种植作物可以 影响细菌群落结构外,还能通过残根、凋落物向土 壤中输入较多的碳氮源供细菌利用,增加微生物的 数量,改变细菌群落结构[30,31]. 这也可能是促进土 壤细菌群落组成发生改变的原因. Urbanová 等[32] 的 研究也发现细菌容易受到作物凋落物的影响. 与细 菌群落组成的门水平结构相比,本研究中细菌属水 平结构的变化更加明显,这应该也与种植模式、种 间关系、根系分泌和地上凋落物等有关. 另外,间作 遮荫对花生产生弱光胁迫,影响了花生的生长发育, 这可能也会对土壤细菌群落结构产生影响.

3.3 间作农田土壤细菌群落对环境因子的响应

任何环境因素改变都可能使土壤微生物群落结 构在一定程度上发生变化[33~35]. 植被类型、经纬、 海拔、气候变化、土壤理化性质和温湿度等环境因 素对土壤微生物具有抑制、促进或无明显作用,是 影响土壤微生物群落组成的重要环境因子[34~37].利 用 RDA 分析不同土壤细菌群落信息,可直观地展现 出土壤环境因子对该地区土壤细菌群落结构的影 响. 本研究发现,土壤有机碳和碱解氮分别是引起5 种土壤细菌群落结构门、属水平产生差异的最主要 环境因子. 这与过往研究中,土壤细菌群落结构组成 受土壤有机质和碱解氮等因素影响的结果类 似[36,38],氮碳是影响土壤细菌群落变化的重要因 子,两者作为土壤微生物的主要能源,对塑造细菌群 落至关重要^[38~42]. Fu 等^[26]和 Zhou 等^[43]研究发现, 间作改善了作物根际土壤微环境,降低了氨化强度, 刺激作物对氮、碳等的吸收和转化,改变了土壤养 分含量,从而导致细菌对土壤环境因子产生不同响 应: Tang 等[21,22] 对木薯花生和甘蔗花生间作系统 的研究也认为,木薯花生和甘蔗花生间作系统可以 通过增加土壤中氮的含量来改善土壤质量,以影响 细菌群落多样性.此外,本研究中环境因子对土壤细 菌门、属水平差异变化的解释度不同,门水平的 92. 24% 远大于属水平的 30. 93%. 这可能是因为土壤受间作或单作影响而引起环境因子发生变化,导致环境因子对不同水平细菌群落的贡献不同. 另外,土壤细菌虽然分布广、适应性强,但特定区域的细菌群落组成受到特定环境因子的调控^[35],而且不同地域或不同学者关于土壤细菌群落对环境因子响应的研究得出的结论也不同^[35~38,43,44].

3.4 间作对农田土壤细菌群落功能的影响

谷子花生间作使土壤细菌群落结构发生变化的 同时,也使土壤细菌功能代谢通路和表型类型产生 了差异. 本研究中, 通过 KEGG 代谢途径利用 PICRUSt 对谷子花生单作及其间作种植模式下土壤 细菌功能进行预测,不同种植模式下农田土壤细菌 共涉及新陈代谢、环境信息处理、遗传信息处理、 细胞过程、人类疾病和有机系统这6个初级代谢通 路,其中新陈代谢相对丰度最高.这表明农田土壤细 菌利用这6类初级功能代谢通路维系生态系统的稳 定;新陈代谢是土壤细菌群落的核心功能,在土壤 细菌生长过程中有着极其重要的作用,受人为影响 较小[45~48].有研究发现,土壤细菌通过代谢活动来 参与土壤物质循环与转化,进而促进植物生长和增 加作物产量,如固氮和解磷等作用的发挥是依靠代 谢提高根系对氮、磷营养元素的吸收[2,11,21]. 这应 该也是氨基酸代谢、碳水化合物代谢和能量代谢等 来维持细菌存活的代谢功能相对丰度较高的原因. 本研究 BugBase 表型预测发现,氧化胁迫耐受、革 兰氏阳性和需氧这3类表型细菌两两之间极显著正 相关,潜在致病性、革兰氏阴性和厌氧这3类两两 之间也极显著正相关,但是这两组间均极显著负相 关. 革兰氏阳性和革兰氏阴性细菌极显著负相关,这 与两类细菌的结构特点有关:需氧和厌氧细菌的极 显著负相关,则与两者对氧气的需求有关;氧化胁 迫耐受表型细菌与应对土壤逆境胁迫有关,潜在致 病性则与土壤病害有关. 本研究发现,间作谷子或花 生土壤较相应单作的氧化胁迫耐受细菌相对丰度增 加,且间作谷子土壤较单作谷子显著增加,可以推测 该谷子花生间作模式可能利于降低潜在土壤病害的 发生. Deng 等[49] 通过研究农田生态系统中细菌功 能对镉污染的生态响应,发现微生物群落中氧化胁 迫耐受表型细菌的变化可能反映了其对恶劣环境的 保护作用,以在剧毒环境中存活.由于一个物种可能 属于多种表型,因此关于细菌 BugBase 表型的预测 分析有待进一步研究.

4 结论

谷子花生间作及其单作土壤细菌群落的菌门组

成相似,均以放线菌门、变形菌门、酸杆菌门和绿 弯菌门为主,但相对丰度各异;细菌菌属组成表现 出与菌门相同的特征. 间作土壤细菌群落 α 多样性 与单作存在差异,但不显著,β多样性则具有显著 差异. 土壤有机碳和碱解氮分别是引起 5 种土壤细 菌群落结构门、属水平产生差异的最主要因子. 通 过 PICRUSt 功能预测发现,这 5 种土壤细菌中,初级 功能新陈代谢的相对丰度最大,次级功能外源生物 降解与代谢的相对丰度波动最大. 在 BugBase 表型 方面,间作谷子或花生土壤较相应单作的氧化胁迫 耐受细菌相对丰度增加,且间作谷子土壤较单作谷 子显著增加. 由此可见,谷子花生间作使土壤细菌群 落多样性、丰富度及代谢功能产生差异,存在降低 潜在土壤病害发生的可能性,可用于调控土壤微生 态环境,以推动黄河下游农田微生态修复和农业可 持续发展.

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