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採货箱泵 (HUANJING KEXUE)

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不同轮作休耕下潮土细菌群落结构特征

南镇武1,刘柱1,代红翠1,张磊2,王娜1,徐杰1,刘开昌1,孟维伟1*,王旭清1*

(1.山东省农业科学院作物研究所,小麦玉米国家工程实验室,济南 250100; 2.山东省烟台市农业科学研究院,烟台 265500)

摘要:本研究旨在明确不同轮作休耕方式对潮土细菌群落的影响,为推动黄河下游冲积平原农田生态修复和促进农业绿色发展提供参考依据.以 2018 年开始的长期轮作休耕定位试验农田土壤为研究对象,采用 Illumina MiSeq 高通量测序技术,通过 Tax4Fun 细菌功能预测工具,分析 4 种轮作休耕方式(长期休耕、冬小麦-夏休耕、冬休耕-夏玉米和冬小麦-夏玉米周年轮作) 定位条件下,土壤细菌群落结构与功能差异,并探究影响农田土壤细菌群落结构及功能变化的环境因子.结果表明,不同轮作休耕方式的土壤样本中共检测到细菌 44 门、146 纲、338 目、530 科、965 属和 2073 种;在 0~20 cm 和 20~40 cm 土层中,主要优势菌群同为放线菌门(Actinobacteria)、变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)和绿弯菌门(Chloroflexi),但 各主要优势菌群的相对丰度在不同轮作休耕方式中存在差异.0~20 cm 土层季节性休耕(冬小麦-夏休耕和冬休耕-夏玉米)较麦玉周年轮作或连续两年休耕的土壤细菌群落更丰富且多样性程度更复杂,20~40 cm 土层则表现出冬小麦-夏休耕的土壤细菌群落更丰富、多样性程度更复杂.通过 Tax4Fun 功能预测发现,不同轮作休耕土壤细菌具有一级功能代谢通路(pathway level 1)6类,二级功能代谢通路(pathway level 1)6类,二级功能代谢通路(pathway level 1)6类,二级功能代谢通路(pathway level 2)40类(其中 18 类相对丰度大于 1.0%),三级功能代谢通路(pathway level 3) 264类;季节性休耕可提高参与新陈代谢、环境信息处理和遗传信息处理等有益细菌代谢通路的相对丰度.根据 RDA 分析,0~20 cm 土层的土壤细菌群落受土壤含水率、全磷、有效磷、速效钾、pH 和碳氮比影响显著(P<0.05),20~40 cm 受土壤全磷和有效磷影响显著(P<0.05).由此可见,不同休耕方式可以改变土壤细菌群落结构、多样性及代谢功能,季节性休耕可以促进农田土壤生态系统的健康与稳定.

关键词:轮作;休耕;土壤细菌;群落结构;功能预测

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Characteristics of Bacterial Community Structure in Fluvo-aquic Soil Under Different Rotation Fallow

NAN Zhen-wu¹, LIU Zhu¹, DAI Hong-cui¹, ZHANG Lei², WANG Na¹, XU Jie¹, LIU Kai-chang¹, MENG Wei-wei¹*, WANG Xu-qing¹*

(1. National Engineering Laboratory of Wheat and Maize, Crop Research Institute, Shandong Academy of Agricultural Sciences, Ji'nan 250100, China; 2. Yantai Academy of Agricultural Sciences, Yantai 265500, China)

Abstract: The aim of this study was to provide a reference for promoting ecological restoration of farmland and the green development of agriculture in the alluvial plain of the lower Yellow River by determining the effects of different rotation fallow patterns on the bacterial community of the fluvo-aquic soil. Farmland soil subject to a long-term rotation fallow experiment since 2018 was studied using Illumina MiSeq high-throughput sequencing technology, and the 'Tax4Fun' bacterial function prediction tool was used to analyze differences in soil bacterial community structure and function under the following four rotation fallow regimes; long fallow (LF), winter wheat and summer fallow (WF), winter fallow and summer maize (FM), and annual rotation of winter wheat and summer maize (WM). The environmental factors affecting changes in the soil bacterial community structure and function were also analyzed. In total, 44 phyla, 146 classes, 338 orders, 530 families, 965 genera, and 2073 species of bacteria were detected in the soil samples from the different rotation fallow regimes, and the dominant bacterial groups were Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi in 0-20 cm and 20-40 cm soil layers. However, the relative abundances of the dominant bacteria groups were varied between the rotation fallow regimes. In the 0-20 cm layer of the seasonal fallow soils (WF and FM), bacteria were more abundant and community diversity was higher than that of the WM and LF soils. In 20-40 cm soil layer, the WF soil was more abundant in bacterial and the community was more diverse. Based on the prediction function of the 'Tax4Fun' tool, six primary metabolic pathways, 40 secondary metabolic pathways (18 types with relative abundance greater than 1%), and 264 tertiary metabolic pathways were identified in the soil bacteria of the different rotation fallow regimes. Seasonal fallow (WF and FM) was found to increase the relative abundance of beneficial bacterial metabolic pathways involved in metabolism, environmental information processing, and genetic information processing. According to RDA analysis, the soil bacterial community in the 0-20 cm soil layer was significantly affected by soil moisture, total phosphorus, available phosphorus, available potassium, pH, and C/N ratio (P < 0.05), and the soil bacterial community in 20-40 cm soil layer was significantly affected by soil total phosphorus and available phosphorus (P < 0.05). Therefore, different fallow patterns were linked to variation in the structure, diversity, and metabolic functions of soil bacterial communities. Based on these results, seasonal fallow practices could promote the health and stability of farmland soil ecosystems. Key words: rotation; fallow; soil bacteria; community structure; function prediction

土壤属于不可再生资源,是农田生态系统的重 要组成部分,较高的地力水平是作物优质稳产的基

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作者简介: 南镇武(1991~),男,硕士,助理研究员,主要研究方向为植物营养与农业生态,E-mail;zhwsouth@163.com

^{*} 通信作者, E-mail; wdlmww@163.com; saaswxq@163.com

础. 当前密集农业为保障我国粮食安全和满足人们对粮食产量的需求做出了巨大贡献,但因耕地的长期高负荷运转,导致土壤肥力下降、耕层变浅、土壤酸化和重金属污染等问题日益严重;耕地质量下降又严重影响着国家粮食安全^[1,2]. 基于这一现状,为推进生态修复治理和耕地质量提升,促进农业可持续发展,我国于2016 年提出了探索实行耕地轮作休耕制度试点方案,推出轮作休耕制度^[3]; 2021 年中央一号文件进一步提出健全耕地休耕轮作制度,以推进农业绿色发展.

休耕是对生态环境脆弱、土壤严重污染的最好 保护,是促使农田生态自我修复、耕地质量提升,实 现"藏粮于地、藏粮于技"的重要手段[3]. 有研究发 现,休耕可以增加土壤养分和储水能力,改善土壤环 境和生物多样性,缓解农业面源污染,以恢复破碎化 的农田生态[4~6].农田生态系统的自我修复同时离 不开土壤微生物的理化效应,土壤微生物既是土壤 形成的作用者,又是衡量农田生态环境健康发展的 重要指标[7,8]. 土壤细菌生物量占土壤微生物总量 的70%~90%[9],其生理类群在土壤物质转化和能 量流动中具有特定的功能,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[10~12].有研究发现,不同土地利用方式、耕作制 度、物料还田及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[9~13]. 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[12,14].

当前关于农田土壤细菌的研究,大多集中于土地利用[11,15]、耕作方式[9,13]、秸秆还田[12,13]及肥料组合[12]等方面,而轮作休耕如何影响土壤细菌群落变化的研究鲜见,明确轮作休耕农田土壤细菌群落结构特征,是揭示轮作休耕土壤肥力变化响应土壤细菌群落结构特征,是揭示轮作休耕土壤肥力变化响应土壤细菌群落结构的必要环节.因此,本文通过研究黄河下游冲积平原潮土细菌群落结构特征及其对不同轮作休耕方式的响应差异,并结合土壤理化性状揭示其驱动因素,通过阐明不同轮作休耕方式影响农田土壤肥力的微生物学机制,以期为推进农田生态修复、耕地质量提升和农业绿色发展提供参考依据.

1 材料与方法

1.1 试验概况

本试验设置于山东省济南市济阳区山东省农业科学院综合试验示范基地(116°58′E, 36°58′N). 地处黄河下游冲积平原,平均海拔20 m; 属暖温带半湿润季风气候,四季分明,光照充足,雨热同期,年均气温12.8℃,年均无霜期195 d,年均日照时数

2 618 h,年均降水量 580 mm. 供试土壤为潮土,发育于黄河冲积母质,表土质地砂壤. 2017 年 10 月至 2018 年 6 月种植济麦 22,麦收后始设长期轮作休耕定位试验. 本试验初始耕层 0~20 cm 土壤有机质 12.1 g·kg⁻¹、全氮 0.7 g·kg⁻¹、全磷 0.8 g·kg⁻¹、全钾 19.2 g·kg⁻¹,碱解氮 50.6 mg·kg⁻¹、有效磷 20.5 mg·kg⁻¹和速效钾 151.9 mg·kg⁻¹,pH 为 8.0. 耕作期冬小麦品种为济麦 22,夏玉米品种为登海 605,播前基施氮磷钾复合肥(15-15-15)750 kg·hm⁻²,冬小麦拔节期、夏玉米大口期追施尿素 225 kg·hm⁻²,其他管理措施同传统耕作,秸秆还田;休耕期无管理措施.

2020年6月麦收后,选取长期休耕(LF,已连续休耕2a)、冬小麦-夏休耕(WF,季节性休耕)、冬休耕-夏玉米(FM,季节性休耕)、冬小麦-夏玉米周年轮作(WM)这4个处理的0~40cm土层分析土壤细菌群落结构特征,每个处理3次重复,计12个小区.2020年5月16日至6月15日自建气象站记录的日均温度(地表距离)与降水量见图1,期间无灌溉.

1.2 样品采集

2020 年 6 月 15 日麦收后,小区"S"形 5 点采集 0~20 cm 和 20~40 cm 土层土壤样品. 同小区同土层样品混合,部分样品直接装入铝盒测定土壤水分,剩余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 0.25 mm 和 1 mm 筛测定土壤理化性状.

1.3 测定方法

土壤理化性状参考文献[16]测定,土壤全氮(TN)采用凯氏定氮法,土壤全磷(TP)采用氢氧化钠碱熔-钼锑抗分光光度法,土壤全钾(TK)采用原子吸收火焰光度法,土壤碱解氮(AN)采用碱解扩散法,土壤有效磷(AP)采用碳酸氢钠-钼锑抗分光光度法,土壤速效钾(AK)采用醋酸铵-原子吸收火焰分光光度法;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).

土壤细菌 DNA 参照土壤 DNA 提取试剂盒 (OMEGA, USA) 说明书进行提取,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 rDNA 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

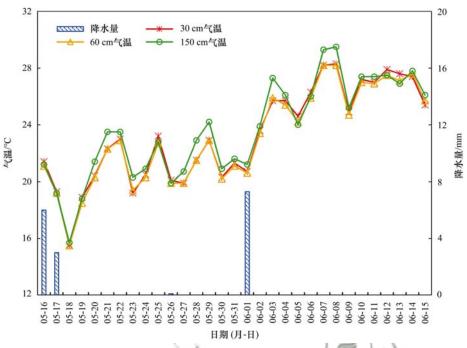


图 1 采样前 31 d 的日均气温与降水量

Fig. 1 Daily average temperature and precipitation of 31 days before sampling

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.

1.4 数据处理

利用美吉生物云平台,经过 QIIME(v1.9.1)软件过滤、拼接、去除嵌合体后,聚类为用于运算分类的 OTU(operational taxonomic units),并按照最小样本序列数进行抽平^[17].采用 RDP classifier 贝叶斯算法对 97% 相似水平的 OTU 代表序列进行分类学分析^[11],置信度阈值为 0.7,比对 Silva (Release132http://www.arb-silva.de)数据库.利用

Mothur 软件(Version 1.31,2)进行 α 多样性(Sobs、ACE、Chaol 和 Coverage)分析^[18]. 基于 Bray-curtis 距离,应用 R 软件制图,采用主坐标分析(PCoA)计算 β 多样性距离矩阵^[11]. 通过 Tax4Fun 将基于 Silva数据库的 16S 分类谱系转化为京都基因和基因组百科全书(kyoto encyclopedia of genes and genomes,KEGG,http://www.genome.jp/kegg/)数据库中原核生物的分类谱系,对 16S RNA 基因序列进行KEGG 功能注释^[18]. 土壤因子与细菌种群分布特征之间的关系利用 R 语言画图进行冗余分析(RDA),研究土壤理化性质对细菌种群分布的影响^[15].

利用 Excel 2019 整理数据,运用 SPSS 26.0 进行单因素方差分析(One-Way ANOVA)和最小显著差异法(LSD)多重比较.

2 结果与分析

2.1 不同轮作休耕农田土壤细菌测序分析

利用 Illumina MiSeq 平台测序结果显示, 24 个土壤样本共获得有效序列1 200 939条,经过优化筛选,基于 97% 的相似性, 24 个样本共获得7 760 OTUs,划分为 44 门、146 纲、338 目、530 科、965 属和2 073种(表1). 20~40 cm土层土壤细菌各分

表 1 土壤全部样本序列信息与细菌分类

Table 1 Sequence information and bacterial classification of all soil samples

土层/cm	序列数/条 -			分类	水平			OTUs
上/云/cm	厅列奴/宋 -	门	纲	I	科	属	种	OTUS
0 ~ 20	611 597	42	135	321	505	921	1 972	7 061
20 ~40	589 342	44	145	332	517	934	1 992	7 237
$0 \sim 40$	1 200 939	44	146	338	530	965	2 073	7 760

加. FM 则减少.

2.2 不同轮作休耕农田土壤细菌群落多样性

将所有数据抽平1次,每个样本得到28993条

高质量序列,各个样本的覆盖度指数显示 0~20 cm

及 20~40 cm 土层土壤 OTUs 涵盖了土壤中 95% 以

上的细菌,说明测序深度可以比较真实地反映土壤

样本的细菌群落,代表细菌群落丰富度与 α 多样性

(表2). 0~20 cm 土层中, WF 的物种丰富度、ACE

指数、Chao 1 指数和香农指数最高, FM 的物种丰

富度和 ACE 指数与 WF 无明显差异, WF 的香农指

数显著高于其他处理(P<0.05). 20~40 cm 土层

中,WF的物种丰富度和ACE指数、Chao 1指数均

显著高于其他处理,LF 则均显著低于其他处理(P

<0.05); WF 的香农指数最高.

类水平的数目均多于 $0 \sim 20$ cm, 但序列数少于 $0 \sim 20$ cm.

不同轮作休耕农田中, 0~20 cm 和 20~40 cm 土壤细菌 OTUs 水平相似性分析产生差异(图 2). 0~20 cm 土层中[图 2(a)], LF、FM、WF 和 WM 的 OTUs 数目分别为4 686、5 106、5 232 和4 724, 特有 OTUs 为 260、392、486 和 300, 共有 OTUs 为2 941. 20~40 cm 土层[图 2(b)]4 个处理的 OTUs 数目依 次为: WF > FM > WM > LF, 与 0~20 cm 土层次序相同;但特有 OTUs 发生变化, LF、FM、WF 和 WM 分别为 361、297、506 和 404; 共有 OTUs 为2 739. 与 0~20 cm 土层相比, 20~40 cm 土层共有 OTUs 数目减少, LF 和 FM 也减少, WF 和 WM 则增加;特有 OTUs 方面, 20~40 cm 土层的 LF、WF 和 WM 增

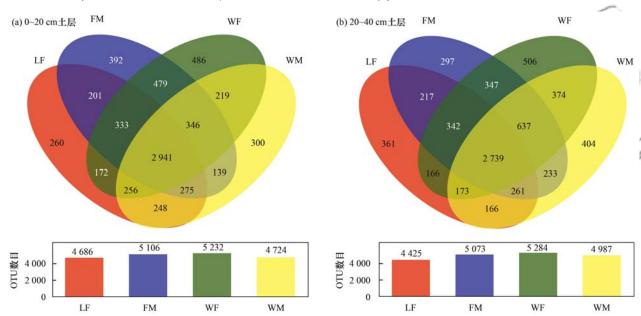


图 2 土壤细菌群落 OTU 水平的 Venn 图

Fig. 2 Venn on OTU level of soil bacterial community

表 2 土壤细菌 α 多样性 $^{1)}$

Table 2 Soil bacterial α-diversity

土层/cm	处理	物种丰富度	ACE 指数	Chao1 指数	香农指数	覆盖度/%
	LF	3 323.3 ± 60.5b	4 663.9 ± 109.7b	4 649.0 ± 78.8a	6.97 ±0.05b	95.92 ± 0.10a
0 ~ 20	FM	$3557.3 \pm 127.6a$	4 993.4 ± 165.1a	4 909. 3 ± 332. 8a	$6.96 \pm 0.08 \mathrm{b}$	$95.59 \pm 0.17b$
0 120	WF	$3691.7 \pm 24.0a$	$5174.5\pm36.3a$	5 116.8 ± 9.2a	$7.17 \pm 0.03a$	$95.46 \pm 0.04b$
	WM	$3300.7\pm70.8\mathrm{b}$	$4634.9\pm110.6\mathrm{b}$	4 782.0 ± 291.1a	$6.91 \pm 0.07 \mathrm{b}$	$95.92 \pm 0.11a$
	LF	$3\ 102.\ 3\pm71.\ 8\mathrm{c}$	$4\ 245.\ 8\ \pm 127.\ 3\mathrm{c}$	$4201.8\pm139.4\mathrm{c}$	$6.82 \pm 0.06\mathrm{c}$	$96.32 \pm 0.15a$
20 ~ 40	FM	$3514.3\pm83.5\mathrm{b}$	$4850.3\pm16.4\mathrm{b}$	$4845.5\pm31.0\mathrm{b}$	$7.07\pm0.09\mathrm{ab}$	$95.75 \pm 0.03b$
20 11 40	WF	$3692.7 \pm 97.2a$	$5\ 164.5 \pm 127.9a$	$5135.0\pm114.8a$	$7.14 \pm 0.06a$	$95.44 \pm 0.10c$
	WM	$3488.7\pm89.6\mathrm{b}$	$4935.6\pm168.3\mathrm{b}$	$4929.9\pm198.3\mathrm{b}$	$7.01 \pm 0.05 \mathrm{b}$	$95.64 \pm 0.17 bc$

¹⁾ 同土层同列不同小写字母表示处理间差异显著(P<0.05)

2.3 不同轮作休耕农田土壤细菌群落物种组成

不同轮作休耕方式下, $0 \sim 20$ cm 和 $20 \sim 40$ cm 土壤细菌群落门水平相对丰度不同(图 3). $0 \sim 20$ cm 土层中[图 3(a)], 放线菌门(Actinobacteria)、

变 形 菌 门 (Proteobacteria)、酸 杆 菌 门 (Acidobacteria)和绿弯菌门(Chloroflexi)是土壤细菌的主要优势菌群,在12个样本中平均相对丰度分别为26.08%、19.90%、17.12%和13.03%,约占

76. 13%; 未被分类细菌约占 1. 16%, 另有 7 类菌门相对丰度大于 1. 0%, 相对丰度小于 1. 0% 的细菌门约占 3. 87%. 在主要优势菌群中, 放线菌门(Actinobacteria)在FM中最丰富(31. 27%), 但在WF中最少(23. 34%); 相反, 绿弯菌门(Chloroflexi)在WF中最丰富(13. 92%), 但在FM中最少(11. 66%); 第二丰富的变形菌门(Proteobacteria), 在WF和FM中相对丰度较高(22. 15%和21. 08%); 而酸杆菌门(Acidobacteria)在LF中最丰富(22. 08%), 且相对丰度高于变形菌门(Proteobacteria, 17. 26%), 在FM中相对丰度最低(12. 93%).

20~40 cm 土层中[图 3(b)],土壤细菌的主要

优势菌群与 0~20 cm 土层相同,在 12 个样本中平均相对丰度分别为 22.34%、21.00%、15.93%和12.37%,约占 71.64%;未被分类细菌约占 1.67%,另有 10 类菌门相对丰度大于 1.0%,相对丰度小于1.0%的细菌门约占 5.01%.与 0~20 cm 土层不同,LF 和 WM 中最丰富的仍为放线菌门(Actinobacteria, 21.23%和 24.64%),而 FM 和 WF中则为变形菌门(Proteobacteria, 23.67%和27.11%);酸杆菌门(Acidobacteria)和绿弯菌门(Chloroflexi)在LF中最丰富(20.33%和13.84%),且高于变形菌门(Proteobacteria, 12.90%);酸杆菌门(Acidobacteria)和绿弯菌门(Chloroflexi)相对丰度分别在WF和FM中最低(13.05%和10.85%).

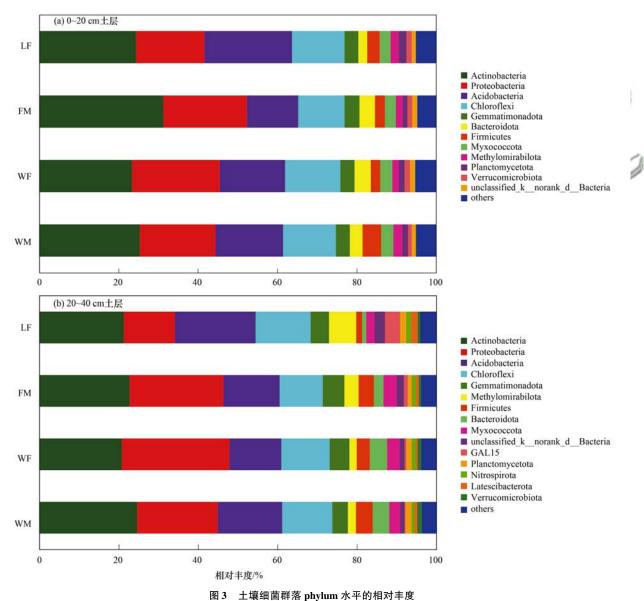
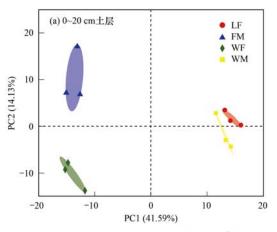


Fig. 3 Community abundance at the phylum level of soil bacterial communities

2.4 不同轮作休耕农田土壤细菌群落组成差异 不同轮作休耕方式下,0~20 cm 和 20~40 cm 土壤细菌群落 OTU 水平基于 Bray Curtis 距离 的 PCoA 分析产生差异(图 4).0~20 cm 土层中 [图 4(a)],以主成分 PC1 和 PC2 为坐标轴构建 二维坐标系的 PCoA 分析, PC1 和 PC2 可分别解

释 41.59% 和 14.13% 群落组成差异,合计达55.72%. LF 位于 PC1、PC2 正值区域; FM 位于 PC1 负值区域和 PC2 正值区域; WF 与 FM 在 PC1 负值区域距离较近,但位于 PC2 负值区域; WM 位于 PC1 正值区域和 PC2 正负值区域两侧,与 LF 距离较近.

20~40 cm 土层中[图 4(b)], PCoA 分析显示



主成分 PC1 和 PC2 分别可以解释 52.11% 和 14.72% 群落组成差异,合计达 66.83%. LF 位于 PC1 正值区域和 PC2 正负值两侧; FM 位于 PC1、PC2 正负值两侧; WF 位于 PC1 正值区域和 PC2 负值区域; WM 位于 PC1、PC2 负值区域.与 0~20 cm 土层相比, LF 和 WM 在 PC1、PC2 上均发生负移, FM 和 WF 均在 PC1 负移、PC2 正移.

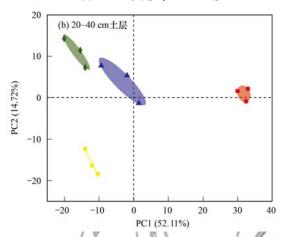


图 4 土壤细菌群落 OTU 水平的主成分分析

Fig. 4 PCoA on OTU level of soil bacterial communities

2.5 不同轮作休耕农田土壤细菌群落功能预测

基于 Silva 数据库的 16S 分类谱系转化为 KEGG 数据库中原核生物的分类谱系,通过 Tax4Fun 对不同轮作休耕 0~40 cm 土壤 16S 的 OTUs 信息进行功能预测. 结果获得一级功能代谢通路(pathway level 1)6 类(表 3); 二级功能代谢通路(pathway level 2)40 类,其中相对丰度大于 1.0% 的二级功能代谢通路包含 18 类(表 4); 三级功能代谢通路(pathway level 3)264 类.

从表 3 可知,在 0 ~ 20 cm 和 20 ~ 40 cm 土壤中,6 类一级功能代谢通路相对丰度均依次为:新陈代谢(metabolism) > 环境信息处理(environmental information processing) > 遗传信息处理(genetic

information processing) > 细胞过程(cellular processes) > 人类疾病(human diseases) > 有机系统 (organismal systems). FM 的新陈代谢功能相对丰度显著高于 WF(P<0.05),但二者与 FM、WM 均差异不显著; LF 的环境信息处理功能相对丰度显著最丰富,WF 则显著最低(P<0.05); WF 的遗传信息处理、人类疾病和有机体系统功能均显著最高,LF 则均显著最低(P<0.05);细胞过程功能则差异不显著. 20~40 cm 土层中,环境信息处理和细胞过程功能差异显著性与0~20 cm 土层相似; FM 和 WF 的新陈代谢功能显著高于 LF 和 WM,WF 和 WM 的遗传信息处理和有机体系统功能显著高于 FM 和 LF(P<0.05);人类疾病中 LF < FM < WF < WM.

表3 土壤细菌群落一级功能代谢通路的相对丰度1)/%

Table 3 Relative abundances of level 1 functional metabolic pathways in soil bacterial communities based on Tax4Fun/%
土层/cm 处理 新陈代谢 环境信息处理 遗传信息处理 细胞过程 人类疾病 有机系统
LF 61. 27 ± 0. 05 ab 20. 09 ± 0. 06a 10. 80 ± 0. 02d 4. 86 ± 0. 05a 2. 02 ± 0. 01d 0. 84 ± 0. 01

	LF	61. 27 \pm 0. 05 ab	20. 09 \pm 0. 06a	10. 80 \pm 0. 02 d	4. $86 \pm 0.05a$	$2.\;02\;\pm0.\;01{\rm d}$	$0.84\pm0.01\mathrm{c}$
0 ~ 20	FM	61. 37 \pm 0. 10a	19. 67 \pm 0. 09b	10. 97 \pm 0. 07 c	4. 87 \pm 0. 04a	$2.12 \pm 0.05 c$	$0.89 \pm 0.02b$
	WF	61. 04 \pm 0. 10c	19. 19 $\pm 0.05 \mathrm{c}$	11. $40 \pm 0.01a$	$4.97 \pm 0.03a$	$2.33 \pm 0.02a$	$0.95 \pm 0.01a$
	WM	61. 12 $\pm 0.09 {\rm bc}$	19. 71 ± 0.06 b	11. 14 \pm 0. 03b	$4.84 \pm 0.13a$	2. 18 ± 0.02 b	$0.88 \pm 0.02b$
	全部样本	61. 2 ± 0. 04a	19. 66 ± 0. 04b	11. 08 ± 0. 03 c	4. 89 ± 0. 04d	2. 16 ± 0. 01e	0.89 ± 0.01f
	LF	60. 93 ±0. 15b	20. 59 ± 0. 20a	$10.63 \pm 0.09 c$	$4.96 \pm 0.02a$	$1.98 \pm 0.03 \mathrm{d}$	0.81 ± 0.01 c
20 ~ 40	FM	61. 22 \pm 0. 07 a	19. 85 \pm 0. 14b	10. 95 \pm 0. 02b	$4.92 \pm 0.06a$	$2.\ 10 \pm 0.\ 02c$	$0.84 \pm 0.02b$
	WF	61. 36 \pm 0. 07a	19. 11 $\pm 0.07 \mathrm{c}$	11. 29 \pm 0. 05 a	$4.98 \pm 0.03a$	$2.24 \pm 0.01 \mathrm{b}$	$0.91 \pm 0.01a$
	WM	60. 85 \pm 0. 04b	19. 68 ± 0.06 b	11. $19 \pm 0.07a$	$4.93 \pm 0.02a$	$2.32 \pm 0.02a$	$0.91 \pm 0.01a$
	全部样本	61. 09 ± 0. 03a	19. 81 ± 0. 06b	11. 01 ± 0. 03 c	4. 95 ±0. 01d	2. 16 ± 0. 01e	0. 87 ± 0. 00f

¹⁾相同土层同列不同小写字母表示处理间差异显著(P<0.05),全部样本同行不同小写字母表示一级功能代谢通路间差异显著(P<0.05)

从表 4 可知,在 0~20 cm 和 20~40 cm 土壤中,相对丰度大于 1.0% 的 18 类二级功能代谢通路总丰度分别为 96.36% ~ 96.63% 和 96.43% ~ 96.69%,其中相对丰度大于 5.0% 的均包含碳水化合物代谢(carbohydrate metabolism)、氨基酸代谢(amino acid metabolism)、膜转运(membrane transport)、信号转导(signal transduction)、辅助因子和维生素的代谢(metabolism of cofactors and vitamins)、能量代谢(energy metabolism)和核苷酸代谢(nucleotide metabolism)这 7 类.相对丰度大于 1.0%的二级功能代谢通路中,LF 与 FM、WF 和 WM 在 0~20 cm 和 20~40 cm 土层分别有 10~11、

9 和 12、13、15 类通路存在显著差异(P < 0.05),FM 与 WF 和 WM 在两土层分别有 9、11 和 11、13 类通路存在显著差异(P < 0.05),WF 与 WM 在两土层则均有 10 类通路存在显著差异(P < 0.05)。0 ~ 20 cm 土层的聚糖生物合成与代谢(glycan biosynthesis and metabolism)、转化(translation)、复制和修复(replication and repair)和细菌性传染病(infectious disease: bacterial)这 4 类二级功能代谢通路在 4 个处理间差异分别显著(P < 0.05),20 ~ 40 cm 土层的能量代谢、膜转运、细菌性传染病 3 类二级功能代谢通路在 4 个处理间差异分别显著(P < 0.05)。

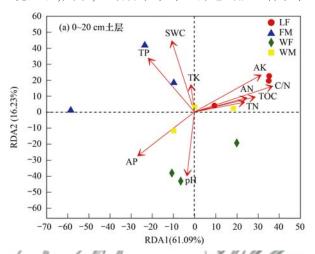
表 4 土壤细菌群落中相对丰度大于1%的二级功能代谢通路1)/%

Table 4 Level 2 functional metabolic nathways with relative abundances of more than 1% in soil bacterial communities based on Tay4Fun

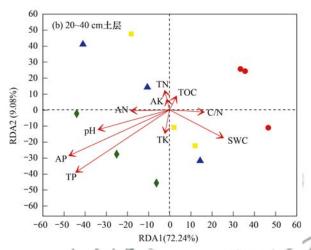
土层/cm	初级功能	次级功能	LF	FM	WF	WM	全部样本
		碳水化合物代谢	12. 97 ± 0. 03a	12. 93 ±0. 03a	12. 93 ± 0. 03a	13. 02 ± 0. 10a	12. 96 ± 0. 06a
		氨基酸代谢	12. 42 ± 0.03 b	12. $59 \pm 0.04a$	12. $43 \pm 0.02b$	12. 33 \pm 0. 01 c	12. 44 ± 0.10
		辅酶和维生素代谢	6.980 ± 0.021 b	$7.075 \pm 0.017a$	7. $068 \pm 0.010a$	6. 987 ± 0.015 b	$7.03 \pm 0.05e$
		能量代谢	$7.068 \pm 0.047a$	7. 057 \pm 0. 030a	$6.980 \pm 0.019a$	6. 951 ± 0. 104a	$7.01 \pm 0.07e$
	新陈代谢	核苷酸代谢	5. $177 \pm 0.015a$	5. 187 ±0. 012a	5. 189 ± 0. 016a	5. $198 \pm 0.033a$	5.19 ± 0.026
	型的化位组	外源生物降解与代谢	$4.481 \pm 0.015a$	$4.434 \pm 0.039a$	$4.\ 260 \pm 0.\ 012c$	4. 326 ± 0.041 b	4.38 ± 0.091
		脂质代谢	3.642 ± 0.008 b	3.633 ± 0.010 b	3.649 ± 0.006 ab	$3.672 \pm 0.022a$	3.65 ± 0.02 j
a 4	101	其他氨基酸代谢	2.725 ± 0.006 b	2. 766 ± 0.007 a	$2.744 \pm 0.002ab$	$2.70 \pm 0.0190c$	2.73 ± 0.03
	(1)	萜类和聚酮类化合物代谢	$2.747 \pm 0.025a$	2.572 ± 0.055 b	2.500 ± 0.039 b	2. 763 ± 0. 113a	2.65 ± 0.13
0~20	0~20	聚糖生物合成与代谢	$2.232 \pm 0.014d$	$2.270 \pm 0.031e$	$2.418 \pm 0.012a$	2. 338 ± 0.006 b	2.31 ± 0.08
) (环境信息处理	膜转运	12. 58 ± 0. 14a	12. 13 ±0. 17b	11. 50 ± 0. 02c	12. 06 ± 0. 17b	12. 07 ± 0. 42
- }	小児信息处理	信号转导	7.510 ± 0.082 b	7. 533 ± 0.096 ab	7. $685 \pm 0.051a$	7. 646 ± 0 . $124ab$	7.59 ± 0.11
R	110	转化	4. 377 ± 0. 006d	4. 455 ±0. 027 c	$4.630 \pm 0.002a$	4. 507 ± 0. 009b	4. 49 ± 0. 10
209 11	遗传信息处理	复制和修复	$4.021 \pm 0.013 d$	4. 095 ± 0. 033 c	4. $296 \pm 0.004a$	4. 173 \pm 0. 007b	4. 15 ± 0. 11
(0)	PTU	折叠、分类和降解	2.220 ± 0.006 b	2.233 ± 0.009 b	2. $279 \pm 0.008a$	2. $267 \pm 0.017a$	2. 25 ± 0. 03
1	细胞过程	细胞运动	2. 292 ± 0. 018b	2. 291 ± 0. 020b	2. 357 ± 0. 010a	2. 316 ± 0. 047ab	2. 31 ± 0. 04
11	细胞过生	细胞生长与死亡	1. 871 ± 0. 020a	1. $851 \pm 0.010a$	1. $859 \pm 0.007a$	1. $829 \pm 0.049a$	1.85 ± 0.03
	人类疾病	细菌性传染病	$1.321 \pm 0.016d$	1. 387 ±0. 040c	1. 578 ± 0. 017a	1. 474 ± 0.016 b	1. 44 ± 0. 10
		碳水化合物代谢	12. 82 ± 0. 02b	12. 97 ±0. 03a	13. 01 ± 0. 03a	13. 00 ± 0. 01a	12. 95 ± 0. 08
		氨基酸代谢	12. 36 ± 0.09 ab	12. 39 \pm 0. 03a	12. $45 \pm 0.04a$	12. 26 \pm 0. 01 b	12. 37 ± 0. 08
		辅酶和维生素代谢	6.967 ± 0.030 b	7. 001 \pm 0. 036b	$7.065 \pm 0.018a$	6. 975 \pm 0. 005b	7.00 ± 0.05
		能量代谢	$7.276 \pm 0.024a$	7. 131 ± 0.034 b	$7.053 \pm 0.019 c$	6. 911 \pm 0. 024d	7. 09 ± 0. 14
	实防 (4)钟	核苷酸代谢	5.135 ± 0.018 b	5. 177 ± 0.015 a	5. $186 \pm 0.002a$	5. 177 \pm 0. 016a	5. 17 ± 0. 02
	新陈代谢	外源生物降解与代谢	$4.439 \pm 0.049a$	$4.413 \pm 0.033a$	$4.380 \pm 0.029a$	4. 245 ± 0.041 b	4.37 ± 0.08
		脂质代谢	$3.602 \pm 0.007 c$	3.635 ± 0.008 b	$3.663 \pm 0.006a$	3. $668 \pm 0.004a$	3.64 ± 0.03
		其他氨基酸代谢	2.701 ± 0.019 b	$2.\ 721 \pm 0.\ 020\mathrm{b}$	$2.753 \pm 0.012a$	2. 707 ± 0.007 b	2. 72 ± 0. 02
20 40		萜类和聚酮类化合物代谢	2.606 ± 0.021 b	$2.670 \pm 0.050a$	2. 588 ± 0.019 b	2. $674 \pm 0.026a$	2.63 ± 0.05
20 ~ 40		聚糖生物合成与代谢	$2.222 \pm 0.031c$	2.273 ± 0.008 b	2. $352 \pm 0.018a$	2. $390 \pm 0.021a$	2. 31 ± 0. 07
	遗传信息处理	膜转运	13. 08 ± 0. 22a	12. 33 ±0. 21b	$11.49 \pm 0.10d$	11. $89 \pm 0.10c$	12. 19 ± 0. 63
	週刊信息处理	信号转导	7.514 ± 0.085 b	7. 521 ± 0.083 b	7. 621 \pm 0. 048b	7. $794 \pm 0.061a$	7. 61 ± 0. 13
		转化	$4.295 \pm 0.035c$	4.426 ± 0.007 b	4. 570 ± 0. 020a	4. $523 \pm 0.028a$	4. 45 ± 0. 11
	环境信息处理	复制和修复	$3.970 \pm 0.038c$	4. 100 ± 0.012 b	4. $246 \pm 0.020a$	4. $211 \pm 0.030a$	4. 13 ± 0. 12
		折叠、分类和降解	$2.181 \pm 0.019c$	2.239 ± 0.004 b	$2.277 \pm 0.006a$	2. $266 \pm 0.013a$	2. 24 ± 0. 04
	细胞量和	细胞运动	2. 314 ± 0. 011b	2. 308 ± 0. 025b	2. 344 ± 0. 019ab	2. 374 ± 0. 012a	2. 33 ±0. 03
	7田田111年	细胞生长与死亡	1. 929 ± 0. 004a	$1.900 \pm 0.017 \mathrm{b}$	1.901 ± 0.006 b	1. 825 ± 0.009 c	1.89 ± 0.04
	人类疾病	细菌性传染病	1. 283 ± 0. 029d	1. 386 ± 0. 024c	1. 484 ± 0. 012b	1. 597 ±0. 018a	1. 44 ± 0. 12

¹⁾相同土层同行不同小写字母表示处理间差异显著(P<0.05),全部样本同列不同小写字母表示二级功能代谢通路间差异显著(P<0.05)

2.6 不同轮作休耕农田土壤细菌群落环境因子分析 不同轮作休耕方式下,0~20 cm 和 20~40 cm 土壤细菌群落结构与土壤理化性质的冗余分析产生 差异(图 5).0~20 cm 土层中[图 5(a)],RDA1 和 RDA2 积累解释变异量可达 77.32%(RDA1: 61.09%; RDA2: 16.23%),能够反映土壤环境因子对土壤细菌群落结构的影响. 置换检验结果显示,土壤含水率(SWC, $r^2=0.852$,P=0.002)、全磷(TP, $r^2=0.666$,P=0.008)、有效磷(AP, $r^2=0.489$,P=0.048)、速效钾(AK, $r^2=0.504$,P=0.038)、pH($r^2=0.614$,P=0.011)、碳氮比(C/N, $r^2=0.539$,P=0.033)为主要影响细菌群落变化的环境因子,其中,土壤含水率与全磷达到极显著水平



(P < 0.01). 20~40 cm 土层中[图 5(b)], RDA1和 RDA2积累解释变异量可达81.32%(RDA1:72.24%; RDA2:9.08%). 置换检验结果显示,全磷(TP, $r^2 = 0.629$, P = 0.014)、有效磷(AP, $r^2 = 0.552$, P = 0.039)为主要影响细菌群落变化的环境因子.有机碳(TOC)、全氮(TN)、碱解氮(AN)、速效钾(TK)对0~40 cm 土层的土壤细菌群落结构影响不显著(P > 0.05),全磷和有效磷则影响显著(P < 0.05).



SWC表示土壤含水率,TOC表示有机碳,TN表示全氮,TP表示全磷,TK表示全钾,AN表示碱解氮,

AP表示有效磷, AK表示速效磷, C/N表示碳氮比

图 5 土壤细菌群落与环境因子间的冗余分析

Fig. 5 Redundancy analysis (RDA) of soil bacterial communities and environmental factors

3 讨论

3.1 不同轮作休耕对农田土壤细菌群落多样性的 影响

不同轮作休耕方式导致黄河下游冲积平原的农 田覆被和土壤理化性状发生变化,进而对土壤微生 物多样性和丰富度产生影响. 0~20 cm 冬小麦-夏 休耕、冬休耕-夏玉米较麦玉周年轮作或连续 2 a 休 耕的土壤细菌群落更丰富且多样性程度更复杂,20 ~40 cm 冬小麦-夏休耕则表现出土壤细菌群落更 丰富、多样性程度更复杂. 这说明季节性休耕较麦 玉周年轮作可以促进土壤细菌的多样性. 可能是因 为季节性休耕较麦玉周年轮作减少了对农田土壤的 翻动,减少了土壤与空气的接触,减缓了土壤有机质 的氧化、矿化,有效提高土壤肥力,利于维持土壤细 菌群落结构的稳定[19~21];也可能因为季节性休耕 较麦玉轮作减少了化肥和农药的使用而更有利于微 生物的生长繁殖,增加细菌种群的多样性[22]. 另外, 传统的麦玉周年轮作频繁翻动土壤,导致土壤结构 恶化,使细菌群落的多样性和丰富度降低[9,21]. 本研 究中连续2 a 休耕土壤细菌群落的丰富度低于季节 性休耕. 这可能因为季节性休耕中小麦或玉米秸秆的还田,在增加有机质输入和改善土壤理化性状的同时^[21,23],利于维持或提高土壤微生物的多样性及活性. 左梅等^[24]在鄂西南山区的研究发现,休耕措施虽然利于提高土壤细菌群落的丰富度,但随着休耕年限的增加,土壤 Chaol 指数和 Shannon 指数呈增加趋势,Simpson 指数呈降低趋势. 这与本研究结果存在差异,可能与取样时间和环境因素有关;此外,本试验未考虑休耕年限方面的问题. 因此,休耕年限对土壤微生物多样性的影响,有待随时间的推移进一步研究.

3.2 不同轮作休耕对农田土壤细菌群落结构的影响不同轮作休耕方式在改变农田土壤细菌群落丰富度和多样性的同时,也促进了土壤细菌群落结构发生变化.本研究发现,4种方式下0~20 cm 和20~40 cm 土层土壤的放线菌门(Actinobacteria)、变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)和绿弯菌门(Chloroflexi)等细菌主要优势菌群没有发生变化,但其丰度在两个土层中产生显著差异.这可能是由于小尺度环境下土壤微生物群落组成较为相近[25];又因不同轮作休耕方式使土壤理化性质

产生变化,导致细菌群落丰度产生差异.此外,地上 植物分类及功能属性也有助于解释微生物多样性和 群落分布的差异[26,27]. 不同植被下土壤细菌群物种 组成和多样性相对稳定,但不同植被条件会造成土 壤中细菌种群在丰度和个别物种上的差异,表现出 各自独特的物种特征[28]. 不同轮作休耕中, 20~40 cm 土层相对丰度大于 1.0% 的细菌门类均多于 0~ 20 cm 土层,这可能也是由于深层土壤较表层受人 为扰动较少而造成的,也可能是因为植物根系垂直 分布及分泌物不同造成的^[20,29]. Youssef 等^[30]的研 究通过排序分析细菌不同的门,发现生境的差异使 细菌群落表现出较大的生态系统多样性. 通过 PCoA 分析发现, 10~20 cm 土层中连续 2 a 休耕和麦玉 周年轮作的簇距离较近,说明这2个处理间细菌群 落结构相似; 而 20~40 cm 土层中这 2 个处理簇相 对分离,说明土壤细菌群落结构存在差异.有研究发 现,不同生境样本的簇分布相对离散,说明不同生境 中细菌群落结构特征存在差异[30,31].

3.3 不同轮作休耕对农田土壤细菌群落功能的影响 细菌群落是土壤有机质分解与矿化的重要参与 者,在驱动土壤养分循环的同时,指示并调节土壤生 态功能[18]. 本研究发现,不同轮作休耕方式使黄河 下游冲积平原农田土壤细菌群落结构发生改变的同 时,也使土壤细菌功能代谢通路发生了相应地变化. 土壤细菌功能代谢通路丰度的波动,也反映了不同 轮作休耕方式土壤细菌群落组成及多样性的变 化[31].农田土壤细菌利用新陈代谢、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类功能代谢通路维系生态系统的稳定.其中, 新陈代谢通路在不同轮作休耕方式中相对丰度均最 大,环境信息处理和遗传信息处理仅次于新陈代谢. 这表明新陈代谢、环境信息处理和遗传信息处理是 土壤细菌的核心功能,受人为影响较小[11,29]. Tax4Fun 功能预测表明,参与代谢最多的细菌类群 与氨基酸、碳水化合物和能量代谢有关:负责环境 信息处理最多的细菌是参与膜运输的菌群,其次是 参与信号转导的菌群; 而在参与遗传信息处理的细 菌中,参与遗传信息转化及复制和修复的细菌群具 有明显的优势. 这与 Xia 等^[29]在黄土高原东南干旱 区关于小麦休耕期不同耕作方式土壤细菌群落功能 预测的研究结果基本一致. 氨基酸代谢主要通过脱 氨作用、转氨作用、联合脱氨或脱羧作用分解成 α-酮酸、胺类及 CO,,是碳代谢和氮代谢的中枢;碳水 化合物合成与代谢则与氮、磷循环呈正相关,间接 说明土壤细菌丰富度越高越有利于氮、磷的转化和 迁移[11,32]. 本研究中休耕与季节性休耕土壤细菌群

氨基酸代谢通路相对丰度均高于麦玉周年轮作;小麦收获后,连续2 a 休耕与冬休耕-夏玉米细菌性传染病二级功能代谢通路则显著低于麦玉周年轮作及冬小麦-夏休耕,这与一级功能代谢通路人类疾病相对丰度的差异性相同;细菌性传染病代谢通路源于致病细菌基因.

3.4 不同轮作休耕农田土壤细菌群落对环境因子的响应

环境因子对土壤微生物具有抑制、促进或无明 显作用,是土壤微生物群落组成的重要影响因 素[33]. 利用 RDA 分析农田土壤细菌信息,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特 征的影响. RDA 分析表明,显著影响 0~20 cm 土层 土壤细菌群落结构的主要环境因子是土壤含水率、 全磷、有效磷、速效钾、pH 和碳氮比, 20~40 cm 土层则是全磷和有效磷.可见,全磷和有效磷对不同 轮作休耕2个土层的土壤细菌群落结构均有显著影 响.有研究发现,富营养条件下,磷素能够削减原有 微生物群落的限制作用,使微生物的代谢活动发生 变化,进而可能会改变微生物的种类组成[34.35]. 另 外,吴宪等[12]的研究发现,潮土细菌群落结构受到 土壤磷的调控,全磷对细菌群落 α 多样性的作用显 著. 这与本研究结果类似,可能是因为细菌生长需要 磷,有效磷对细菌具有促进作用.但在黄土高原半干 旱区的研究发现,土壤全氮、全钾和速效氮含量是 影响9种轮作休耕方式土壤细菌群落结构的主要环 境因子[36]. 这与本试验存在差异,可能是地域环境、 作物种类及取样时间不同造成的.目前,关于环境因 子对土壤细菌群落的影响,不同地域或不同学者得 出的结论不同[21,33~36];另外,土壤细菌群落受水热 条件的影响较大,而水和热又不能隔离.因此,不同 轮作休耕农田土壤细菌群落结构特征对环境因子的 响应有待深入研究.

4 结论

不同轮作休耕方式 20~40 cm 土层中,土壤细菌在门、纲、目、科、属、种及 OTU 水平上菌群数量均多于 0~20 cm 土层,但 0~20 cm 土壤细菌在不同分类水平上均存在 20~40 cm 土层没有的特有类群;冬小麦收获后,0~20 cm 土层季节性休耕(冬小麦-夏休耕和冬休耕-夏玉米)的土壤细菌群落更丰富、多样性程度更复杂,20~40 cm 土层则是冬小麦-夏休耕;2个土层中,主要优势菌群同为放线菌门(Actinobacteria)、变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)和绿弯菌门(Chloroflexi).通过 Tax4Fun 功能预测发现,不同轮作休耕土壤细

菌具有一级功能代谢通路 6 类,二级功能代谢通路 40 类,三级功能代谢通路 264 类;季节性休耕可以提高参与新陈代谢、环境信息处理和遗传信息处理等有益细菌的代谢功能.根据 RDA 分析,0~20 cm 土层的土壤细菌群落受土壤含水率、全磷、有效磷、速效钾、pH 和碳氮比影响显著,20~40 cm 受土壤全磷和有效磷影响显著。由此可见,在黄河下游冲积平原农田中,不同轮作休耕方式和土壤深度均可使土壤细菌群落多样性、丰富度及代谢功能产生差异;合理的季节性休耕可以促进农田土壤生态系统的健康与稳定.

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