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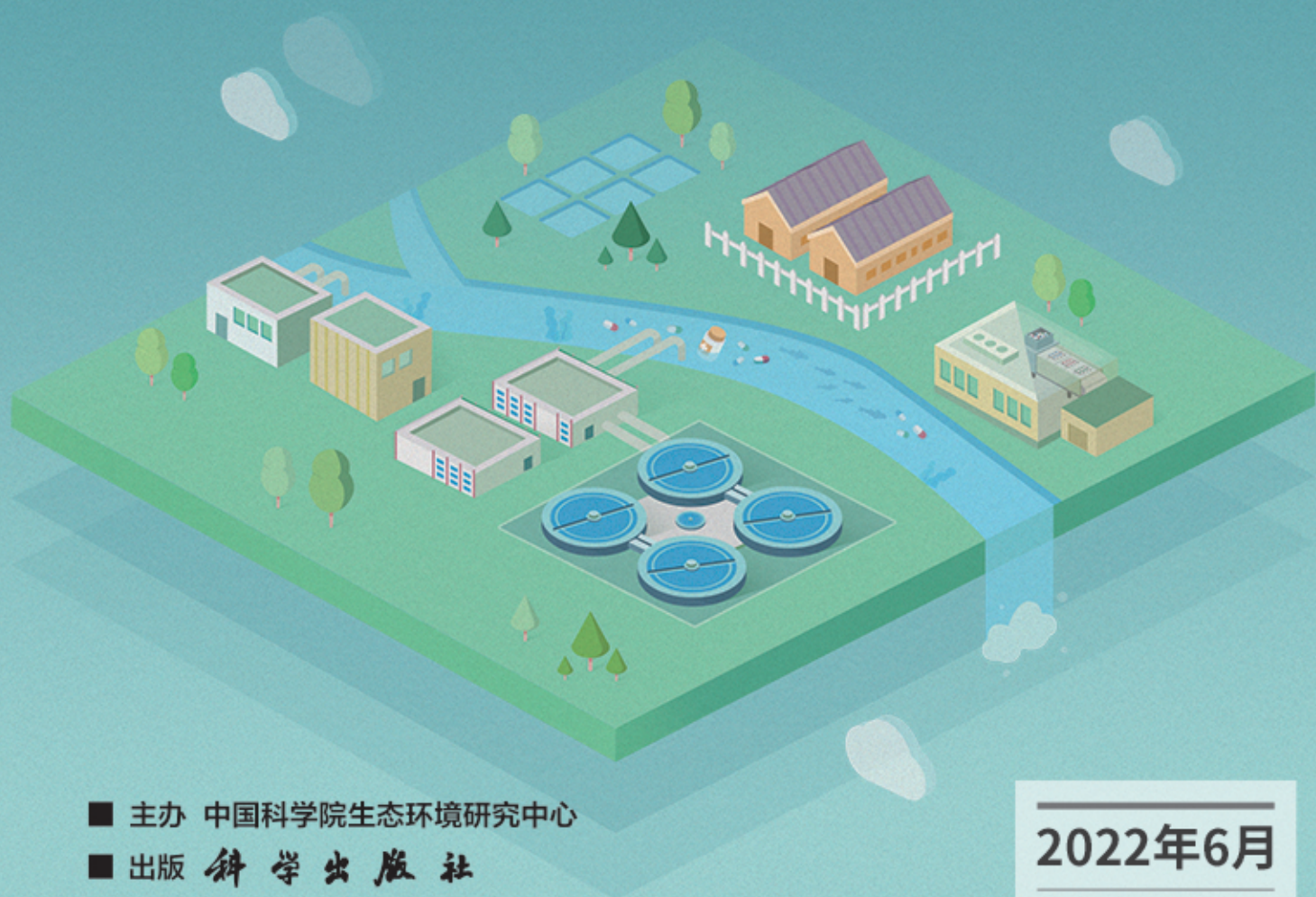
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长江中游典型饮用水水源中药物的时空分布及风险评价

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目次

COVID-19 管控期间气象条件变化对京津冀 PM _{2.5} 浓度影响	邱雨露, 陈磊, 朱佳, 马志强, 李梓铭, 郭恒, 唐颖潇 (2831)
新冠疫情管控措施对郑州市 PM _{2.5} 浓度、粒径分布、组分和来源的影响	黄兵役, 王申博, 和兵, 薛若雨, 高更宇, 张瑞芹 (2840)
COVID-19 管控期间苏州市 PM _{2.5} 中金属元素浓度变化及来源解析	缪青, 杨倩, 吴也正, 魏恒, 周民锋, 张晓华, 邹强 (2851)
2015 ~ 2019 年南京北郊碳质气溶胶组成变化	谢添, 曹芳, 章炎麟, 林煜棋, 范美益, 宋文怀, 鲍孟盈, 项妍琨, 赵祝钰, 杨笑影, 谢锋, 张煜炯, 俞浩然, 张子金, 邢佳莉 (2858)
基于受体和化学传输的综合模型解析重庆 PM _{2.5} 来源	彭超, 李振亮, 曹云攀, 蒲茜, 方维凯, 王晓宸, 汪凌韬 (2867)
保定市冬季 PM _{2.5} 的氧化潜势特征及其影响来源分析	吴继炎, 杨池, 张春燕, 范美益, 吴爱坪, 章炎麟 (2878)
南京江北新区 PM _{2.5} 中水溶性有机氮的污染特征及其来源	关璐, 丁铨, 张毓秀, 胡建林, 于兴娜 (2888)
广西十万大山背景点 PM _{2.5} 中非极性有机气溶胶组成及来源解析	邢佳莉, 曹芳, 王谦, 张煜炯, 章炎麟 (2895)
大气多环芳烃区域迁移转化模型比较与关键影响因素: 以京津冀地区为例	张馨露, 刘世杰, 韩美丽, 苏超, 张志鹏, 马琳琳, 李洋, 程苗苗 (2906)
基于过程分析的京津冀区域典型城市臭氧成因	唐颖潇, 姚青, 蔡子颖, 丁净, 樊文雁, 杨旭, 韩素芹 (2917)
天津市 PM _{2.5} -O ₃ 复合污染特征及气象影响分析	肖致美, 李源, 孔君, 李鹏, 蔡子颖, 高璟, 徐虹, 戴运峰, 邓小文 (2928)
2016 ~ 2020 年山东省空气质量时空分布特征及影响因素分析	周梦鸽, 杨依, 孙媛, 张凤英, 李永华 (2937)
河南省臭氧污染趋势特征及敏感性变化	晏洋洋, 尹沙沙, 何秦, 秦凯, 张瑞芹 (2947)
热带气旋对珠三角秋季臭氧污染的影响	赵伟, 吕梦瑶, 卢清, 高博, 梁小明, 刘明, 孙家仁, 陈来国, 范绍佳 (2957)
武汉市夏季大气挥发性有机物实时组成及来源	苏维峰, 孔少飞, 郑煌, 陈楠, 祝波, 全继宏, 祁士华 (2966)
运城市夏季大气挥发性有机物污染特征及来源解析	温肖宇, 赵文婷, 罗淑贞, 张强, 王姝涛, 马俊杰, 刘新罡 (2979)
我国地表水新烟碱类杀虫剂对水生生物安全的威胁	范丹丹, 刘红玲, 杨柳燕 (2987)
长江中游典型饮用水水源中药物的时空分布及风险评价	武俊梅, 魏琳, 彭晶倩, 何鹏, 施鸿媛, 汤冬梅, 吴振斌 (2996)
内蒙古东北部地区地下-地表饮用水源多环芳烃污染特征与风险	张坤峰, 昌盛, 付青, 樊月婷, 王思瑞, 孙兴滨, 王山军 (3005)
不同尺度土地利用方式对地表水环境质量的影响及驱动机制	宋静雯, 张学霞, 姜东旸, 赵丞豪, 李鹏飞 (3016)
高原湖泊周边浅层地下水: 氮素时空分布及驱动因素	李桂芳, 杨恒, 叶远行, 陈清飞, 崔荣阳, 陈安强, 张丹 (3027)
青海湖沉积物重金属分布及其潜在生态风险分析	张雅然, 车霏霏, 付正辉, 许野, 李薇 (3037)
东江湖表层沉积物重金属污染特征与潜在生态风险评价	赵晓亮, 李响, 卢洪斌, 卢少勇, 王涛, 张森霖, 国晓春, 张静, 弥启欣, 刘晓贺, 宋书峰 (3048)
湖泊沉积物有机磷释放动力学特征及水质风险	刘哲哲, 倪兆奎, 刘思儒, 李晓秀, 王圣瑞 (3058)
长三角一体化示范区青浦区水体表层沉积物有机质分布特征、来源解析及污染评价	张智博, 段艳平, 涂耀仁, 罗鹏程, 高峻 (3066)
香溪河流域微塑料的分布特征及其迁移规律分析	陈圣盛, 李卫明, 张坤, 熊伟唯, 张续同, 刘子健 (3077)
城市水体微塑料垂向分布下附着细菌群落结构和功能响应	陈玉芳, 闫振华, 张燕, 赵海洲 (3088)
2015 ~ 2020 年洪泽湖浮游植物群落结构及其环境影响因子	屈宁, 邓建明, 张祯, 蔡永久, 龚志军, 李明 (3097)
嘉兴南湖不同湖区浮游植物群落结构特征与环境因子关系	王雅雯, 李迎鹤, 张博, 郭云艳, 陈俊伊, 韩松 (3106)
近 20 年来广东省农业面源污染负荷时空变化与来源分析	葛小君, 黄斌, 袁再健, 王栋栋, 王泉泉, 陈佳村, 谢真越 (3118)
长江上游平原丘陵区农业非点源污染输出特征和驱动机制	谭少军, 刘洋, 朱小婕, 刘荷, 邵景安, 邓华 (3128)
高分辨率数据驱动的流域非点源污染输出风险评估方法	顾晶晶, 冶涛涛, 董甲平, 蒋云钟, 曹引, 赵红莉 (3140)
不同面源强度影响下城市河流溶解性有机质光谱特征变化	陈旭东, 高良敏 (3149)
生态沟渠-生物滞留池组合控制农村径流污染	石雷, 杨小丽, 吴青宇, 王亦铭, 徐佳莹 (3160)
不同水力扰动强度对老化 PSMPs 在泥水两相间迁移的影响	吴香香, 艾萍, 李大鹏 (3168)
北京市中心城区屋面径流污染特征及来源分析	席玥, 郭婧, 陶蕾, 田颖, 陈吉吉, 吴悦, 徐藤, 荆红卫, 刘保献 (3177)
不同植被绿色屋顶径流水质年际变化特征	章孙逊, 张守红, 葛德, 闫婧, 杨航, 王任重远, 魏良怡, 张成玉 (3187)
可见光促有机物诱导铁还原的多相类芬顿体系强化效能与机制	曹丝雨, 许路, 付权超, 金鑫, 石炬, 金鹏康 (3195)
4 种典型抗生素在反硝化体系中的去除特性	唐佳, 陈茜, 覃牧川, 唐溪, 唐崇俭 (3204)
农业废弃物基生物炭对水溶液中镉的吸附效果与机制	龚沛云, 孙丽娟, 宋科, 孙雅菲, 秦秦, 周斌, 薛永 (3211)
腐殖酸-重金属对 ANAMMOX 菌脱氮性能的影响及其动力学分析	李芸, 崔楠, 熊星星, 黄志远, 李泽兵, 王东亮, 李朝明, 许丹, 李军 (3221)
2000 ~ 2020 年西南地区植被 NDVI 对气候变化和人类活动响应特征	徐勇, 黄雯婷, 窦世卿, 郭振东, 李欣怡, 郑志威, 靖娟利 (3230)
黄河三角洲湿地不同植被类型下土壤营养元素空间分布及其生态化学计量学特征	孙德斌, 栗云召, 于君宝, 杨继松, 杜朝红, 孙丹丹, 凌越, 马元庆, 周迪, 王雪宏, 赵佳怡 (3241)
青藏高原东北部地区表层土壤中全氟化合物的分布特征及来源解析	温祥洁, 陈朝辉, 徐维新, 吴小娟, 郝云庆, 刘伟, 印红玲, 方淑红 (3253)
西南典型“退耕还林”区土地利用/覆被变化对土壤中硒及重金属含量的影响	刘永林, 刘属灵, 吴梅, 田兴磊, 刘双燕 (3262)
贵州普定喀斯特关键带土壤重金属形态特征及风险评价	张倩, 韩贵琳 (3269)
南丹盆地东部山区土壤锆分布特征及其影响因素分析	董秋瑶, 赖书雅, 宋超, 温皓天, 严明疆, 杨振京 (3278)
神农架川金丝猴栖息地重金属污染特征及风险评价	严佳莉, 于紫玲, 余辉亮, 向明灯, 王传华 (3288)
石灰泡石钝化后两种轮作模式对重度镉污染农田土壤的利用及修复	许璐, 周春海, 刘梅, 孔辉, 李元, 黄志红 (3299)
水稻磷盈亏对镉吸收转运的影响	谭文韬, 霍洋, 周航, 仇银燕, 曾鹏, 辜娇峰, 廖柏寒 (3308)
改良剂调控下水稻镉累积和土壤溶解性有机质光谱特征的响应	罗会龙, 陈娟, 张云慧, 袁贝, 杨宾, 张昊, 杜平 (3315)
土壤真菌群落对五台山亚高山草甸退化的响应	罗正明, 赫磊, 刘晋仙, 胡砚秋, 周妍英, 郑庆荣, 柴宝峰 (3328)
小麦与不同作物多样化轮作对土壤真菌群落的影响	靳海洋, 岳俊芹, 闫雅倩, 张德奇, 杨程, 张素瑜, 李向东, 邵运辉, 方保停, 王汉芳, 秦峰 (3338)
重庆农田土壤有机碳稳定性同位素空间分布特征	廖宇琴, 龙娟, 木志坚, 文首鑫, 李翠莲, 杨志敏, 赵秀兰 (3348)
长江三角洲 2018 年土壤 NO 排放特征	廖加强, 薛金, 王文锦, 朱永慧, 朱安生, 黄凌, 王杨君, 李莉 (3357)
基于多源数据的城市扩张中热环境演变及响应	梁建设, 白永平, 杨雪蕊, 高祖桥, 李玲蔚, 张春悦, 王倩 (3365)
《环境科学》征订启事 (3004) 《环境科学》征稿简则 (3047) 信息 (3252, 3298, 3327)	

小麦与不同作物多样化轮作对土壤真菌群落的影响

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摘要: 为明确华北平原冬小麦与不同作物多样化轮作下的土壤真菌群落差异, 为生态可持续种植制度的构建和优化提供理论依据, 采用实时荧光定量 PCR 和高通量测序技术研究了连续冬小麦-夏玉米 M、冬小麦-夏花生 (夏玉米) PM 和冬小麦-夏大豆 (夏玉米) SM 轮作处理的土壤真菌群落丰度、组成和多样性。结果表明, 与连续冬小麦-夏玉米处理相比, 轮作花生 PM2 和大豆 SM2 处理显著降低了土壤真菌 ITS 序列拷贝数, 轮作花生或大豆处理增加了土壤真菌群落丰富度和多样性。非度量多维尺度分析 (NMDS) 结果显示, 不同轮作茬口之间土壤真菌群落存在明显分离, 轮作作物对土壤真菌群落结构的影响达显著水平。华北平原砂壤质潮土中不同作物轮作处理的土壤真菌群落均以 Ascomycota 为优势菌门, 以 Sordariomycetes 和 Eurotiomycetes 为优势菌纲。不同轮作茬口土壤真菌群落组成存在差异显著的类群, *Neocosmospora*、*Plectosphaerella* 和 *Gibellulopsis* 等潜在病原真菌在冬小麦-夏花生 (夏玉米) 轮作处理中显著富集, 而 *Penicillium* 和 *Zopfiella* 等潜在有益真菌在冬小麦-夏大豆 (夏玉米) 轮作处理中显著富集。与连续冬小麦-夏玉米处理相比, 轮作花生或大豆处理增加了病理营养型、病理-共生营养型和腐生-共生营养型土壤真菌的相对丰度, 而腐生营养型土壤真菌相对丰度有所降低。综上, 在连续冬小麦-夏玉米轮作体系中, 加入夏花生或夏大豆替代夏玉米进行不同周期轮作, 可增加土壤真菌群落丰富度和多样性, 显著影响土壤真菌群落结构; 其中, 夏大豆茬口利于土壤潜在有益真菌的富集。

关键词: 轮作; 土壤; 真菌群落; ITS 序列; 微生物多样性

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Response of Soil Fungal Communities in Diversified Rotations of Wheat and Different Crops

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Abstract: Crop-soil microorganism interactions and feedback are critical to soil health and crop production. The aim of this study was to clarify the difference in soil fungal communities under diversified rotations of wheat and different crops in the North China Plain and to provide a theoretical basis for the construction and optimization of ecological sustainable planting systems. The soil fungal community abundance, composition, and diversity of continuous winter wheat-summer maize M, winter wheat-summer peanut (summer maize) PM, and winter wheat-summer soybean (summer maize) SM treatments were studied using real-time quantitative PCR and high-throughput sequencing technology. The results showed that, compared with those of the continuous winter wheat-summer maize treatment, the peanut rotation treatment PM2 and soybean rotation treatment SM2 significantly reduced soil fungal ITS sequence copy numbers ($P < 0.05$); there was no significant difference in soil fungal ITS sequence copy numbers between other rotation treatments and those of the control ($P > 0.05$). Rotation treatments with peanut or soybean increased soil fungal community richness (Chao1 and ACE indices) and diversity (Shannon and InvSimsim indices), in which the community richness of all rotation treatments and the community diversity of SM1/SM2 treatments varied significantly ($P < 0.05$). The result of non-metric multidimensional scaling (NMDS) analysis showed that the soil fungal community among different rotation crops were obviously separated. The rotation crops significantly affected soil fungal community structure (PERMANOVA; $r^2 = 0.350$, $P = 0.001$; ANOSIM; $r = 0.478$, $P = 0.001$). Ascomycota (73.67%–85.48%) was the dominant phylum, whereas Sordariomycetes (30.53%–48.19%) and Eurotiomycetes (11.12%–31.19%) were the dominant classes of the fungal communities of sandy-loam fluvo-aquic soil in the North China Plain. There were significantly different taxa of soil fungal communities in different rotations. Potential pathogens such as *Neocosmospora*, *Plectosphaerella*, and *Gibellulopsis* were significantly enriched in the rotations of winter wheat-summer peanut (summer maize), whereas potential beneficial fungi such as *Penicillium* and *Zopfiella* were significantly enriched in the rotations of winter wheat-summer soybean (summer maize). Compared with that under the continuous winter wheat-summer maize treatment, rotations with peanut or soybean increased the relative abundance of pathotroph, pathotroph-symbiotroph, and saprotroph-symbiotroph fungi and decreased the relative abundance of saprotroph fungi. The soil fungal community richness and structure were significantly

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related to soil organic carbon and available nutrients, and the Shannon diversity index was significantly related to soil mineral nitrogen and available phosphorus. In summary, on the basis of continuous winter wheat-summer maize rotation in the North China Plain, adding summer peanut or summer soybean instead of summer maize for rotations with different interval years could increase the richness and diversity of soil fungal communities and significantly change soil fungal community structure. In particular, summer soybean as the preceding crop had a positive effect on the enrichment of potential beneficial fungi.

Key words: crop rotation; soil; fungal community; ITS sequence; microbial diversity

土壤微生物群落是生态系统生物化学循环过程的关键参与者^[1], 是植物生产力的重要驱动者^[2]. 在农业生态系统中, 土壤微生物群落多样性和活性会受到作物种植的影响^[3,4], 同时, 微生物活动直接或间接影响作物生产过程的植物营养、生长调节和生物防治等关键环节^[5,6], 作物-土壤微生物相互作用与反馈对土壤健康和作物生产至关重要^[7]. 真菌是土壤微生物群落的主要成员之一, 在作物生产上可分为有害真菌和有益真菌, 有害真菌可侵染作物引起植物病害, 有益真菌能够抑制病原菌、促进植物生长和分解植物残体等^[8]. 充分了解农业管理实践对土壤真菌群落的影响, 对发展生态可持续农业生产具有重要意义.

随着集约化种植强度的增加, 现代农业生产的一个突出特点是种植制度的简化^[3,4], 作物多样性的降低可能导致农业生态系统功能和服务减少. 有研究表明, 在连作条件下, 玉米的生物量和产量会由于土壤微生物的负反馈而降低^[9]; 连续单一栽培花生会显著增加土壤病原真菌的相对丰度, 减少潜在有益真菌, 造成土壤真菌群落生态失衡和花生产量降低^[10]; 连作大豆减弱了根际土壤真菌群落网络结构, 加强了潜在病原真菌之间的正向互作, 导致土壤功能退化和大豆产量下降^[11,12]. 作物种植多样化被认为是提高农业生态系统生物多样性^[13]和增加气候变化条件下粮食生产稳定性^[14,15]的有力措施之一. 通过轮作增加时间上的作物多样性可恢复地上-地下的正相互作用^[16], 充分利用水分和养分等自然资源, 最大限度地利用生态位和土壤生物多样性^[17], 具有增强土壤生态系统功能的潜力, 对维持农业系统中土壤服务功能至关重要^[18,19]. 有研究表明, 作物轮作显著改变了土壤细菌和真菌群落多样性、组成和网络^[20]; 随着轮作作物从 1 种增加到 5 种, 土壤团聚体、有机碳和全氮增加^[16]; 与简单轮作相比, 更多样化的轮作增加了土壤微生物群落代谢多样性和活性^[4,16], 增加了作物生物量和产量^[21]. 通过 Meta 分析, 与连作相比, 轮作作物产量平均增加 20%, 且豆科作物的轮作效益更高^[22]; 调查结果表明, 与连作小麦相比, 小麦与豆科作物轮作具有明显的经济优势^[23].

受光温水资源的影响, 不同作物种类和轮作顺序的选择具有地域性. 在华北平原, 冬小麦-夏玉米、

冬小麦-夏花生和冬小麦-夏大豆等一年两熟制是主要种植制度, 其中, 以连续冬小麦-夏玉米周年轮作为主导. 有研究表明, 与冬小麦-夏玉米一年两熟制相比, 冬小麦-夏花生种植模式具有较高的净收益和较低的单位净产值碳排放^[24], 花生茬口的土壤含水量显著高于玉米茬口, 可提高后茬冬小麦的净光合速率, 显著提高小麦籽粒产量^[25]; 与玉米茬口相比, 大豆茬口和玉米大豆间作茬口显著增加后茬小麦的穗数和穗粒数, 增加小麦籽粒产量, 提高氮肥利用率^[26]; 与玉米相比, 花生或大豆作为前茬作物可增加土壤速效养分含量, 增加小麦产量 9.57% ~ 10.32%^[27]; 与玉米-小麦种植体系相比, 花生-小麦和大豆-小麦具有更高的当量产量和收益, 具有较高的土地利用效率和生产效率^[28]. 鉴于多样化轮作的诸多优势, 在华北平原有必要探索发展冬小麦与不同作物(夏玉米、夏花生和夏大豆)多样化轮作的种植模式, 不同作物轮作下土壤真菌群落的差异及其影响因子值得深入地研究. 基于此, 本研究以常年冬小麦-夏玉米周年轮作为基础, 加入夏花生或夏大豆替代夏玉米进行不同周期轮作, 利用多年定位试验, 分析了小麦与不同作物多样化轮作对土壤真菌群落的影响, 以期对生态可持续种植制度的构建和优化提供理论依据.

1 材料与方法

1.1 研究地点

本研究地点位于河南现代农业研究开发基地(河南省新乡市平原新区, 35°00' N, 113°41' E). 该区域累年年平均气温 14.4℃, 累年月平均气温 0℃(1 月)至 26.9℃(7 月); 累年年平均降水量 566.2 mm, 约三分之二的降水量集中于 6 ~ 9 月. 土壤为黄河冲积物发育的砂壤质潮土, 其 0 ~ 20 cm 土壤中 ω (有机碳)为 4.29 g·kg⁻¹, ω (全氮) 0.31 g·kg⁻¹, ω (全磷) 0.87 g·kg⁻¹, ω (全钾) 19.65 g·kg⁻¹, pH 值 8.52. 研究基地处于华北平原, 该区域传统以冬小麦-夏玉米一年两熟为主要种植制度.

1.2 试验设置

以常年冬小麦-夏玉米周年轮作为基础, 加入夏花生或夏大豆替代夏玉米进行不同周期轮作, 设置 1 个冬小麦-夏玉米处理(M)、3 个冬小麦-夏花生

(夏玉米)处理(PM1、PM2和PM3)和3个冬小麦-夏大豆(夏玉米)处理(SM1、SM2和SM3),共计7个轮作处理,作物种植顺序如表1所示.田间试验处理始于2015年6月,每个处理设3个重复,共21个

小区,小区长宽6 m×5 m,四周以深2 m的混凝土隔开.冬小麦10月播种,次年6月初收获;随后播种夏玉米、夏花生或夏大豆,9月底收获.除轮作处理外,各小区田间管理措施一致.

表1 不同轮作处理的作物种植顺序

Table 1 Cropping sequences of different rotations

处理	2015~2016年	2016~2017年	2017~2018年	2018~2019年	2019~2020年	2020~2021年
M	玉米-小麦	玉米-小麦	玉米-小麦	玉米-小麦	玉米-小麦	玉米-小麦
PM1	花生-小麦	玉米-小麦	花生-小麦	玉米-小麦	花生-小麦	花生-小麦
PM2	花生-小麦	玉米-小麦	玉米-小麦	花生-小麦	玉米-小麦	花生-小麦
PM3	花生-小麦	玉米-小麦	玉米-小麦	玉米-小麦	花生-小麦	花生-小麦
SM1	大豆-小麦	玉米-小麦	大豆-小麦	玉米-小麦	大豆-小麦	大豆-小麦
SM2	大豆-小麦	玉米-小麦	玉米-小麦	大豆-小麦	玉米-小麦	大豆-小麦
SM3	大豆-小麦	玉米-小麦	玉米-小麦	玉米-小麦	大豆-小麦	大豆-小麦

1.3 测定项目与方法

1.3.1 土壤样本采集与微生物总DNA提取

于2020年9月30日,使用土钻(内径3 cm)采集作物收获后的行间土壤样品,取样深度0~20 cm,每个小区随机取5个样点混合作为该小区的土壤样本.冷藏箱带回实验室后,除去石块和植物残体,过2 mm筛混匀,保存于-80℃.

称取0.5 g冷冻土壤,使用FastDNA Spin Kit for Soil和FastPrep Instrument(MP Biomedicals, USA)提取土壤微生物基因组DNA,采用NanoDrop 2000(Thermo Scientific, USA)进行DNA纯度和浓度检测,1%琼脂糖凝胶电泳进行DNA完整性检测.

1.3.2 实时荧光定量PCR

以土壤微生物基因组DNA为模板,采用引物ITS3F(5'-GCATCGATGAAGAACGCAGC-3')和ITS4R(5'-TCCTCCGCTTATTGATATGC-3')^[29,30]进行实时荧光定量PCR(qPCR),测定土壤真菌ITS序列拷贝数.qPCR反应中的DNA Polymerase、SYBR Green I和dNTPs等使用ChamQ SYBR Color qPCR Master Mix(Cat. No. Q411-02,南京诺唯赞生物科技股份有限公司,中国),qPCR仪使用Applied Biosystems 7300 Real-Time PCR System(Applied Biosystems, USA).qPCR反应体系包含:10 μL 2×ChamQ SYBR Color qPCR Master Mix、0.8 μL Forward Primer(5 μmol·L⁻¹)、0.8 μL Reverse Primer(5 μmol·L⁻¹)、0.4 μL 50×ROX Reference Dye 1、2 μL Template DNA和6 μL dd H₂O.qPCR反应条件为:95℃预变性3 min;95℃变性5 s,58℃退火30 s,72℃延伸1 min,40个循环.将已知浓度含有目的序列的质粒DNA进行10倍梯度稀释,随样品同时进行qPCR,制作标准曲线.每个样本和标准曲线各3个复孔,根据标准曲线计算样本的真菌ITS序列拷贝数.

1.3.3 土壤真菌ITS序列扩增与高通量测序

以土壤微生物基因组DNA为模板,采用引物ITS3F(5'-GCATCGATGAAGAACGCAGC-3')和ITS4R(5'-TCCTCCGCTTATTGATATGC-3')^[29,30]进行真菌ITS序列的PCR扩增,PCR反应中的DNA Polymerase、Buffer和dNTPs等使用TransStart FastPfu DNA Polymerase(Cat. No. AP221-02,北京全式金生物技术有限公司,中国),PCR仪使用GeneAmp PCR System 9700(Applied Biosystems, USA).PCR反应体系包含:4 μL 5×TransStart FastPfu Buffer、2 μL 2.5 mmol·L⁻¹ dNTPs、0.8 μL Forward Primer(5 μmol·L⁻¹)、0.8 μL Reverse Primer(5 μmol·L⁻¹)、0.4 μL TransStart FastPfu DNA Polymerase、0.2 μL BSA、10 ng Template DNA和ddH₂O补充至20 μL.PCR反应条件为:95℃预变性3 min;95℃变性30 s,55℃退火30 s,72℃延伸45 s,35个循环;72℃最后延伸10 min.每个样本3个重复,PCR反应后将同一样本的产物混合,2%琼脂糖凝胶电泳检测,使用AxyPrep DNA Gel Extraction Kit(Cat. No. AP-GX-250, Axygen, USA)切胶回收目的DNA片段,Tris-HCl洗脱DNA,2%琼脂糖电泳检测.使用QuantiFluor-ST Handheld Fluorometer(Promega, USA)采用PicoGreen荧光染料法进行DNA定量,按相应体积比例混合,Illumina MiSeq测序平台进行PE300高通量测序.

1.3.4 数据统计分析

Illumina MiSeq下机数据使用FLASH^[31]对两端测序序列进行拼接(overlap≥10 bp),采用Fastp对原始数据进行质量控制和数据过滤^[32],根据barcode区分样本数据,得到优化数据.使用USEARCH^[33]以97%相似性进行OTU聚类(UPARSE)^[33,34]和嵌合体检查去除(UCHIME)^[35].使用RDP Classifier^[36]对OTU进行分类注释,采用

UNITE^[37]数据库. 按最小样本序列数进行抽平, 以抽平后的有效数据进行后续微生物群落多样性和组成分析.

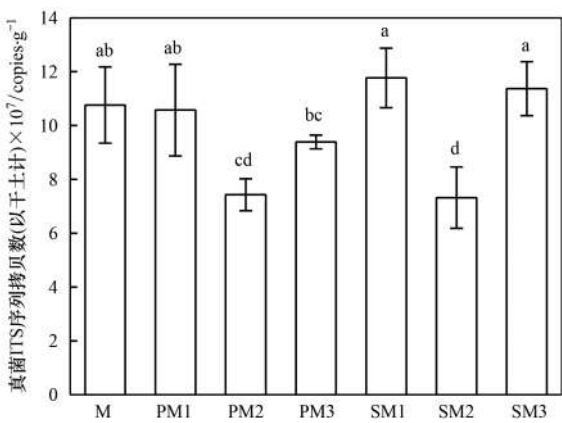
使用 Mothur 进行 α 多样性分析^[38,39]. β 多样性分析采用基于 Binary Jaccard 距离算法的非度量多维尺度分析 (non-metric multidimensional scaling, NMDS), 通过置换多元方差分析 (permutational multivariate analysis of variance, PERMANOVA) 和相似性分析 (analysis of similarities, ANOSIM) 评估不同处理对真菌群落结构的影响. 采用 Circos 对不同处理群落组成数据进行可视化^[40]. 采用线性判别分析工具 LEfSe (linear discriminant analysis effect size) 分析不同轮作茬口的差异物种^[41], LDA 阈值设置为 3.5. 采用 FUNGuild 对土壤真菌营养方式在 OTU 水平进行分类注释^[42].

采用单因素方差分析 (one-way ANOVA) 比较不同处理间的土壤真菌 ITS 序列拷贝数和真菌群落 α 多样性指数, 多重比较采用 LSD 法 ($P < 0.05$). 采用 Pearson 相关性分析研究 ITS 序列拷贝数和真菌群落 α 多样性指数与土壤性质的相关关系; 通过 Mantel test 检验群落结构与土壤性质的相关关系.

2 结果与分析

2.1 不同作物轮作对土壤真菌群落丰度的影响

采用实时荧光定量 PCR (qPCR) 测定不同轮作茬口土壤真菌 ITS 序列拷贝数的结果如图 1 所示, 与连续冬小麦-夏玉米处理相比, 冬小麦-夏花生 (夏玉米) PM2 处理和冬小麦-夏大豆 (夏玉米) SM2 处理的土壤真菌 ITS 序列拷贝数显著降低 ($P < 0.05$). 冬小麦-夏花生 (夏玉米) PM1、PM3 处理和冬小麦-夏大豆 (夏玉米) SM1、SM3 处理的土壤真菌 ITS 序列拷贝数与对照相比差异未达显著水平



误差线表示标准差, 不同字母表示差异达显著水平 ($P < 0.05$)

图 1 不同轮作茬口的土壤真菌群落丰度

Fig. 1 Abundance of soil fungal community in different crop rotations

($P > 0.05$).

2.2 ITS 序列测序数据统计

Illumina MiSeq 测序数据经过拼接质控后, 21 个样本共得到 1 400 274 条优化序列, 每个样本 33 961 ~ 74 991 条, 平均序列长度 312 bp. 以 97% 相似性对非重复序列进行 OTU 聚类, 按最小样本序列数进行抽平, 每个样本 30 765 条有效序列, 共对应 1 658 个 OTU. 注释后这些 OTU 归属于 432 个属 (Genus)、224 个科 (Family)、113 个目 (Order)、54 个纲 (Class) 和 17 个门 (Phylum). 根据稀释曲线 (图 2), 随着序列数量的增加, 各个样本的群落覆盖度和群落多样性 (Shannon 指数) 均趋于平缓, 表明抽平后的序列数据量趋近饱和, 能够覆盖样本中真菌群落的绝大部分物种, 足够进行后续的真菌群落分析.

2.3 不同作物轮作对土壤真菌群落 α 多样性的影响

土壤真菌群落 α 多样性分析结果表明, 与连续冬小麦-夏玉米处理相比, 轮作花生或大豆处理显著增加了土壤真菌群落丰富度 (Chao1 指数和 ACE 指

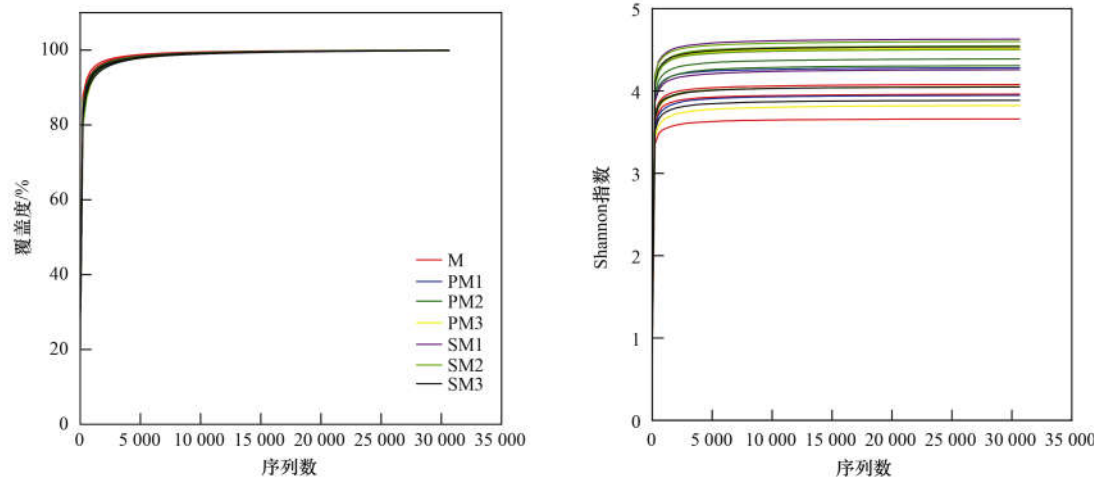


图 2 基于群落覆盖度和 Shannon 指数的真菌群落稀释曲线

Fig. 2 Rarefaction curves of fungal community based Good's coverage and Shannon index

数, $P < 0.05$, 表 2)。冬小麦-夏花生(夏玉米)和冬小麦-夏大豆(夏玉米)处理的土壤真菌群落多样性(Shannon 指数和 InvSimpson 指数)与对照相比有所增加,其中 SM1 和 SM2 处理与对照相比差异达显著水平($P < 0.05$)。轮作花生或大豆的不同种植顺序处理间土壤真菌群落丰富度和多样性差异未达显著水平($P > 0.05$)。

表 2 不同轮作茬口的土壤真菌群落 α 多样性¹⁾
Table 2 The α diversity of soil fungal community

in different crop rotations				
处理	Chao1 指数	ACE 指数	Shannon 指数	InvSimpson 指数
M	485b	491b	3.89b	17.33b
PM1	624a	625a	4.23ab	27.78ab
PM2	606a	598a	4.24ab	24.15ab
PM3	600a	588a	4.12ab	25.29ab
SM1	635a	635a	4.45a	40.03a
SM2	615a	614a	4.54a	39.19a
SM3	603a	602a	4.15ab	23.89ab

1) 同列数值后不同小写字母表示处理间差异达显著水平($P < 0.05$)

2.4 不同作物轮作对土壤真菌群落结构的影响

土壤真菌群落 β 多样性非度量多维尺度分析(NMDS)结果如图 3 所示,不同作物轮作处理分别聚集在一起,在第一坐标轴或第二坐标轴具有明显分离,而同种作物的不同种植顺序轮作处理之间没有明显分离,表明不同作物轮作处理之间土壤真菌群落结构存在明显差异。置换多元方差分析(PERMANOVA)和相似性分析(ANOSIM)结果均表明,不同轮作作物对土壤真菌群落结构的影响达显著水平(PERMANOVA: $r^2 = 0.350$, $P = 0.001$; ANOSIM: $r = 0.478$, $P = 0.001$)。

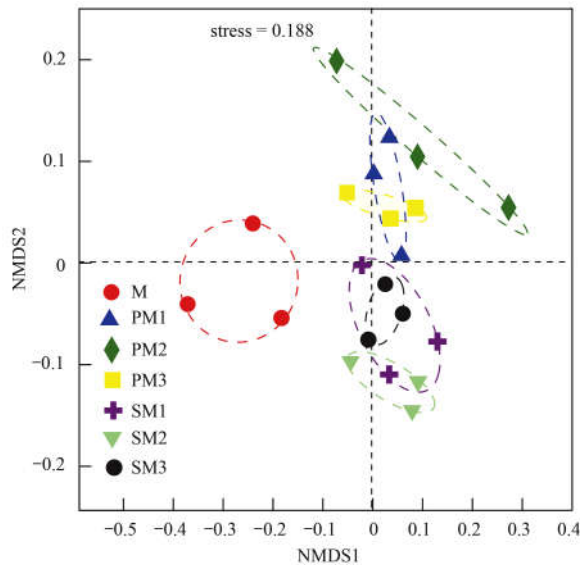


图 3 不同轮作茬口土壤真菌群落结构的非度量多维尺度分析
Fig. 3 Non-metric multidimensional scaling (NMDS) analysis of soil fungal community structure in different crop rotations

2.5 不同作物轮作对土壤真菌群落物种组成的影响

在门水平,不同作物轮作处理的土壤真菌群落均以 Ascomycota 为优势类群,相对丰度高达 73.67% ~ 85.48% (图 4)。其次为 Mucoromycota (3.91% ~ 6.97%)、Zoopagomycota (1.20% ~ 6.84%)、Basidiomycota (0.61% ~ 5.56%) 和 Mortierellomycota (0.59% ~ 2.99%)。unclassified Fungi 占真菌群落的 2.57% ~ 10.22%。

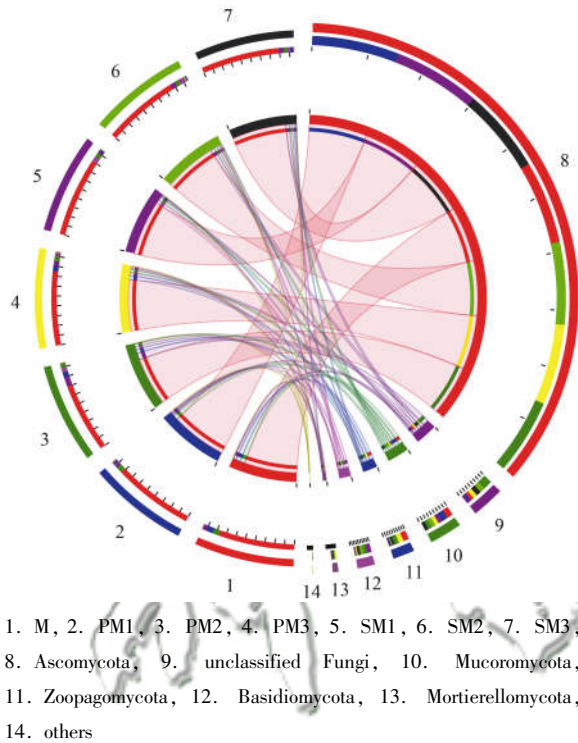
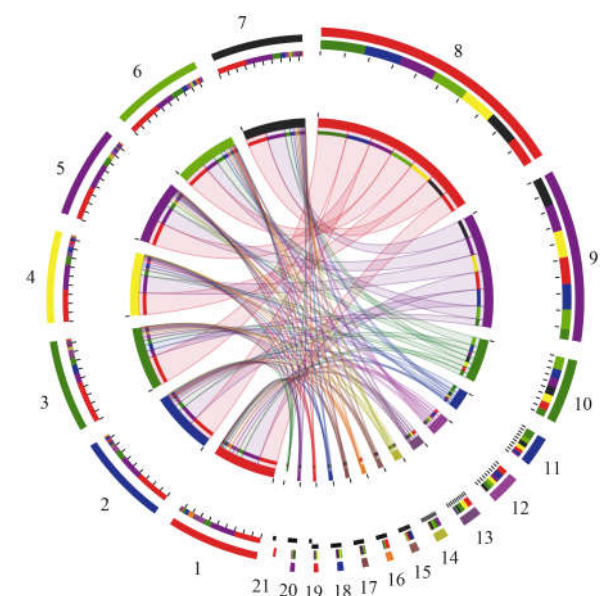


图 4 不同轮作茬口的门水平土壤真菌群落组成
Fig. 4 Soil fungal community compositions in different crop rotations at phylum level

在纲水平,不同作物轮作处理的土壤真菌群落均以 Sordariomycetes 和 Eurotiomycetes 为优势类群,相对丰度分别为 30.53% ~ 48.19% 和 11.12% ~ 31.19% (图 5)。另外,还鉴定出相对丰度大于 1% 的真菌纲 10 个,其中相对丰度在各处理土壤中均大于 1% 的类群有: Dothideomycetes (7.58% ~ 14.35%)、Mucoromycetes (3.91% ~ 6.97%) 和 unclassified Zoopagomycota (1.20% ~ 6.84%)。

以 LDA 3.5 为阈值,对不同作物轮作处理土壤真菌群落组成进行线性判别分析,结果如图 6 所示,共识别出 21 个差异类群。在属水平,Striaticonidium、Preussia、Meyerozyma 和 Chrysosporium 在连续冬小麦-夏玉米处理中显著富集; Neocosmospora、Trichocladium、Plectosphaerella、Podospira、Gibellulopsis 和 unclassified Bionectriaceae 在冬小麦-夏花生(夏玉米)轮作处理中显著富集; Penicillium 和 Zopfiella 在冬小麦-夏大豆(夏玉米)



1. M, 2. PM1, 3. PM2, 4. PM3, 5. SM1, 6. SM2, 7. SM3, 8. Sordariomycetes, 9. Eurotiomycetes, 10. Dothideomycetes, 11. unclassified Fungi, 12. Mucoromycetes, 13. unclassified Zoopagomycota, 14. Agaricomycetes, 15. Leotiomyces, 16. Pezizomycetes, 17. unclassified Ascomycota, 18. others, 19. Mortierellomycetes, 20. Pezizomycotina cls Incertae sedis, 21. Saccharomycetes

图5 不同轮作茬口的纲水平土壤真菌群落组成
Fig. 5 Soil fungal community compositions in different crop rotations at class level

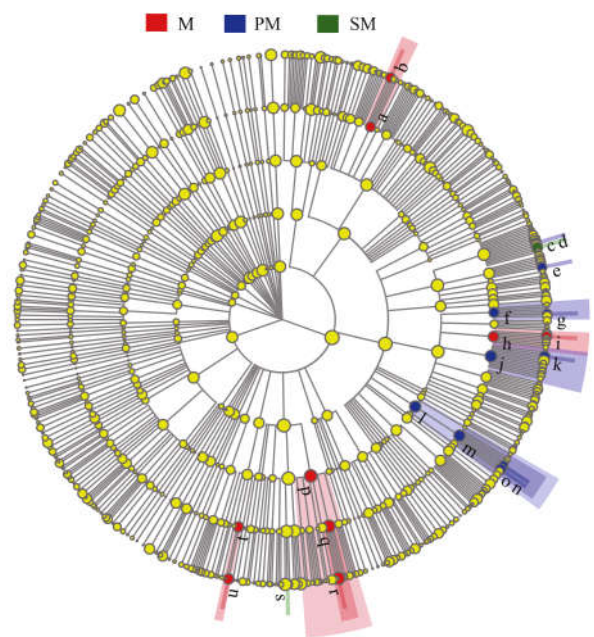
轮作处理中显著富集。

2.6 不同作物轮作对土壤真菌营养方式的影响

通过 FUNGuild 注释分析,不同轮作茬口的土壤真菌营养方式划分为病理营养型(pathotroph)、共生营养型(symbiotroph)和腐生营养型(saprotroph),以及病理-共生营养型(pathotroph-symbiotroph)、病理-腐生营养型(pathotroph-saprotroph)、腐生-共生营养型(saprotroph-symbiotroph)和病理-腐生-共生营养型(pathotroph-saprotroph-symbiotroph)等兼性营养方式(图7)。腐生营养型真菌的相对丰度较高,占土壤真菌群落的36.80%~59.33%。与连续冬小麦-夏玉米处理相比,轮作花生或大豆处理增加了病理营养型、病理-共生营养型和腐生-共生营养型土壤真菌的相对丰度,而腐生营养型土壤真菌相对丰度有所降低。

2.7 土壤真菌群落与土壤养分的相关性

Pearson 相关性分析结果显示,不同作物轮作处理的土壤真菌群落丰度和多样性 InvSimpson 指数与土壤有机碳和速效氮磷钾含量相关性未达显著水平($P>0.05$,表3)。土壤真菌群落丰富度与土壤有机碳、无机氮和速效钾含量显著负相关,而与土壤有效磷含量显著正相关($P<0.05$)。土壤真菌群落多样性 Shannon 指数与土壤无机氮含量显著负相关,



a. f_Sporormiaceae, b. g_Preussia, c. g_Trichocladium, d. g_Zopfiella, e. g_Podospora, f. f_Bionectriaceae, g. g_unclassified_f_Bionectriaceae, h. f_Stachybotryaceae, i. g_Striaticonidium, j. f_Nectriaceae, k. g_Neocosmospora, l. o_Glomerellales, m. f_Plectosphaerellaceae, n. g_Plectosphaerella, o. g_Gibellulopsis, p. o_Onygenales, q. f_Onygenales_fam_Incertae_sedis, r. g_Chrysosporium, s. g_Penicillium, t. f_Debaryomycetaceae, u. g_Meyerozyma

图6 不同轮作茬口的土壤真菌群落差异物种分析

Fig. 6 Differential taxa analysis of soil fungal communities in different crop rotations

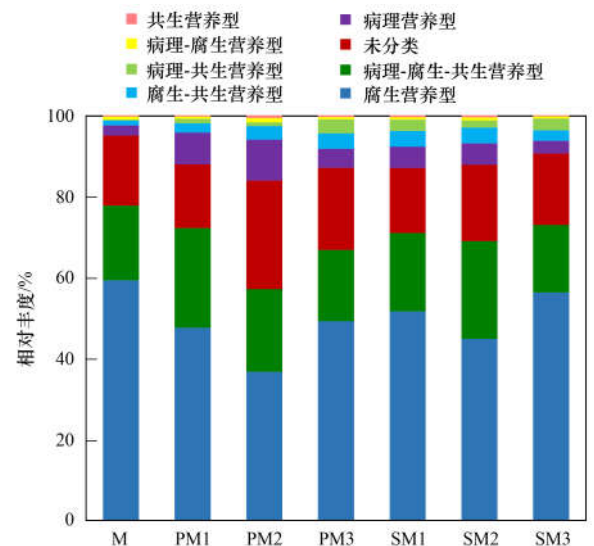


图7 不同轮作茬口的土壤真菌营养方式相对丰度

Fig. 7 Relative abundance of soil fungal trophic mode in different crop rotations

而与土壤有效磷含量显著正相关($P<0.05$)。

Mantel test 分析结果显示,不同作物轮作处理的土壤真菌群落结构与土壤有机碳、无机氮、有效磷和速效钾含量显著相关($P<0.05$,表4)。

表 3 土壤真菌群落丰度和 α 多样性指数与土壤有机碳和速效养分的 Pearson 相关系数¹⁾Table 3 Pearson correlation coefficients between abundance, α diversity indices of soil fungal community, soil organic carbon, and available nutrients

土壤性质	真菌 ITS 序列拷贝数	Chao1 指数	ACE 指数	Shannon 指数	InvSimpson 指数
有机碳	0.337	-0.490 *	-0.491 *	-0.287	-0.122
无机氮	0.044	-0.675 **	-0.670 **	-0.438 *	-0.313
有效磷	-0.178	0.608 **	0.603 **	0.489 *	0.389
速效钾	0.011	-0.619 **	-0.607 **	-0.216	-0.126

1) * 表示 0.05 水平显著相关, ** 表示 0.01 水平显著相关

表 4 土壤真菌群落结构与土壤有机碳和速效养分的 Mantel test 相关性

Table 4 Mantel test correlations between soil fungal community structure, soil organic carbon, and available nutrients

土壤性质	r 值	P 值
有机碳	0.367	0.004
无机氮	0.545	0.001
有效磷	0.445	0.011
速效钾	0.393	0.010

3 讨论

群落丰富度代表生态系统中的物种数量,是群落 α 多样性基本的衡量指标,而群落多样性是群落丰富度和均匀度的综合反映.为排除不同指标计算方法的干扰,本研究同时采用 Chao1 指数和 ACE 指数表征群落丰富度,采用 Shannon 指数和 InvSimpson 指数表征群落多样性,不同指标计算方法的结果一致.与连续冬小麦-夏玉米处理相比,轮作花生或大豆处理增加了土壤真菌群落丰富度和多样性(表 2),这与前人在其他作物上的研究结果相一致.有研究表明,随马铃薯连作时间的延长,土壤真菌群落丰富度和多样性显著降低^[43];与谷子连作相比,谷子轮作大豆、籽粒苋或藜麦有利于提高土壤真菌群落丰富度和多样性^[44];与玉米连作相比,玉米-大豆轮作提高了土壤真菌群落 Shannon 指数^[45]. Venter 等^[3]的研究通过 Meta 分析表明,地上和地下生物多样性之间具有相关性,轮作作物多样性的提高可增加土壤微生物群落丰富度(15.11%, $n = 26$)和多样性(3.36%, $n = 43$),且轮作时间越长,对微生物群落丰富度的正效应越强.植物通过根系分泌物和植物残体为土壤微生物提供营养^[46],通过多样化轮作增加时间上的作物多样性,能够在一定程度上增加土壤有机输入的数量、质量和化学多样性^[47],更多样化的碳源可支持多样化微生物类群的繁殖和生长^[3],因此作物多样化对土壤真菌多样性的增加效应可能归因于多样化的根系分泌物和植物残体.由于更广泛的微生物能够同时支持多种生态系统功能^[48],土壤微生物多样性被认为是维持土壤质量和健康的关键^[49],土壤真菌多样性的增加可能会对农业生态系统功能和可持续性产生有益影响

响^[50].同时,轮作对土壤真菌群落多样性的影响因作物而不尽相同.有研究显示,与黄瓜单作相比,番茄-芹菜-黄瓜-大白菜轮作可降低土壤真菌群落丰富度和多样性^[51];与连作处理相比,轮作大豆处理显著提高了土壤真菌群落的 Shannon 指数,而轮作小麦、玉米处理与连作处理相比差异未达显著水平^[52].不同作物轮作对土壤真菌群落多样性影响差异的原因还需进一步深入研究.

本研究中,在连续冬小麦-夏玉米周年轮作的基础上,加入夏花生或夏大豆替代夏玉米进行不同周期轮作,显著改变了土壤真菌群落结构(图 3).作为重要的营养物质和信号化学物质,植物可通过根系分泌物改变土壤微生物群落^[17].不同植物的根系分泌物存在差异,因此每种植物会选择特定的微生物类群^[46].首先,多样化轮作为地下生物提供了多样化的碳源,不同的碳源刺激了特定微生物类群的繁殖和生长,进而影响土壤微生物群落结构.其次,某些作物的根系分泌物中含有独特的代谢成分,对特定类群的微生物存在抑制或刺激作用,例如,花生根系分泌物中的酚酸^[53]、大豆根系分泌物中的异黄酮^[54,55]和小麦玉米根系分泌物中的苯并噁唑啉酮^[56,57]等均可以促进土壤微生物群落的变化.另一方面,在秸秆全量还田条件下,不同作物轮作处理土壤具有不同种类的秸秆输入,不同生物化学性质的有机物质能够刺激特定的真菌分解者^[45],例如,玉米秸秆有利于生长相对缓慢的真菌分解者,而大豆秸秆促进生长快速的真菌分解者^[58].因此,多样化轮作处理在一定时间内增加了作物秸秆的种类,利于更广泛的真菌物种存在^[45].

本研究中,华北平原砂壤质潮土中土壤真菌群落以 Ascomycota 为优势菌门,这与前人在华北平原的研究结果一致^[59,60].另外,在宁夏中部干旱带^[44]、黄土高原半干旱区^[61]、长江中下游平原水旱轮作区^[62]和台州湾滨海滩涂地^[63],土壤真菌群落在纲水平的优势类群有所差别,而门水平均以 Ascomycota 为优势类群.通过 LEfSe 分析结果显示, *Neocosmospora*、*Plectosphaerella* 和 *Gibellulopsis* 等在冬小麦-夏花生(夏玉米)轮作处理中显著富集(图

6). 有研究表明, *Neocosmospora* 可侵染花生^[64,65]、大豆^[66]、柑橘^[67]和火龙果^[68]等作物引起茎基腐病; *Plectosphaerella* 可引发卷心菜^[69]和茼蒿^[70]等园艺作物的根茎腐病^[71]; *Gibellulopsis* 可引发甜菜萎蔫病^[72]和茼蒿苗腐病^[73]等真菌性病害. 由此, 在连续冬小麦-夏玉米轮作中加入夏花生进行不同周期轮作, 可增加病原真菌的相对丰度, 在生产上要更加注重病害的防治. 另外, 在冬小麦-夏大豆(夏玉米)轮作处理中显著富集了 *Penicillium* 和 *Zopfiella* (图 6). 有研究表明, *Penicillium* 是一种植物促生菌, 具有溶磷活性^[74], 还可以通过激活多种防御信号诱导作物对病原菌的抗性^[75]; 从猕猴桃植株中分离得到的内生真菌 *Zopfiella* 能够抑制引起猕猴桃溃疡病病原菌 *Pseudomonas syringae* 的生长^[76]. 以上分析表明, 在连续冬小麦-夏玉米轮作中加入夏大豆进行不同周期轮作, 可增加潜在有益真菌的相对丰度, 具有一定的优势.

有研究表明, 前茬作物的种植对后茬作物根际微生物群落具有显著影响^[77,78], Meta 分析结果显示, 轮作对后续作物产量的遗留效益可持续 2~3 a^[22]. 由此, 不同轮作茬口对土壤真菌群落的影响差异在下茬冬小麦生长期内的遗留效应值得进一步深入研究.

4 结论

(1) 在华北平原常年冬小麦-夏玉米周年轮作的基础上, 加入夏花生或夏大豆替代夏玉米进行不同周期轮作, 可增加土壤真菌群落丰富度和多样性, 显著影响土壤真菌群落结构.

(2) 不同轮作茬口土壤真菌群落组成存在差异显著的类群, *Neocosmospora*、*Plectosphaerella* 和 *Gibellulopsis* 等潜在病原菌在冬小麦-夏花生(夏玉米)轮作处理中显著富集, 而 *Penicillium* 和 *Zopfiella* 等潜在有益真菌在冬小麦-夏大豆(夏玉米)轮作处理中显著富集.

(3) 与连续冬小麦-夏玉米周年轮作相比, 轮作花生或大豆可增加病理营养型、病理-共生营养型和腐生-共生营养型土壤真菌的相对丰度.

(4) 不同作物轮作处理的土壤真菌群落丰富度和群落结构与土壤有机碳、无机氮、有效磷和速效钾含量显著相关.

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CONTENTS

Impacts of Changes in Meteorological Conditions During COVID-19 Lockdown on PM _{2.5} Concentrations over the Jing-Jin-Ji Region	QIU Yu-lu, CHEN Lei, ZHU Jia, <i>et al.</i> (2831)
Influence of COVID-19 Prevention and Control Measures on PM _{2.5} Concentration, Particle Size Distribution, Chemical Composition, and Source in Zhengzhou, China	 HUANG Bing-yi, WANG Shen-bo, HE Bing, <i>et al.</i> (2840)
Concentration Variation and Source Analysis of Metal Elements in PM _{2.5} During COVID-19 Control in Suzhou	MIAO Qing, YANG Qian, WU Ye-zheng, <i>et al.</i> (2851)
Changes in Carbonaceous Aerosol in the Northern Suburbs of Nanjing from 2015 to 2019	XIE Tian, CAO Fang, ZHANG Yan-lin, <i>et al.</i> (2858)
Source Apportionment of PM _{2.5} Based on Hybrid Chemical Transport and Receptor Model in Chongqing	PENG Chao, LI Zhen-liang, CAO Yun-qing, <i>et al.</i> (2867)
Analysis on the Characteristics of Oxidation Potential and Influence Sources of PM _{2.5} in Baoding City in Winter	WU Ji-yan, YANG Chi, ZAHNG Chun-yan, <i>et al.</i> (2878)
Pollution Characteristics and Sources of Water-soluble Organic Nitrogen in PM _{2.5} in Jiangbei New Area, Nanjing	GUAN Lu, DING Cheng, ZHANG Yu-xiu, <i>et al.</i> (2888)
Organic Aerosols and Source Analysis of Fine Particles in the Background of Shiwanda Mountain, Guangxi	XING Jia-li, CAO Fang, WANG Qian, <i>et al.</i> (2895)
Comparison of Regional Transportation and Transformation Models of Atmospheric Polycyclic Aromatic Hydrocarbons and Research on Key Influencing Factors: Take the Beijing-Tianjin-Hebei Region as Example	ZHANG Xin-lu, LIU Shi-jie, HAN Mei-li, <i>et al.</i> (2906)
Exploring Formation of Ozone in Typical Cities in Beijing-Tianjin-Hebei Region Using Process Analysis	TANG Ying-xiao, YAO Qing, CAI Zi-ying, <i>et al.</i> (2917)
Characteristics and Meteorological Factors of PM _{2.5} -O ₃ Compound Pollution in Tianjin	XIAO Zhi-mei, LI Yuan, KONG Jun, <i>et al.</i> (2928)
Spatio-temporal Characteristics of Air Quality and Influencing Factors in Shandong Province from 2016 to 2020	ZHOU Meng-ge, YANG Yi, SUN Yuan, <i>et al.</i> (2937)
Trend Changes in Ozone Pollution and Sensitivity Analysis of Ozone in Henan Province	YAN Yang-yang, YIN Sha-sha, HE Qin, <i>et al.</i> (2947)
Effects of Tropical Cyclones on Ozone Pollution in the Pearl River Delta in Autumn	ZHAO Wei, LÜ Meng-yao, LU Qing, <i>et al.</i> (2957)
Real-time Composition and Sources of VOCs in Summer in Wuhan	SU Wei-feng, KONG Shao-fei, ZHENG Huang, <i>et al.</i> (2966)
Pollution Characteristics and Source Apportionment of Atmospheric Volatile Organic Compounds in Summer in Yuncheng City	WEN Xiao-yu, ZHAO Wen-ting, LUO Shu-zhen, <i>et al.</i> (2979)
Neonicotinoid Insecticides Threaten Surface Waters at the National Scale in China	FAN Dan-dan, LIU Hong-ling, YANG Liu-yan (2987)
Spatiotemporal Distribution and Risk Assessment of Pharmaceuticals in Typical Drinking Water Sources in the Middle Reaches of the Yangtze River	 WU Jun-mei, WEI Lin, PENG Jing-qian, <i>et al.</i> (2996)
Pollution Characteristics and Risks of Polycyclic Aromatic Hydrocarbons in Underground and Surface Drinking Water Sources in Northeast Inner Mongolia	 ZHANG Kun-feng, CHANG Sheng, FU Qing, <i>et al.</i> (3005)
Impact of Land Use Types at Different Scales on Surface Water Environment Quality and Its Driving Mechanism	SONG Jing-wen, ZHANG Xue-xia, JIANG Dong-yang, <i>et al.</i> (3016)
Shallow Groundwater Around Plateau Lakes: Spatiotemporal Distribution of Nitrogen and Its Driving Factors	LI Gui-fang, YANG Heng, YE Yuan-hang, <i>et al.</i> (3027)
Distribution and Potential Ecological Risk Assessment of Heavy Metals in Sediments of Lake Qinghai	ZHANG Ya-ran, CHE Fei-fei, FU Zheng-hui, <i>et al.</i> (3037)
Analysis of Heavy Metal Pollution Characteristics and Potential Ecological Risks of Surface Sediments in Dongjiang Lake	ZHAO Xiao-liang, LI Xiang, LU Hong-bin, <i>et al.</i> (3048)
Kinetic Release Characteristics of Organic Phosphorus of Sediment-water and Water Quality Risks	LIU Zhe-zhe, NI Zhao-kui, LIU Si-ru, <i>et al.</i> (3058)
Distribution Characteristics, Source Analysis, and Pollution Evaluation of Organic Matter in Surface Sediments of Qingpu District, Yangtze River Delta Integration Demonstration Area	 ZHANG Zhi-bo, DUAN Yan-ping, TU Yao-jen, <i>et al.</i> (3066)
Distribution Characteristics of Microplastics and Their Migration Patterns in Xiangxi River Basin	CHEN Sheng-sheng, LI Wei-ming, ZHANG Kun, <i>et al.</i> (3077)
Community Structure and Microbial Function Responses of Biofilms Colonizing on Microplastics with Vertical Distribution in Urban Water	 CHEN Yu-fang, YAN Zhen-hua, ZHANG Yan, <i>et al.</i> (3088)
Community Structure of Phytoplankton and Environmental Impact Factors in Lake Hongze from 2015 to 2020	QU Ning, DENG Jian-ming, ZHANG Zhen, <i>et al.</i> (3097)
Structural Characteristics of Zooplankton and Phytoplankton Communities and Its Relationship with Environmental Factors in Different Regions of Nanhu Lake in Jiaxing City	 WANG Ya-wen, LI Ying-he, ZHANG Bo, <i>et al.</i> (3106)
Temporal and Spatial Variation Characteristics and Source Analysis of Agricultural Non-point Source Pollution Load in Guangdong During the Past 20 Years	 GE Xiao-jun, HUANG Bin, YUAN Zai-jian, <i>et al.</i> (3118)
Output Characteristics and Driving Mechanism of Agricultural Non-point Source (AGNPS) Pollutant in Plain and Valley Region of Upper Yangtze River, China	 TAN Shao-jun, LIU Yang, ZHU Xiao-jie, <i>et al.</i> (3128)
Risk Assessment Method of Non-point Source Pollution Output for Watershed Using High Resolution Data	GU Jing-jing, YE Yun-tao, DONG Jia-ping, <i>et al.</i> (3140)
Spectral Characteristics Change in Dissolved Organic Matter in Urban River Under the Influences of Different Intensities of Non-point Source Pollution	CHEN Xu-dong, GAO Liang-min (3149)
Combination of Ecological Ditch and Bioretention Pond to Control Rural Runoff Pollution	SHI Lei, YANG Xiao-li, WU Qing-yu, <i>et al.</i> (3160)
Influence of Different Hydraulic Disturbance Intensities on the Migration of Aged PSMPs Between Sediment and Water	WU Xiang-xiang, AI Ping, LI Da-peng (3168)
Analysis of Pollution Characteristics and Sources of Rainfall Runoff from Roofs in the Central District of Beijing	XI Yue, GUO Jing, TAO Lei, TIAN Ying, <i>et al.</i> (3177)
Inter-annual Changes in Runoff Quality from Green Roofs with Different Vegetation	ZHANG Sun-xun, ZHANG Shou-hong, GE De, <i>et al.</i> (3187)
Effectivity of Multiphase Fenton-like System of Iron Reduction Induced by Bisphenol A Authigenic Photoelectron	CAO Si-yu, XU Lu, FU Quan-chao, <i>et al.</i> (3195)
Removal Characteristics of Four Typical Antibiotics in Denitrification System	TANG Jia, CHEN Xi, QIN Mu-chuan, <i>et al.</i> (3204)
Adsorption Capacity and Mechanism of Biochar Derived from Typical Agricultural Wastes for Cadmium in Aqueous Solutions	GONG Pei-yun, SUN Li-juan, SONG Ke, <i>et al.</i> (3211)
Effect of Humic Acid-Heavy Metals on the Nitrogen Removal Performance of ANAMMOX Bacteria and Its Kinetic Analysis	LI Yun, CUI Nan, XIONG Xing-xing, <i>et al.</i> (3221)
Responding Mechanism of Vegetation Cover to Climate Change and Human Activities in Southwest China from 2000 to 2020	XU Yong, HUANG Wen-ting, DOU Shi-qing, <i>et al.</i> (3230)
Spatial Distribution and Eco-stoichiometric Characteristics of Soil Nutrient Elements Under Different Vegetation Types in the Yellow River Delta Wetland	 SUN De-bin, LI Yun-zhao, YU Jun-bao, <i>et al.</i> (3241)
Distribution Characteristics and Source Apportionment of Perfluoroalkyl Substances in Surface Soils of the Northeast Tibetan Plateau	 WEN Xiang-jie, CHEN Zhao-hui, XU Wei-xin, <i>et al.</i> (3253)
Effect of Land Use/Land Cover Change on the Concentration of Se and Heavy Metals in Soils from a "Return Cropland to Forest" Area, Southwest China	 LIU Yong-lin, LIU Shu-ling, WU Mei, <i>et al.</i> (3262)
Speciation Characteristics and Risk Assessment of Soil Heavy Metals from Puding Karst Critical Zone, Guizhou Province	 ZHANG Qian, HAH Gui-lin (3269)
Distribution Characteristics and Influencing Factors of Germanium in Soil in the Eastern Mountainous Area of the Nanyang Basin	DONG Qiu-yao, LAI Shu-ya, SONG Chao, <i>et al.</i> (3278)
Heavy Metal Pollution Characteristics and Risk Assessment of Golden Snub-nosed Monkey (<i>Rhinopithecus roxellana</i>) Habitat in Shennongjia Mountains	 YAN Jia-li, YU Zi-ling, YU Hui-liang, <i>et al.</i> (3288)
Utilization and Remediation of Heavily Cadmium-Contaminated Agricultural Soils by Two Crop Rotation Patterns After Lime and Sepiolite Passivation	 XU Lu, ZHOU Chun-hai, LIU Mei, <i>et al.</i> (3299)
Effects of Phosphorus Sufficiency and Deficiency on Cadmium Uptake and Transportation by Rice	TAN Wen-tao, HUO Yang, ZHOU Hang, <i>et al.</i> (3308)
Responses of Cd Accumulation in Rice and Spectral Characteristics of Soil Dissolved Organic Matter Regulated by Soil Amendments	LUO Hui-long, CHEN Juan, ZHANG Yun-hui, <i>et al.</i> (3315)
Responses of Soil Fungal Communities to Subalpine Meadow Degradation in Mount Wutai	LUO Zheng-ming, HE Lei, LIU Jin-xian, <i>et al.</i> (3328)
Response of Soil Fungal Communities in Diversified Rotations of Wheat and Different Crops	JIN Hai-yang, YUE Jun-qin, YAN Ya-qian, <i>et al.</i> (3338)
Spatial Characterization of Stable Isotope Composition of Organic Carbon from Farmland Soils in Chongqing	LIAO Yu-qin, LONG Juan, MU Zhi-jian, <i>et al.</i> (3348)
Characteristics of Soil NO Emissions in the Yangtze River Delta Region for Year 2018	LIAO Jia-qiang, XUE Jin, WANG Wen-jin, <i>et al.</i> (3357)
Thermal Environment Evolution and Response Mechanism of Urban Sprawl Based on Multi-source Data	LIANG Jian-she, BAI Yong-ping, YANG Xue-di, <i>et al.</i> (3365)