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复合菌群接种剂在热区农业可持续发展中的应用

杨腊英[1], 赵青云[2], 周登博[3], 郭立佳[1], 周游[1], 杨扬[1], 郭志凯[3], 汪军[1], 梁昌聪[1], 黄俊生[1*]

1. 中国热带农业科学院环境与植物保护研究所, 热带作物生物育种全国重点实验室, 农业农村部热带作物有害生物综合治理重点实验室, 国家肥料微生物种质资源库(海南), 海口 571101;
2. 中国热带农业科学院香料饮料研究所, 万宁 571533;
3. 中国热带农业科学院热带生物技术研究所, 海口 571101
* 联系人, E-mail: h888111@126.com

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摘要 高温多雨的天气导致热区农业面临着病虫害的多发与频发等诸多挑战. 目前, 木霉、芽孢杆菌和链霉菌等微生物已经被广泛应用于保障热带农业可持续发展和环境友好生产中, 且接种不同功能微生物的组合作为植物生长促进剂和生物防治剂具有更大的潜力. 本文综述常见的几类微生物及其制剂在热带农业可持续发展中的应用, 概述其功能微生物的作用机制, 包括重寄生、产生抗生素等直接作用机制, 以及竞争空间和营养物质、激活宿主植物防御能力和修饰根际微生物群等间接作用机制, 并展望未来复合菌群在农业生产应用中的研究方向和热点.

关键词 根际促生菌, 菌根菌, 木霉, 复合菌群, 可持续农业

随着世界人口增长, 人类面临的最大问题之一是如何满足日益增长的粮食需求[1,2]. 世界热带地区面积达5300多万平方千米, 涉及亚洲、大洋洲、非洲、拉丁美洲四大洲近100个国家和地区, 超10亿人口. 热带作物产业用占4%的全球土地总面积养活15%的全球人口, 然而高温多雨的天气导致热区农业面临着病虫害多发与频发等诸多挑战, 减少作物中病原微生物和害虫造成的损失是可持续农业必须解决的三个基本问题之一. 据估计, 害虫每年使全球农业生产力降低18%~25%[3], 而病原微生物直接造成10%~15%的损失[4]. 因此, 发展能够养活子孙后代的可持续农业系统需要制定尊重环境和健康的新生物战略[5].

微生物在农业系统中起着重要作用, 是土壤恢复力和可持续性的关键生物驱动力之一[6], 它们可通过直接养分供应、生产植物生长促生物质、提高植物对非生物胁迫的耐受性、直接作为生物农药应对生物胁迫的作用和诱导植物防御来提高农业生产力[7,8]. 改造植物和土壤微生物群对于促进农业中有益的共生关系至关重要. 外源微生物的应用直接改变农业系统中存在的土著有益微生物种群[9]. 农业中使用的主要生物接种剂包括植物促生菌(plant growth-promoting rhizobacteria, PGPR)等生物刺激剂, 以及苏云金芽孢杆菌

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(*Bacillus thutingiensis*)和木霉(*Trichoderma* spp.)等生物防治剂(biological control agents, BCA)[10]. 将具有互补特征的多个物种组装在一起形成合成微生物菌群，在过去十年中得到迅速发展[11]. 发展微生物复合菌群最常见的目标是利用单个微生物的能力和它们之间的相互作用来创造更高效的生态系统, 以提高其生产力, 并通过有效的代谢功能改善土壤健康[12]，同时对植物产生协同效应[13]. Li等人[14]通过荟萃分析2010~2020年应用微生物的相关文献，发现应用微生物接种剂后作物平均产量增加32%，而Liu等人[15]通过荟萃分析发现，与单一菌种接种相比，施用复合菌群生物肥料的估计效应值明显增加(平均增加48%).

本文综述木霉(*Trichoderma* spp.)、芽孢杆菌(*Bacillus* spp.)和链霉菌(*Streptomyces* spp.)等微生物及其产品在热带农业可持续发展中的应用，概述微生物促进植物生长的作用机制以及微生物复合菌群的直接与间接生防机制, 并分析利用微生物复合菌群的策略, 展望复合菌群在农业生产应用中的未来研究方向和热点.

1 不同功能微生物单独或联合接种在典型热带作物上的应用

1.1 菌根真菌生物接种剂

菌根真菌是广泛存在于土壤中的微生物，能与陆地上超过80%的植物物种(约20万种)根系形成互利互惠的共生关系，其作用主要是改善植物营养、提高植物抗逆性和抵御病虫害侵染的能力，菌根真菌的应用在可持续农业和生态系统中发挥着重要作用. 国外自1928年开始橡胶树菌根真菌的研究并在其对橡胶树生长与抗病性方面取得良好进展[16]，高秀兵与李增平[17]调查发现球囊霉属(*Glomus*)是海南橡胶树根际丛枝菌根真菌(arbuscular mycorrhiza, AM)分离频率最高属. 香蕉根系具有不同的AM种类[18~20]，且可促进组培香蕉苗生长[18]，同时菌根可增强香蕉苗的耐盐性[20]、诱导香蕉对线虫的抗性[21]、降低香蕉枯萎病发病率和病情指数[22]. 番木瓜AM种类多样[23,24]，具有促进作物生长与提高产量[25]，防控茎基腐烂病[26]与苗期病害[27]的作用. 在科特迪瓦的木薯田间试验中发现，*Rhizophagus*属真菌主导丛枝菌根真菌群落[28]，速效磷含量较低的木薯种植土壤中AM多样性较高[29].

1.2 农业中的木霉生物接种剂

在农业应用中, 木霉能够促进植物生长, 提高植物对非生物胁迫的耐受性，并作为生防制剂抵抗植物病原菌，是近几十年来最具农业可持续发展和科学潜力的微生物群之一[30,31]. 木霉对橡胶树胶孢炭疽病和橡胶树棒孢霉落叶病[32]、橡胶疫霉落叶病[33]、火龙果溃疡病[34,35]、芒果炭疽病[36]、芒果焦腐病[37]、木薯炭疽病[38]、咖啡炭疽病[39]、胡椒炭疽病[40]等叶部与果实病害病原菌以及香蕉枯萎病[41~43]、香草兰枯萎病[44]、胡椒疫霉根腐病[45]等土传病害病原菌均具有良好的生防活性，对峙培养抑菌率或离体接种实验或盆栽实验防效在42%~84%之间. 木霉能够提高香蕉苗的生长速率23.3%~25%[46,47]、提高香蕉产量8%[43]，并能提高芒果果实中营养物质含量7%[48].

1.3 植物促生菌PGPR与细菌生物接种剂BCA

对植物有益的细菌种类繁多，可用于提高作物生产力和土壤健康. 这些细菌可定殖在根际，也可内生或附生, 其中假单胞菌(*Pseudomonas* spp.)、芽孢杆菌(*Bacillus* spp.)、根瘤菌(*Rhizobium* spp.)、农杆菌(*Agrobacterium* spp.)、伯克霍尔德氏菌(*Burkholderia* spp.)、无色杆菌(*Achromobacter* spp.)、微球菌(*Micrococcus* spp.)、黄杆菌(*Flavobacterium* spp.)、欧文氏菌(*Erwinia* spp.)以及链霉菌等放线菌最为突出[49]. 科研工作者已开展芒果炭疽病菌[50~53]、芒果细菌性黑斑病[54,55]、橡胶树白粉病[56]、橡胶树炭疽病[57]、橡胶树白根病[58]、香蕉枯萎病菌[59~61]、香蕉炭疽病菌[62]、番木瓜炭疽病菌[63,64]、番木瓜枯萎病[65]、香草兰根(茎)腐病菌与疫病菌及细菌性软腐病菌[66]、木薯细菌性枯萎病菌[67,68]、胡椒根腐病[69]与枯萎病[70]、火龙果炭疽病[71,72]、莲雾软腐病菌[73]、剑麻斑马纹病菌[74]、咖啡叶锈病[75,76]等病原菌的生防细菌筛选与应用研究，对各种病害的室内或田间防控起到良好的应用效果，对峙培养的抑菌率在45%~100%之间, 盆栽或田间防控效果在38%~86%之间.

1.4 复合菌群生物接种剂

在自然界中，99%的微生物以复合菌群的形式存在，并被用于环境修复、食品工业和人类健康. 菌根真菌、木霉、内生真菌以及其他PGPR之间的联合应用已取得较好进展，详见相关综述文章[77~80]. 在典型

热带作物上，90%以上的复合微生物接种剂对作物生长具有较好的促进作用．AM菌与其他菌联合接种中，AMF与内生丝状真菌(*Mortierella* sp.)联合应用可显著促进油梨生长[81]；两种AMF与铜绿假单胞菌(*Pseudomonas aeruginosa*) 联合施用后显著提高对油棕茎基腐病的防治效果[82]；AMF和肠杆菌属(*Enterobacter* sp.)的泥炭生物制剂可降低橡胶幼苗白根病的发生并促进植株生长[83]，且共接种硅酸钙后的效果显著增强[84]; AM菌与假单胞菌(*Pseudomonas* sp.)或与哈茨木霉(*T. harzianum*)共同施用促进番木瓜植物生长，降低病害发生率[26,27]；AMF与褐球固氮菌(*Azotobacter chroococcum*)联合应用促进芒果幼苗生长[85]．在不同木霉联用或者与其他PGPB尤其是芽孢杆菌(*Bacillus* sp.)或假单孢杆菌(*Pseudomonas* sp.) 联合应用中, 绿色木霉(*T. viride*)和哈茨木霉(*T. harzianum*)的联用降低胡椒炭疽病的发病率，防控效果略高于两个菌株的单用效果[40]；哈茨木霉(*T. harzianum*)与假单孢杆菌(*Pseudomonas* sp.)的应用可促进胡椒苗生长[86]与降低胡椒茎基腐病发生率[87]、减少番木瓜根系寄生的根结线虫虫卵量[88]、促进香草兰植株生长[89]与降低由尖孢镰刀菌(*Fusarium oxysporum*), 立枯丝核菌 (*Rhizoctonia solani*)以及齐整小核菌(*Sclerotium rolfsii*)引起的病害发生率[90], 哈茨木霉(*T. harzianum*)与枯草芽孢杆菌(*B. subtilis*)共同接种可促进番木瓜植株生长[91]; 联合施用哈茨木霉(*T. harzianum*)、伯克霍尔德氏菌(*Burkholderia* sp.)、类芽孢杆菌(*Paenibacillus* sp.)以及解淀粉芽孢杆菌(*B. amyloliquefaciens*)或木霉、芽孢杆菌(*Bacillus* sp.)、假单胞菌(*Pseudomonas* sp.)以及链霉菌(*Streptomyces* sp.)可降低香蕉枯萎病发病率[92,93]; 联合施用深绿木霉(*T. atroviride*) 、芽孢杆菌(*Bacillus* sp.)和假单孢菌(*Pseudomonas* sp.)菌悬液使香蕉植株生物量的增加超过单一微生物菌剂应用效果，且对穿孔线虫(*Radopholus similis*)的防治效果超过60%[94]; 共同施用深绿木霉(*T. atroviride*)与两种假单孢菌(*Pseudomonas* sp.)后降低油梨根腐病发病率[95]; 接种绿色木霉(*T. viride*)与假单孢菌(*Pseudomonas* sp.)降低由尖孢镰刀菌香草兰专化型(*F.oxysporum* f. sp. *vanillae*)和香草兰刺盘孢(*Colletotrichum vanilla*)引起的香草兰植株病害发生率[96]; 接种棘胞木霉(*T. asperellum*)和蜡样芽孢杆菌(*B. cereus*)促进油棕苗生长[97]. 不同细菌的联合应用中, 施用芽孢杆菌(*Bacillus* sp.)与假单胞菌(*Pseudomonas* sp.)促进香蕉苗生长, 提升植株耐盐性[98].

2　微生物复合菌群的协同作用机制

早期的土壤微生物接种剂产品大多是基于单一种类和菌株的微生物接种剂. 随着深入研究发现, 单一微生物接种剂应用于复杂的环境条件可能不是最好的策略．由于土壤微生物群落的高度复杂性和土壤中定殖的生态位多样性，接种具有有益特性的相容微生物混合物更能促进微生物接种剂在土壤中定殖和增殖．这种具有冗余能力的多菌株菌群的发展越来越普遍，许多微生物接种剂包含两个或两个以上的属/种．通过有针对性地设计微生物群落，将具有不同功能的微生物(如促生和抗病微生物)联合起来，复合菌群内的微生物可以通过协同合作促进目标菌株的定殖和发挥作用[99],不同微生物之间的主要协同作用方式见图1．这些复合菌群具有多种互补功能(例如, 解磷菌与菌根真菌，拮抗微生物与抗性诱导剂等)，复合菌群如何相互填补并以协同方式来提高接种效率见表1.

2.1　促进植物生长的微生物复合菌群的作用机制

AMF、木霉、不同的PGPRs间相互共接种在促进不同作物生长、增加养分吸收和/或提高产量方面具有重要的协同效应(表2)，与其产生铁载体、磷酸盐溶解酶、植物生长促进酶(如1-氨基环丙烷-1-羧酸脱氨酶(ACC-deaminase))和植物激素(主要是吲哚乙酸IAA和细胞分裂素)直接相关．在许多研究中，已经可以确定微生物引起植物相关效应的作用机制，但在许多描述性研究中只报告协同作用.

(1) 促进植物对营养物质的吸收. N, P, K, Fe等营养元素在植物生长发育过程中发挥着重要作用，而金属微量元素(Fe, Mn, Cu, Zn, Mo和Ni)与土壤微生物群丰度、多样性和功能亦密切相关[100], 不同微生物菌剂的联合应用具有活化植物所需矿质营养元素的作用．AMF与*Mortierella* sp.共同接种油梨树根系后，可以促进P溶解并增加P的供应，进而促进植物生长，增加植物组织中的营养成分[81]. 木霉-假单胞菌相互作用促进植物对N和P的吸收利用，胡椒或香草兰植株生物量显著高于接种单一微生物菌剂[86,89]．在油棕上联合接种木霉与蜡样芽孢杆菌后，通过产生铁载体及提高P的生物有效性促进植株生长[97].

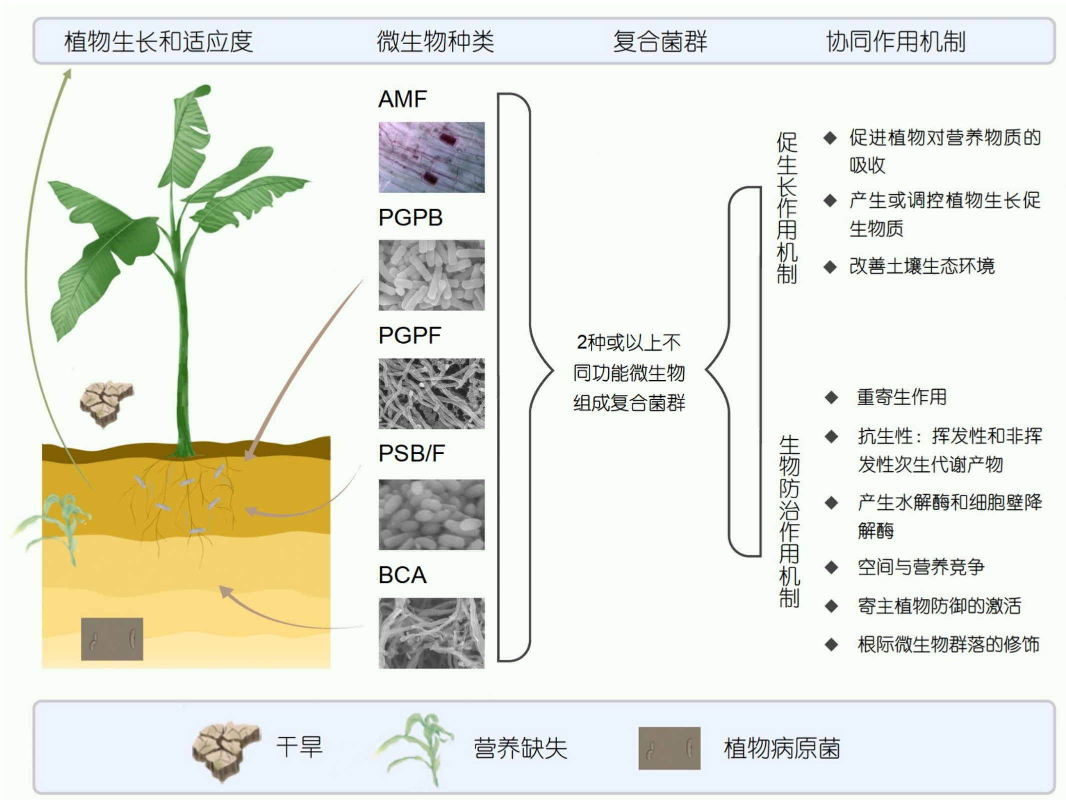

图 1 复合微生物菌群协同作用机制. 不同功能微生物菌群对作物生长发育都会产生影响，主要包括促生长与生物防治两个方面; 其协同作用机制也体现为不同的方式. 图中AMF为丛枝菌根菌, PGPB为植物促生细菌, PGPF为植物促生真菌, PSB/F为溶磷细菌或真菌, BCA为生物防治剂

Figure 1 Synergistic mechanisms of microbial consortium. Different functional microbial consortia have an impact on crop growth and development, including growth promotion and biological control, and their synergistic mechanisms are also manifested in different ways. AMF, arbuscular mycorrhizal fungi; PGPB, plant growth-promoting bacteria, PGPF, plant growth-promoting fungi, PSB/F; phosphate-solubilizing bacteria or fungi; BCA, biological control agent

(2) 产生或调控植物生长促生物质. 在提供营养物质的同时, 微生物作为PGP的主要作用机制之一是产生促生长类化合物，如激素吲哚乙酸IAA. 木霉和芽孢杆菌细胞悬浮液的共接种因IAA产量的协同增加, 导致这两种微生物在油棕作物中促生长能力的协同增加[97].

(3) 改善土壤生态环境. 土壤微生物不仅参与养分循环和有机质转化，还通过多种生物化学和生物物理机制改变土壤生境；这种微生物介导的土壤性质的改变又可以对微生物组的组装产生局部影响，具有明显的生态后果[101]. Li等人[102]研究发现, 土壤酸化引起的土壤微生物组的变化和特定微生物过程的破坏可能对植物健康起关键作用. 而微生物接种剂不仅能够活化土壤中的养分，还可以在一定程度上改善土壤物理性质，改变相关土壤酶活性，创造有利于作物生长的土壤生态环境. 如Li等人[103]研究发现，适当施用生物有机肥配施化肥改善土壤性质, 重塑细菌和真菌生态, 从而提高香蕉的产量和品质. Zheng等人[104]研究发现联合施用不同PGP以及番茄青枯病无毒病原菌菌株，可显著性提高土壤脲酶活性，且冗余分析发现根际土壤的pH、有机碳含量等理化参数与番茄青枯病的发病率(disease incidence, DI)或种群呈负相关.

2.2 作为生防制剂的微生物复合菌群的直接与间接作用机制

近年来，木霉菌、芽孢杆菌、假单孢杆菌等不同生防制剂的组合使用越来越受到人们的关注，其在协同防控典型热带作物农业病虫害中已有较多研究报道(表2). 尽管迄今为止开展的许多研究描述协同作用(既

表 1　微生物主要功能特征以及复合菌群的优缺点

Table 1　The main functional characteristics of microorganisms, and advantages and disadvantages of bacterial consortia

特征	复合菌群优势	复合菌群缺点
不需要特异性(例如, 与植物或其他土壤生物的关系)	可以在土壤中自我维持, 而不需要特定的植物或微生物来定殖	复合菌群可以单独在土壤中生存, 因此具有更强存活力, 很难将其从土壤中移除
抗(耐)生物与非生物因子的胁迫能力	复合菌群对其耐受性产生潜在的协同或相加作用	在压力和极端条件下, 可能会表现出对抗性
植物生长的促进	联合作用可能比单独作用时诱导更高的植物生产力	也可能诱导非作物植物种类的生长
难分解碳向易分解碳的转化	整个菌群能够利用不可利用的碳作为能量来源, 尤其复合菌群中包含腐生真菌时优势更明显, 同时也使其能够被其他土壤生物利用	不同微生物对可利用碳的竞争可能发生在特定的胁迫条件下
土壤理化性质的改善	改善土壤的理化参数, 提高养分和金属元素的有效性	与接菌前相比, 可能降低接菌点微生物组的变异性
促进其他土壤生物的生存力和/或恢复力(生态促进)	在土壤和植物水平上都具有潜在的叠加和或协同效应	可能允许其他细菌(如致病细菌)的移动和存活, 以及它们在田间的潜在传播

有直接的也有间接的)所涉及的作用机制, 但在一些有趣的描述性研究中, 这些机制是未知的.

(1) 重寄生作用.　重寄生作用是木霉菌最具特征的行为. 细菌的存在可以协同增加木霉的寄生活性, 在体外, 由于木霉对真菌寄生的增加, 绿色木霉和荧光假单胞菌的共接种协同降低卵菌致病疫霉(*Phytophthora infestans*)的菌丝生长[105].

(2) 抗生性: 挥发性和非挥发性次生代谢产物. 木霉、芽孢杆菌等BCAs可产生丰富多样的挥发性和非挥发性次生代谢产物, 这些次生代谢产物对植物病原菌具有高效的抑菌作用. 而不同BCAs的共培养发酵协同提高对不同农业病原菌具有生物杀菌作用的非挥发性次级代谢产物种类及产量[106~109]. 例如, 由于代谢产物Koninginin A和mevastatin的协同产生, 木霉-枯草芽孢杆菌共培养的发酵滤液使真菌禾谷镰孢菌的体外生长降低54%[110].

(3) 产生水解酶和细胞壁降解酶. 木霉等BCAs具有很强的产胞外水解酶能力, 能够有针对性地降解不同植物病原菌的细胞壁. 哈茨木霉与荧光假单孢杆菌共接种后, 协同产生β-1,3-葡聚糖酶、β-1,4-葡聚糖酶和脂肪酶裂解酶, 从而降低胡椒茎基腐病的发生率[87]; 绿色木霉与荧光假单孢杆菌共接种后, 协同产生β-1,3-葡聚糖酶与蛋白酶, 从而降低香草兰主要病害发生率[96].

(4) 空间与营养竞争. BCAs的另外一个直接作用机制是对空间和营养物质的竞争, 微生物能够在新的生态位中成功定殖于根际和浅根组织[111]. AMF与肠杆菌共接种橡胶根系后, 因增加AMF孢子密度和AMF的根系定殖率而促进橡胶苗生长[83]; 哈茨木霉-荧光假单胞菌组合施用后由于增强木霉在番木瓜根系的定殖从而对抗南方根结线虫(*Meloidogyne incognita*)[88];从香蕉植物根际分离的木霉、芽孢杆菌、假单胞菌和链霉菌微生物组合在一起施用后, 减少香蕉枯萎病发病率[93], 在这些组合中, 由绿色木霉、绿针假单胞菌和贝莱斯芽孢杆菌组成的联盟是最有效的, 结合对空间、营养物质和抗生素化合物的竞争.

(5) 寄主植物防御的激活. BCAs对农业害虫和病原菌的主要间接作用机制是植物防御的局部和系统激活, 是由微生物-植物分子对话引起植物对微生物相关分子模式的识别, 并激活植物对潜在生物胁迫的防御[112]. 例如, 绿色木霉和哈茨木霉的联合接种可提高超氧化物歧化酶(superoxide dismutase, SOD)的活性来降低胡椒炭疽病的发生[40]; 木霉-AM菌共接种提高不同防御酶的活性, 如多酚氧化酶(polyphenol oxidase, PPO)、过氧化物酶(peroxidase, POD)和SOD[113], 促进番木瓜植株内植物防御酚类化合物积累[91].

(6) 根际微生物群落的修饰. BCAs另一个重要的间接作用机制是改变/调控根际微生物区系, 根际微生物群落能够为植物抵抗病原微生物侵染提供前线防御[114~116]. 外源接种功能微生物可重塑土壤微生物菌群, 促使植株健康, 提升产量和品质[117]. 同时土壤微生物组的变化可用于预测植物生长对微生物接种反应的变化[118]. 目前报道较多的木霉-细菌组合的良好协

表 2 不同功能微生物共接种对典型热带作物生长和病虫害防控的影响

Table 2 The effects of co-inoculation of different functional microorganisms on growth and pest control of typical tropical crops

微生物种类	作物	协同效应	作用机制	参考文献
聚生球囊霉(*Glomus Fasciculatum*), 被孢霉属(*Mortierella* sp.)	油梨	促进植物生长; 增加植物组织中的营养成分	P溶解作用与P供应增加	[81]
根内球囊霉(*G. intraradices*), 明球囊霉(*G. clarum*), 铜绿假单胞菌(*Pseudomonas aeruginosa*)	油棕	降低苗圃和田间的油棕茎基腐病的发生率	未鉴定	[82]
摩西球囊霉(*G. mosseae*), 肠杆菌属(*Enterobacter* sp.)	橡胶	促进植物生长; 显著增加根和地上部硅含量以及叶片营养元素(N, P, K, Ca)含量	AMF孢子密度和根系定殖率均提高	[83]
摩西球囊霉(*G. mosseae*), (*Trichoderma harzianum*)	番木瓜	改善植株生长, 降低根腐病病害严重程度	未鉴定	[26]
摩西根内球囊霉(*G. intraradices*), 摩西球囊霉(*G. mosseae*), 幼套球囊霉(*G. etunicatum*), 微白巨孢囊霉(*Gigaspora albida*), 假单胞菌(*Pseudomonas* sp.)	番木瓜	促进植物生长, 降低*Fusarium oxysporum*引起的苗期病害的发生率	未鉴定	[27]
聚生球囊霉(*G. fasciculatum*), 褐球固氮菌(*Azotobacter chroococcum*)	芒果	促进芒果幼苗的生长.	未鉴定	[85]
绿色木霉(*T. viride*), 哈茨木霉(*T. harzianum*)	胡椒	降低胡椒炭疽病的发生	提高叶绿素含量, 降低H_2O_2含量, 显著性增加SOD酶活性	[40]
哈茨木霉(*T. harzianum*), 荧光假单胞菌(*P. fluorescens*)	胡椒	促进植物生长 降低胡椒茎基腐病的发生率	N和P的养分吸收较高 合成β-1,3-葡聚糖酶, β-1,4-葡聚糖酶和脂肪酶裂解酶	[86] [87]
哈茨木霉(*T. harzianum*), 荧光假单胞菌(*P. fluorescens*)	番木瓜	根结线虫卵量减少	空间竞争: 根系的定殖	[88]
哈茨木霉(*T. harzianum*), 荧光假单胞菌(*P. fluorescens*)	香草兰	促进植物生长 降低由*Fusarium oxysporum*, *Rhizoctonia solani* 和 *Sclerotium rolfsii*引起的病害发生率	N和P的养分吸收较高 未鉴定	[89] [90]
哈茨木霉(*T. harzianum*), 枯草芽孢杆菌(*B. subtilis*)	番木瓜	促进植物生长	酚类化合物的积累	[91]
哈茨木霉(*T. harzianum*), 洋葱伯克霍尔德氏菌(*Burkholderia cepacia*), 土地类芽孢杆菌(*Paenibacillus terrae*), 解淀粉芽孢杆菌(*B. amyloliquefaciens*)	香蕉	降低枯萎病发生率	未鉴定	[92]
木霉菌(*Trichoderma* sp.), 芽孢杆菌(*Bacillus* sp.), 假单孢菌(*Pseudomonas* sp.), 链霉菌(*Streptomyces* sp.)	香蕉	降低枯萎病发生率	空间与营养物质的竞争	[93]
深绿木霉(*T. atroviride*), 芽孢杆菌(*Bacillus* sp.), (*Pseudomonas* sp.)	香蕉	促进植物生长, 降低穿孔线虫的种群密度和根系穿透能力	未鉴定	[94]
深绿木霉(*T. atroviride*), 绿针假单胞菌(*P. chlororaphis*), 类产碱假单胞菌(*P. pseudoalcaligenes*)	油梨	降低油梨根腐病病害发生率	未鉴定	[95]
绿色木霉(*T. viride*), 荧光假单孢菌(*P. fluorescens*)	香草兰	降低由*F. oxysporum* f. sp. *vanillae* and *Colletotrichum vanilla*引起的病害发生率	合成β-1,3-葡聚糖酶、蛋白酶	[96]
棘孢木霉(*T. asperellum*), 蜡样芽孢杆菌(*B. cereus*)	油棕	促进植物生长	产铁载体、P供磷以及产吲哚乙酸	[97]
芽孢杆菌(*Bacillus* sp.), 假单胞菌(*Pseudomonas* sp.)	香蕉	促进香蕉苗生长及提高植株耐盐性	启动WRKY转录因子介导的对非生物和生物胁迫的保护	[98]

同效果, 如哈茨木霉-枯草芽孢杆菌联合施用后, 根际有益细菌和有益真菌多样性和丰度都有所增加, 并且对豆类根腐病[119]或马铃薯苍痂病[120]等病原菌具有很强的拮抗能力.

虽然多项研究在菌根菌、木霉、PGPR菌等共接种的生物防治效果方面取得积极的结果, 但所涉及的

分子机制报道尚少, Kaleh等人[98]研究发现, 芽孢杆菌与假单孢菌共同接种后, 启动WRKY转录因子介导的对非生物和生物胁迫的保护, 从而促进香蕉苗生长及提高植物耐盐性. 在未来研究中, 加深研究者对微生物如何调节与生物防治相关的基因表达的理解将是有趣的, 如水解酶产生基因、抗菌肽基因和铁载体产生基因.

3　利用微生物复合菌群的策略和未来研究展望

接种不同微生物复合菌系对植物的促生作用可能大于其各组分的促生作用之和, 如果研究和开发得当, 可能会产生协同增效效应, 亦有相关研究说明不同菌之间的联合应用不一定产生协同作用, 例如, Castillo等人[121]研究发现, 哈兹木霉和球囊菌联合施用对枯萎病有显著的抑制作用, 但不具有协同作用; 同时发现当两种生物防治剂同时施用于香蕉根部时, 可能存在竞争效应. 另Ramírez-Cari˜no等人[122]甚至发现木霉与芽孢杆菌组合对番茄植株中尖孢镰刀菌的抑制效果不如单独接种. 因此, 若要不同功能菌株联合应用后产生协同效应, 需要考虑多种因素: (ⅰ) 潜在形成生物菌剂的候选微生物兼容性, 需要针对每种情况单独进行研究. 一些具有抗真菌能力的细菌, 如一些芽孢杆菌属和假单胞菌属, 可对真菌产生拮抗作用, 而这两类微生物其生物膜的形成是成功的关键因素. (ⅱ) 另一个重要影响因素是生物菌剂配方, 不同配方体现的协同效果可能不一样, 例如, 在以滑石粉为载体、羧基甲基纤维素为黏合剂的配方中, 只有木霉协同产生促生长化合物[123], 而在用阿拉伯胶包被的细胞中, 豆瘤根瘤菌除协同增加细菌根瘤形成外, 还协同产生促生长物质[124]. 因此, 开发的技术和配方都必须确保微生物的细胞和容量在可接受的时间内存活, 并且细胞浓度高、无污染和易于在农业中应用. (iii) Laabas等人[125]研究显示在田间自然情况下共接种固氮菌与根际促生菌对鹰嘴豆的生长与结瘤模式无促进作用, 强调土壤条件在决定接种成功方面的重要性; Kavoo-Mwangi等人[47]通过接种不同微生物接种剂对3种香蕉组培苗存活率与生长的影响, 发现以微生物为基础的商业接种剂的效果取决于土壤类型和植物发育阶段; 不同土壤类型、不同品种及其不同发育阶段的棉花根际微生物群落结构存在动态变化[126]; 根际微生物接种剂对植物生长的促进作用受土壤营养条件的影响, 细菌接种的有益效果在营养缺乏的土壤中比在营养丰富的土壤中最佳[127]; Zhou等人[128]研究单作和轮作对花生根际微生物群抑制根腐病能力的影响, 结果发现与轮作相比, 单作导致微生物群落对根腐病的抑制效果较差, 且是由单作导致的关键根际分类群的枯竭而引起; 在豆科-谷类间作系统中, 生物接种剂可作为提高作物耐旱性和磷缺乏性的手段[129]; 气候变化改变土壤细菌的生态策略[130], 导致土壤有机碳微生物矿化增加[131], 更多关于气候变化对不同气候敏感土壤生态系统中土壤微生物影响详见文献综述[132]. 因此, 使用过程中除考虑微生物复合菌群及其需要的配套相应技术外, 还需综合考虑作物种类、土壤类型、田间管理措施以及气候环境等因素(图2).

针对有益微生物联合应用的对象、作用机制以及与其他化学制剂协同应用方面仍存在一定差距, 今后将需拓宽以下3个方面的相关研究: (ⅰ) 不同有益微生物联合应用的研究主要集中在农业病害的防治上, 对害虫的防治研究较少, 对病毒的防治研究更少, 目前报道的有利用微生物组来调节植物对棉花卷曲病的抗

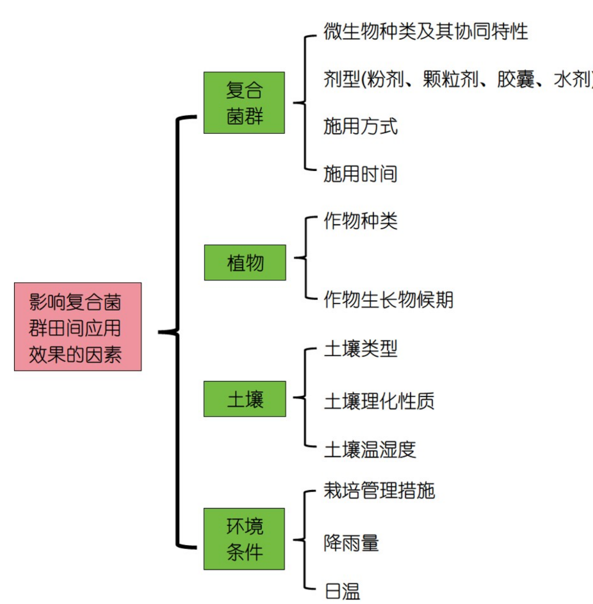

图 2　影响复合菌群田间应用效果的因素分析. 微生物、植物、土壤, 以及气候环境为影响复合菌群田间应用效果的主要因素

Figure 2　Factors influencing the effects of microbial consortium inoculants in field application. The main factors include microorganisms, plants, soil, and climatic environment

性[133]. 此外, 关于共接种微生物对植物非生物胁迫耐受性的影响研究亦较少. 因此, 需要针对这些具体方面进行更多的研究. (ii) 虽然微生物对植物生长促进和生物防治机制是已知的, 但触发两者协同作用的机制往往是未知的. 在未来研究中应确定这些机制, 以开发更高效稳定的BCA制剂. (iii) 在目前的农业背景下, 需要限制化学农药的使用, 同时将病虫害水平维持在经济损失阈值以下, 部分研究表明新型替代品与当前化学农药共接种获得相似的疾病减少值. 开展这类微生物与化学农药联合使用可能会产生进一步的协同增效作用, 增强其有效性. (iv) 需要用跨学科的方法来了解有益土壤微生物组的组成、动态和部署, 从而为通过接种外源微生物菌群来恢复和保护健康的土壤生态系统来推动减轻或扭转环境损害.

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Applications of microbial consortium inoculants in the sustainable development of tropical agriculture

YANG LaYing[1], ZHAO QingYun[2], ZHOU DengBo[3], GUO LiJia[1], ZHOU You[1], YANG Yang[1], GUO ZhiKai[3], WANG Jun[1], LIANG ChangCong[1] & HUANG JunSheng[1]

1 National Key Laboratory for Tropical Crop Breeding, Key Laboratory of Integrated Pest Management on Tropical Crops, Ministry of Agriculture and Rural Affairs, National Collection of Microbial Resource for Fertilizer (Hainan), Environment and Plant Protection Institute, Chinese Academy of Tropical Agricultural Sciences, Haikou 571101, China;
2 Spice and Beverage Research Institute, Chinese Academy of Tropical Agricultural Sciences, Wanning 571533, China;
3 Institute of Tropical Bioscience and Biotechnology, Chinese Academy of Tropical Agricultural Sciences, Haikou 571101, China

High temperature and rainy weather bring many challenges such as frequent occurrences of pests and diseases to tropical agriculture. At present, microorganisms such as *Trichoderma*, *Bacillus* and *Streptomyces* have been widely used to ensure sustainable and environmentally friendly production of tropical agriculture, and the combination of different functional microorganisms has greater potential as plant growth promoters and biological control agents. In this paper, the application of several types of common microorganisms and their products in the development of tropical sustainable agriculture was reviewed. The mechanisms of functional microorganisms were summarized, including direct mechanisms such as hyperparasitism and antibiotic production, and indirect mechanisms such as competition for space and nutrients, activation of host plant defense ability and modification of rhizosphere microflora. The future research directions and hotspots of microorganism consortia in agricultural production and applications were prospected.

plant growth-promoting rhizobacteria, Mycorrhiza, *Trichoderma* spp., consortium, sustainable agriculture

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