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微生物组学对植物病害微生物防治研究的启示

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摘要：植物病害的微生物防治研究主要集中在植物、病原菌和生防菌三者的互作关系上，相对忽视了植物微生物组/群的作用。越来越多的研究表明，植物内生微生物、根围土壤微生物和叶围微生物均不同程度地参与了植物防病的机制。为了更好地了解相关进展，本文选择部分代表性研究，详述了植物微生物组/群的构成，并结合案例介绍了植物微生物组/群对寄主植物的防/致病作用、对植物病原菌致病性的影响，以及施用生防菌对植物微生物组/群的影响。微生物组学的发展为生防机制领域提出了新的研究思路，有利于发现更加科学的防治手段。

关键词：微生物组，植物病害，微生物防治

利用微生物生防菌(biological control agents, BCAs)，例如木霉(*Trichoderma* spp.)[1–2]、盾壳霉(*Coniothyrium* spp.)[3]和芽孢杆菌(*Bacillus* spp.)[4]等，可防治由细菌、真菌和线虫引起的作物病害。关于微生物生防机制的研究集中在：(1) 二元互作(binary interaction)，如植物和病原菌[5]、植物和生防菌[6]以及生防菌和病原菌[7]之间的互作关系；(2) 三元互作(ternary interaction)，如生防菌诱导植物抗性拮抗病原菌[8]的关系。随着对微生物生防菌防病机制越来越深入的了解，

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以及对其发酵工艺和菌剂研制的不断改进，很多菌剂登记成为活体微生物农药[9]。目前微生物菌剂的研发偏重于前期在实验室条件下对生防菌株的筛选和优化，对于菌剂在田间使用后受到影响的研究相对匮乏。我们在研究中发现，一些在实验室条件下筛选得到的高效生防菌，在田间使用后其防治效果并不稳定，受环境影响较大，经常出现定殖数量降低、防病效果明显减弱等情况。越来越多的研究表明，植物内生微生物、根围土壤微生物和叶围微生物均不同程度地参与了植物、生防菌和病原菌间的互作。随着植物微生物组学的逐步发展，为我们揭示了更为复杂的生防关系网络，这些成果为植物病害的微生物防治研究打开了新思路。

1 植物微生物组/群的构成

植物微生物组/群由根围微生物(rhizosphere microbe)、内生微生物(endophytes)和叶围微生物(phyllosphere microbe)构成。不同区域的微生物群体经由植物本体进行物质和能量交流，与植物共同组成有机整体。植物微生物组/群的构成复杂，其种群多样性、偏好性和丰度受寄主植物和环境的双重影响，是植物与土壤、大气交互作用的媒介。

1.1 根围微生物群落

根围微生物组被认为是植物的“第二基因组”(secondary genome)，为植物提供由微生物衍生的(microbe-derived)化合物以及相应的特性[10–12]。研究估算，在根围约有 10^6–10^9 cells/cm^2 的微生物群落定殖[13]。根围微生物因土壤类型或植物类型的不同，其组成结构具有显著的差异[11]。根围微生物群落的形成由土壤理化性质、植物根系分泌物、植物内生菌[14]和植物激素[15]等因素共同影响并演替而来[11]。另外，在植物种子传播期，由种子携带的、来自母本植物的微生物群落也参与了新生植物土壤环境中的微生物组成多样性[16]。

1.2 植物内生微生物群落

植物内生微生物包括真菌和细菌，其中对内生真菌及其代谢产物的研究较为丰富。从各类作物[17–22]、木本植物、苔藓[23]、蕨类植物[24]和地衣[24]中分离的内生真菌主要包括链格孢属(*Alternaria* spp.)、刺盘孢属(*Colletotrichum* spp.)、镰刀菌属(*Fusarium* spp.)、赤霉菌属(*Gibberella* spp.)、小丛壳菌属(*Glomerella* spp.)、球座菌属(*Guignardia* spp.)、小光壳属(*Leptosphaerulina* spp.)、黑孢属(*Nigrospora* spp.)、茎点霉属(*Phoma* spp.)、拟茎点霉属(*Phomopsis* spp.)和炭角菌属(*Xylaria* spp.)等[25]。内生细菌主要分离自农作物[26–28]，种类涵盖变形菌门(Proteobacteria，占 90%)、放线菌门(Actinobacteria)、浮霉菌门(Planctomycetes)、疣微菌门(Verrucomicrobia)和酸杆菌门(Acidobacteria)[29]等 5 个门。植物内生微生物的多样性主要受寄主植物种类的影响，另外，植物生长地域的温度变化特征[30–33]、土壤重金属等环境因素对植物内生微生物多样性及丰度也具有影响[25]。

1.3 叶围微生物群落

叶围指植物体表能够栖息微生物的所有区域，包括茎表面(caulosphere)、花表面(anthosphere)、果实表面(carposphere)和叶表面(phylloplane)，全球的叶围面积估算约 10^9 km^2，其上定殖有数百种微生物种类[34–36]，其中大部分为细菌[37]。不同植物间的叶围微生物群落组成差异性很大，并易受到群落生态和大气环境因子的影响[38–41]。在自然条件下，季节性作物的叶围微生物群落组成具有时间动态变化规律和演替的特征[42]。叶围微生物被

认为是植物与大气环境交互响应的媒介[43–44]，对揭示植物与环境因子间的响应机制十分重要。然而针对叶围微生物群落结构及演替特征的研究正处于初期阶段，其作用被普遍忽视。目前在防治叶部病害时，一些菌剂在田间的防治效果较差，对于叶际微生物基础研究的欠缺可能是菌剂防效差的重要原因。

2 植物微生物组/群对寄主植物的防/致病作用

植物微生物组/群主要通过下列途径对寄主植物产生防病作用：(1) 促进植物对营养的吸收及直接促生作用；(2) 转化环境中的营养物质，增加植物生长所需营养；(3) 提高植物耐受(非)生物胁迫的能力；(4) 诱导植物对病原微生物的系统抗性；(5) 与病原微生物互作调节植物的抗病性等[13]。对寄主植物具有防病促生作用的微生物有木霉属(*Trichoderma* spp.)、球囊霉属(*Glomus* spp.)等。根围土壤中的木霉比如哈茨木霉(*T. harzianum*)、绿木霉(*T. virens*)等可引起寄主植物的系统抗病性，其作用机制是研究热点。Sarrocco 等人研究发现绿木霉 I10 中的 2 个多聚半乳糖醛酸内切酶基因 *tvpg1* 和 *tvpg2* 的表达引起了番茄的对灰霉菌(*Botrytis cinerea*)的诱导性系统抗性(induced system resistance，ISR)作用[45]；Alkooranee 等人报道哈茨木霉 TH12 通过调节水杨酸(salicylic acid，SA)信号途径，引起了油菜对核盘菌(*Sclerotinia sclerotiorum*)的 ISR 作用，其培养滤液则引起油菜的系统获得性抗性(systemic acquired resistance，SAR)[46]。另外，根围植物促生菌(plant growth-promoting rhizobactria，PGPR)和丛枝菌根真菌(arbuscular mycorrhizal fungi，AMFs)对寄主植物具有促生作用，其中 PGPR 主要通过固氮、解磷、解钾和矿化有机质等途径增加植物可利用养分和分泌植物生长激素的途径直接促进植物生长，AMFs 主要通过促进植物对磷的吸收及扩大根系吸收表面积等途径产生促生作用[47]。PGPR 和 AMFs 具有协同作用关系[48]，促进植物的生长发育，间接提高了植物对病害的抑制能力[47]。除此之外，植物微生物组/群中还存在致病微生物，例如青霉菌(*Penicillium* spp.)、附球霉属(*Epicoccum* spp.)等，和对植物无防/致病作用的微生物，包括毛壳菌属(*Chaetomium* spp.)、匍柄霉属(*Stemphylium* spp.)，目前对这 2 类植物微生物的关注相对较少[49]。反之，寄主植物的生长发育也可影响微生物群落的形成，如寄主植物通过其挥发性有机物(volatile organic compound，VOC)的抑菌作用或作为碳源的补给作用，影响叶围微生物群落的形成和定殖水平。反之，定殖的叶围微生物群还可影响植物生理特性并调整植物生化途径，进而影响 VOCs 的组成[42]。

3 植物微生物组/群对植物病原微生物致病性的影响

植物微生物组/群可通过重寄生、分泌抗生物质或空间营养竞争等作用直接拮抗病原微生物，还可通过诱导植物抗性或 BCAs 活性间接抑制病原微生物的致病性。Busby 等人以日本虎杖(*Fallopia japonica*)和美洲辽杨(*Populus trichocarpa*)为研究对象，首次系统揭示了植物内生真菌与病原微生物之间的互作关系[49]。研究表明，木霉属(*Trichoderma* spp.)、短梗霉属(*Aureobasidium* spp.)、镰刀菌属(*Fusarium* spp.)、青霉属(*Penicillium* spp.)、毛壳菌属(*Chaetomium* spp.)、生赤壳属(*Bionectria* spp.)、

毕赤酵母属(*Pichia* spp.)和假丝酵母(*Candida* spp.)是这 2 种植物内生菌中主要的致病微生物拮抗菌。其中木霉是常见的生防菌，对灰霉菌、核盘菌、丝核菌(*Rhizoctonia solani*)等多种病原菌具有拮抗作用[7,50–51]，而镰刀菌的拮抗作用以前并不被人熟知，该研究扩展了对生防菌范围的认知。值得注意的是，植物内生微生物对不同病原菌的作用方式不同，例如，对于 *F. japonica* 叶锈病的病原菌 *Puccinia polygoni-amphibii* var. *torvariae*，其内生微生物中既存在协同病原菌如拟茎点霉菌(*Phomopsis* spp.)，也存在病原菌拮抗菌如链格孢菌(*Alternaria* spp.)和茎点霉菌(*Phoma* spp.)，还存在无协同/拮抗作用的炭疽菌(*Collectotrichum* spp.)和拟盘多毛孢菌(*Pestalotiopsos* spp.)[49]。另外，在不同的植物和环境中，不宜简单地将一种植物内生微生物界定为病原菌拮抗菌或协同病原菌，例如镰刀菌和青霉菌，其生态角色兼具病原菌拮抗菌、病原菌协助菌以及自身即是病原菌 3 种[52–53]。即使同一种拮抗菌对不同的病原菌的拮抗作用也具有差异，如深绿木霉(*T. atroviride*)对丝核菌、核盘菌和腐霉菌(*Pythium ultimum*)的拮抗作用呈现不同的特征[54]。

4 施用 BCAs 对植物微生物组/群的影响

BCAs 通常来源于自然生境，经筛选并通过原生质体融合等技术增强其综合防病效果。根据农业生产需要，BCAs 的施用目标和区域往往与其来源地的植被及土壤生态差异很大。研究表明施用 BCAs 对土著植物微生物组/群的构成具有影响作用。例如，绿色木霉(*T. viride*) GB7 和沙雷氏菌(*Serratia plymuthica*)同时接种后 2–4 周显著改变了生菜根围微生物群结构，提高了物种均匀度(species evenness)[55]；同时喷施解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*) FZB42、哈茨木霉 T22 和球孢白僵菌(*Beauveria bassiana*) ATCC74040 一个月后，草莓的叶围微生物中真菌的构成和多样性受到影响，而其细菌多样性并未见明显差异[56]。在 BCAs 影响植物微生物组/群的研究中，对根围微生物组/群的报道显著多于叶围微生物。不过也有研究者认为 BCAs 不是植物微生物组/群的主要影响因素，例如施用假单胞菌(*Pseudomonas. jessenii*)后，生菜根围细菌群落的扩增子测序结果出现显著差异，但这种差异仅发生在冲积土壤，而未出现在沙地和黄土中[57]。还有一些报道讨论了 BCAs 施用后微生物组/群的自我调节作用，即 BCAs 对植物微生物的影响是较为短暂的，在停施后一段时间可基本恢复至未处理的微生物群落结构[58–62]。由于寄主植物和环境因子的复杂性，BCAs 对植物微生物组/群的影响方式、程度和规律还需进一步研究和阐明。我们对生防木霉菌的研究发现，木霉菌对不同作物的病害防治效果具有很大差异，其中不排除植物微生物组/群对木霉定殖和防效的影响。但目前有关植物微生物组/群对 BCAs 防治效果的影响作用鲜见报道，需要进一步深入研究。

5 小结

研究者很早就注意到，与植物共生的微生物群落中含有相当数量的 BCAs。通过平板培养等方法可分离并筛选获得高效 BCAs，成为针对植物病害的可持续施用的“绿色农药”。我们前期筛选的高效木霉生防菌菌剂，田间应用于不同作物后，出现了防病效果不稳定的情况。目前我们的研究

集中于木霉对不同病原菌的不同生防机制，主要方向为利用组学技术解析木霉对立枯丝核菌、畸雌腐霉菌的重寄生机制[63]，分析木霉消除草酸作用与防治灰霉病之间的关联机制等木霉防治病害的生防机制[64]，但缺乏对微生物组学的研究。多项研究提出，对生物防治的研究应该从对单一的BCAs扩展到与植物关联的微生物种群中[65–67]。鉴于在菌剂应用中出现的问题，将来的研究工作中我们将重视微生物组/群在木霉生防机制中的作用。

微生物组学研究中的高通量测序技术(next generation sequencing，NGS)、单分子实时测序技术(single molecule real-time，SMRT)结合传统平板培养技术，可帮助人们把握微生物组的全貌，获得更加真实的植物微生物群落的分类、功能等，从而深入揭示植物微生物组/群与植物病害的关系、与病原菌或BCAs的相互作用，建立可信的生防体系互作模型，为生物防治提出新思路。除了技术革新，微生物组学对植物病害微生物防治领域研究的思维模式带来了更为深远的影响，即从关注简单的二元、三元互作模式拓展至对植物微生物组全局的考量。例如，当界定一种微生物对植物有益或有害时，除了考察该菌株对植物本身的作用，更要考虑其如何影响了植物自身的微生物生态。当研究病原菌病理特性时，应加入对微生物组分析的步骤，不仅分析病原菌与BCAs的相互作用，还要分析病原菌与微生物组的相互影响[68]。一些新的组学研究思路或对生防研究具有借鉴意义，如Bai等人从模式植物拟南芥(*Arabidopsis thaliana*)叶片和根中分离到400多种可培养细菌，并在拟南芥无菌苗中重建了根和叶的微生物组，开创了定义微生物组的研究模式[69]。定义微生物组的研究思路或可被生防领域借鉴，用于在实验室条件下研究BCAs、病原菌与植物间的互作机制，更准确地揭示生防菌的防病机理。另外，BCAs对施用地植物微生物群落结构的影响也正在受到关注。一些报道称BCAs施用后，植物微生物群结构出现了变化[60–62,70]，但也有研究表明，土壤性质、试验条件和生理特性比BCAs对根围微生物的影响更持久[61,71–72]。Massarta等人认为，如果施用BCAs一段时间后，根围微生物群落可以恢复至对照水平，那么该BCAs可定义为环境友好型生防菌剂[13]。可见，微生物组学技术和思路为微生物防治提供了更深入的研究空间。

综上所述，微生物组学的发展可帮助人们更全面地认识植物病害，并采用更科学的手段加以防治。

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Enlightenment from microbiome research towards biocontrol of plant disease

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Abstract: Studies on biocontrol of plant diseases mainly focus on interactions among plant, pathogen, and biocontrol agents (BCAs), but ignore the role of associated microbiome of plants. Increasing numbers of studies have revealed the essential roles of plant endophytes, rhizosphere microbiota and phylloplane microflora in resistance to plant diseases. Basing on selected representative reports, we reviewed the composition of plant microbiome, its anti-pathogenic and pathogenic effects for plants, and its effect on pathogenicity of phytopathogen as well as the effect of BCAs on native microbiome. Progress in microbiome researches provides novel perspectives toward plant diseases and biological control, which will help to develop more scientific methods for plant disease management.

Keywords: microbiome, plant disease, microbial biocontrol

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