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植物内生菌影响土壤微生物区系的研究进展*

武佳蕊 王宏伟 谢星光 戴传超**

(南京师范大学生命科学学院/江苏省微生物与功能基因组学重点实验室/江苏省微生物资源产业化工程技术研究中心 南京 210023)

摘 要 土壤微生物区系是土壤生态环境的重要组分，其结构的稳定性对作物的健康生长至关重要。本文重点综述了植物内生菌对土壤微生物区系的调节作用，调节机制及潜在应用，指出了植物内生菌影响土壤微生物区系研究中出现的问题。一些植物内生菌不仅对植物生长有益，还可以显著改善土壤微生物区系，主要表现在对土壤微生物种类及数量、微生物生物量、酶活性及相关酶基因表达的影响，这可能是内生菌在土壤中和植物体内引发的多种效应的综合。植物内生菌可以在土壤中作为腐生菌与土壤微生物存在生态位竞争，通过产生某些抗菌活性物质和有机酸影响土壤微生物生长，通过降解复杂有机物如木质素、酚类化感物质等调节微生物区系，并吸收和转运重金属降低其对土壤微生物区系的危害等等。最后提出了今后的研究方向。

关键词 土壤微生物区系 植物内生菌 生态竞争 降解作用 拮抗作用

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Advances in the study of endophytes effects on soil microflora

WU Jiarui, WANG Hongwei, XIE Xingguang, DAI Chuanchao

(College of Life Sciences, Nanjing Normal University/Jiangsu Key Laboratory for Microbes and Functional Genomics/Jiangsu Engineering and Technology Research Center for Industrialization of Microbial Resources, Nanjing 210023, China)

Abstract Soil microflora is an important part of soil ecological environment. The stability of soil microflora plays an important role in plant growth. Except for the plant growth promoting ability, some endophytes also significantly impact soil microflora. In this review, quantities of studies are summarized and effects of endophytes on soil microflora and the regulatory mechanisms are also discussed. Endophytes not only improve soil microbial composition and biomass, but also enhance soil enzyme activities and the expression of related enzyme genes. The mechanisms of these effects mediated by endophytes are complex. Living in soil, endophytes occupy the same niches and struggle for the sources of carbon and nitrogen with soil microbes. Meantime, endophytes provide plenty of carbon and nitrogen sources for soil microbes by degrading litters in the soil. They also produce some antimicrobial active substances and organic acids to affect soil microbes. In addition, endophytes regulate soil microorganisms by promoting the release and degradation of complex organic compounds, such as ligin and phenolic allelochemicals. Furthermore, endophytes reduce the toxicity of heavy metal in soil. In addition, the application of endophytes is discussed. The deficiencies in the existing researches are pointed out and the further researches are also put forward.

Keywords Soil microflora; Endophyte; Ecologic competition; Degradation; Antagonistic action

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土壤微生物区系(soil microflora)是指在某一特定环境和生态条件下土壤中所存在的微生物种类、数量以及参与物质循环的代谢活动强度，是土壤生态环境中重要的一部分，且易受到人类农业生产活动影响[1−2]。土壤微生物区系失衡，会影响作物营养物质吸收，病害加重，甚至导致连作障碍[3−7]。植物内生菌(endophyte)是一定阶段或全部阶段生活于健康植物的组织和器官内部且不会引起宿主植物明显危害的一类微生物[4−7]。植物内生菌不仅能够促进宿主植物的生长，也能增强植物的抗性，同时一些内

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** 通讯作者: 戴传超，主要从事微生物生态学的研究。E-mail: daichuanchao@njnu.edu.cn
武佳蕊，研究方向为微生物多样性。E-mail: 1223750170@qq.com
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生菌也可作为腐生菌在土壤中生存[8]。与使病原菌产生抗药性, 且对人、畜和环境都有严重危害的化学农药相比, 植物内生菌不仅能够抑制病原微生物, 而且具有无毒、无害、无污染和不易产生抗药性等优点[9]。虽然前人已对土壤微生物区系的宏生态变化模型、土壤微生物区系变化的原因以及植物内生真菌优化土壤环境[10−13]等方面进行了相关综述, 且植物内生菌改善土壤微生物区系在农业和森林生态系统中也有涉及, 但关于植物内生菌影响土壤微生物区系方面却一直未有详细综述。本文主要从植物内生菌在农业方面对土壤微生物区系的调节作用及其机制、植物内生菌作为土壤调节剂在农业上的潜在应用、植物内生菌研究中存在的问题等方面进行重点综述, 并展望了植物内生菌调节土壤微生物区系的研究前景。

1 植物内生菌对土壤微生物区系的调节作用

关于植物内生菌的研究报道已经有很多, 但大部分研究主要集中在以下几个方面[7]: ①植物内生菌与植物生长的关系; ②植物内生菌的次生代谢物质种类及其作用; ③植物内生菌在生物防治方面的应用等。而目前关于植物内生菌直接影响土壤微生物区系研究的内容很少, 主要集中在对土壤中微生物种类、 数量以及代谢强度的影响等方面[14−17]。

1.1 植物内生菌对土壤微生物种类和数量的调节

土壤中添加植物内生菌能够改变土壤中微生物的种类和数量。在花生(*Arachis hypogaea*)和草莓(*Fragaria ananassa*)连作土壤中添加植物内生真菌拟茎点霉(*Phomopsis liquidambari*)B3菌株、拟茎点霉(*Phomopsis* sp.)NJ4.1菌株和角担子菌(*Ceratobasidum stevensii*)B6菌株后均能提高土壤中细菌和放线菌数量, 减少霉菌数量[14−16]。*C. stevensii* B6能够显著抑制连作西瓜(*Citrullus lanatus*)土壤中尖孢镰刀菌(*Fusarium oxysporum*)的生长[17]。与玉米(*Zea mays*)等作物共生的白僵菌(*Beauveria bassiana*)可以增加土壤中真菌和细菌的数量, 但却抑制放线菌的生长[18]。此外, 土壤中接种根瘤菌(*Rhizobiaceae*)可以增加菜豆(*Phaseolus vulgaris*)根际土壤中细菌群落的丰富度, 在开花期和收获期使土壤中α和γ变形菌纲(*Alpha-* and *Gammaproteo bacteria*)、厚壁菌门(*Firmicutes*)和放线菌(*Actinobacteria*)的数量增多, 根瘤菌属的丰度增加, 并且这种增加受到时间和接种距离的限制[19]。

1.2 植物内生菌对土壤微生物生物量的影响

土壤微生物生物量(soil microbial biomass, SMB)指土壤中个体体积小于5×10^3 μm^{3}的活微生物总量, 包括土壤微生物生物量碳(soil microbial biomass carbon, SMBC)、土壤微生物生物量氮(soil microbial biomass nitrogen, SMBN)、土壤微生物生物量磷(soil microbial biomass phosphorus, SMBP)等, 能够预示土壤有机质等土壤理化性质的变化趋势。在连作花生土壤中添加内生菌*P. liquidambari* B3后, 由于内生菌自身带来的SMBC、SMBN和内生菌胞内外营养物质的释放促进了其他土壤微生物增殖使处理组萌发期SMBC、SMBN均显著高于对照组[11]; 在花生萌发期, 含B3的处理SMBC、SMBN分别比对照组高93.6%、76.8%, 且两者在花生的整个生长期呈现出先增大后减少的趋势。

1.3 植物内生菌对土壤酶活和有关酶基因表达的影响

土壤酶是土壤中产生专一生物化学反应的生物催化剂。土壤酶参与土壤中各种生物化学过程, 如腐殖质的分解与合成, 动植物残体和微生物残体的分解, 有机化合物的水解与转化以及某些无机化合物的氧化、还原反应。土壤酶的活性大致反映了某一土壤生态状况下生物化学过程的相对强度。施加内生菌*P. liquidambari* B3可以提高连作花生和连作草莓土壤环境中蔗糖酶和过氧化氢酶的活性, 与对照相比分别提高28.3%和22.4%[14,16]。在近期研究中, 根际土壤样本中细菌编码固氮还原酶基因(*nif*H)、氨单加氧酶基因(*amo*A)和亚硝酸还原酶基因(*nir*k)被定量[20]。接种根瘤菌可改变土壤中*nif*H基因的多样性; 接种不同的根瘤菌对不同土壤中氮转化基因也会造成影响, 比如在对紫花苜蓿(*Medicago sativa*)接种更多的有效根瘤菌后, 在开花期可以观察到高数量的*amo*A拷贝[21]。

2 植物内生菌调节土壤微生物区系的机制

土壤接种植物内生菌, 会明显改善土壤微生物区系, 使连作土壤的微生物结构从真菌主导型向细菌主导型转变[22−23], 造成这种变化的可能机制如下:

2.1 生态位竞争

生态位(ecological niche)指一个种群在生态系统中, 在时间空间上所占据的位置及其与相关种群之间的功能关系与作用。每种微生物的生长都必须有适当的营养物质供给, 在土壤中添加内生菌后, 土著微生物间、内生菌与土著微生物间都存在竞争关系。内生菌可以与病原菌形成营养竞争的对抗关系, 一些内生菌可以消耗氮、碳、氧或其他适宜病原菌生长所需的微量元素(如铁), 抑制病原菌的生长和代谢。荧光假单胞杆菌(*Pseudomonas fluorescens*)能产生一种黄绿色铁载体与病菌竞争铁, 导致病菌

因得不到铁元素而死亡，但在铁充足的情况下，此种竞争却不明显[24]。内生真菌*C. stevensii* B6与尖孢镰刀菌存在养分和生存空间的竞争，两者在土壤中呈此消彼长的趋势[25]。

2.2　产生生理活性物质，影响土壤微生物的生长

土壤中不仅有促进碳氮循环的微生物，还有许多土传植物病原菌如疫霉菌(*Phytophthora*)、镰刀菌(*Fusarium*)、腐霉菌(*Pythium*)等。植物内生菌产生的抗菌活性物质能够抑制植物病原菌的生长，这是其作为生防菌的原因之一[26]。研究者已分别从穿心莲(*Andrographis paniculata*)、杜香(*Rhododendron tomentosum*)、余甘子(*Emblica officinalis*)等植株中分离出了具有抗菌活性的内生细菌、真菌和放线菌[27−32]。从植物组织内分离的内生细菌能够显著降低由黄萎病菌(*Verticillium dahlia*)和枯萎病菌(*Fusarium oxysporum* f. sp. Lycopersici)引起的发病症状[33]；内生真菌印度梨形孢(*Piriformospora indica*)不仅能有效抑制由 *V. dahiae* 引起的番茄病害[34]，而且能够抵抗小麦白粉病菌(*Blumeria graminis f.* sp.)的侵染[35]；内生放线菌暗蓝色链霉菌(*Streptomyces caeruleatus* GIMN4^T)对油菜黄单胞菌(*Xanthomonas campestris* pv. Glycine)具有抑制作用[36]。

目前关于植物内生菌产生的抗菌活性物质主要有：①细胞壁降解酶类。细胞壁降解酶类如几丁质酶、β-1,3-葡聚糖酶等能够降解土壤中某些微生物的细胞壁，抑制微生物的生长，改变土壤微生物区系结构。Quecine 等[37]发现内生菌链丝菌属(*Streptomyces* spp.)拮抗作用越强，产几丁质酶的能力就越强，并通过电子显微镜观察到几丁质酶可降解真菌细胞壁。芦苇内生真菌(*Choiromyces aboriginum*)可通过产生 β-1,3-葡聚糖酶降解植物病原真菌细胞壁进而使内生菌菌丝寄生于病原菌中而降解病原真菌的细胞质[38]。②抗菌肽(antimicrobial peptides, AMPs)。AMPs 是一类含有 6~100 个氨基酸的小分子多肽，对细菌和真菌具有广泛的抑制作用[39]。Tejesvi 等[40]从杜香中分离出的三线镰刀菌(*Fusarium tricinctum*)能够产生抑制肉葡萄球菌(*Staphylococcus carnosus*)、白色念珠菌(*Candida albicans*)的抗菌肽物质，并首次利用分子生物学方法对其进行了序列分析。此外，植物内生菌还能产生一些萜类、挥发性物质以及酚类、生物碱、醌类、脂肪族化合物(布雷菲德菌素)等抗菌活性物质[41−45]。

植物内生菌还可以释放有机酸，不仅能够作为土壤中某些微生物的碳源，而且也能与Ca^{2+}、Fe^{3+}、Fe^{2+}、Al^{3+}等金属离子螯合使难溶性磷酸盐溶解，促进土壤中的磷循环和土壤微生物对磷的吸收和利用[46−47]。

2.3　降解复杂有机物，调节土壤微生物区系

随着世界人口增加，粮食及经济作物生产压力大，作物的连年耕种导致土壤中不仅存在许多如植物凋落物、秸秆等占用大量碳、氮源物质，而且还存在通过多种途径释放到土壤中的酚类化感物质。这些酚类化感物质能够对土壤微生物和植物产生毒性，严重影响土壤微生物区系的结构，从而导致了连作障碍。内生菌降解有机物对土壤微生物区系影响主要表现在两个方面：一是降解复杂有机物，为其他微生物提供碳源、氮源等营养物质；二是降解一些酚类化感物质，减少其对土壤微生物产生的化感作用。

2.3.1　降解秸秆、凋落物提供碳源和氮源

在自然条件下，凋落物的分解过程缓慢，并受各种生物和非生物因素限制。作为先锋分解者，拟茎点霉属(*Phomopsis*)已被证明能加快凋落叶分解和土壤氮素转化[48−49]。秸秆中的木质素只有 13%~25%，却是限制秸秆快速降解的关键因素[50−51]。木质素结构复杂，只能被少数土壤微生物降解利用，造成土壤中大量的碳源流失，很多微生物因得不到所需的碳源而死亡。木质素的分解与木质素降解酶漆酶、纤维素酶、木聚糖酶等有关[52−53]。*P. liquidambari* B3 能够在体外分泌漆酶，加速木质素的降解，改变土壤微环境[54−56]；球毛壳菌(*Chaetomium globosum*)能够降解纤维素，且具有编码纤维素酶和糖水解酶基因的功能[57]。内生菌能将凋落物降解成对安息香酸、香草酸等一些土壤微生物可以利用的小分子物质从而促进土壤中碳、氮源的有效利用。

2.3.2　降解酚类化感物质，降低其对土壤微生物的毒害作用

土壤中的酚类化感物质不仅能够通过抑制代谢酶的活动和扰乱生长素的合成对种子萌发和生长产生负面影响[58]，而且也会通过改变种群和群落结构破坏土壤的微生物平衡[59]。*P. liquidambari* B3 能将对羟基苯甲酸(4-hydroxybenzoic acid, 4-HBA)分解为3,4-二羟基苯甲酸、顺式-己二烯二酸和邻苯二酚，解除其对土壤微生物和植物的危害[59−62]，使植物的生长环境得到改善，进而增加植物根系分泌物的种类和数量，提高微生物的数量和多样性[55]；*P. liquidambari* B3 还能降解含氮的杂环化合物吲哚[52]和土壤中难降解的多环芳烃(PAHs)菲[63−64]。目前已从植物中分离出了多种能够降解 PAHs 的内生菌，如降解菲的 *C. stevensii*、假单胞菌属 Ph6-*gfp* (*Pseudomonas* sp. Ph6-*gfp*)、纳西杆菌属(*Naxibacter* sp.)[65−67]，降解芘的葡萄球菌 BJ06 (*Staphylococcus* sp. BJ06)、*Burkholderia fungorum* DBT1[68−69]等。

2.4 吸收土壤重金属，调节土壤微生物区系结构

随着工业发展，大量被排放到河流中的重金属离子经农业灌溉富集到农田中导致土壤重金属离子的超标。这不仅破坏了土壤微生物区系的平衡，而且通过食物链，最终给人类的健康带来极大的危害[70]。重金属严重影响土壤微生物区系：①抑制土壤酶活[71]。Cd、Zn、Pb 3种重金属都能够抑制土壤中过氧化氢酶和脲酶的活性。其抑制机理一方面可能是重金属离子与这些酶的活性部位结合，形成较稳定络合物，产生与底物的竞争性抑制作用；另一方面可能由于重金属通过抑制土壤微生物的生长和繁殖，减少体内酶的合成和分泌，最后导致土壤酶活性下降。②抑制土壤微生物对土壤中凋落物的分解和土壤碳、氮的矿化[72−74]。③减少土壤中真菌种数[75]。

土壤微生物虽可在土壤滤沥过程中通过分泌有机酸络合并溶解土壤中的重金属，但这种能力却很有限[76]。植物内生菌对重金属具有抗性，可与植物联合作用用于土壤修复：从植物组织中分离出的95株分别属于茎点霉属(*Phoma*)、链格孢属(*Alternaria*)、派伦霉属(*Peyronellaea*)的内生真菌对Pb-Zn具有抗性[77]；从龙葵(*Solanum nigrum*)、海洲香薷(*Elsholtzia splendens*)中分离出的内生细菌可分别促进宿主植物对土壤中Cd、Cu的吸收[78−79]。内生真菌和细菌对重金属的抗性机制不同：真菌菌丝接触污染面积大，菌丝中的超氧化物歧化酶(SOD)和氧化氢酶(CAT)活性会随重金属离子(Cd^{2+}、Pb^{2+})浓度的升高而升高，从而消除由重金属浓度升高而增加的活性氧[80]；植物内生细菌则可以通过产生铁载体促进植物对重金属的吸收[81]。由于内生菌与植物能够形成稳定的共生关系，且不会与土壤微生物产生竞争，因此利用内生菌−植物联合对土壤中重金属的修复已成为土壤修复的一项重要技术[82]。

3 植物内生菌作为土壤调节剂的应用

作为土壤调节剂植物内生菌有很多优点：与化学防治法相比植物内生菌不仅不会造成环境污染，而且不会使病原菌产生耐药性，具有生态农业可持续性；利用内生菌作为植物增产剂比培育高产量新品种更加高效。目前植物内生菌在植物病原菌防治，改善连作障碍等方面得到了应用。

植物内生菌可分泌抗菌活性物质而抑制土壤中土传病原菌的生长，减少病原菌对作物的侵染，降低植物病害。西瓜连作土壤中施加*C. stevensii* B6菌后的4周内能够有效控制尖孢镰刀菌的数量。其原因可能是由于*C. stevensii* B6在土壤中与尖孢镰刀菌一方面竞争营养，另一方面产生了抑制镰刀菌生长的活性物质，从而抑制了镰刀菌的生长[17]。植物体内生菌莫海威芽孢杆菌(*Bacillus mojavensis*)能够产生表面活性剂Leu7-surfactin，从而抑制玉米串珠镰刀菌(*Fusarium verticillioides*)的生长[83]。Kilani-Feki等[84]证实在荧光假单胞菌(*Pseudomonas fluorescens*)的藤黄菌绿素和吩嗪基因簇中隐匿有抗真菌活性的基因。

引起连作障碍的主要原因之一是土壤微生物区系的变化。连作土壤微生物多样性呈单一化趋势，植物病原真菌得到富集，不仅不利于土壤中微生物种群的平衡，而且易导致植物根部病害的发生，使作物产量逐年降低[85]。目前已将内生菌应用到缓解农作物连作障中：接种*P. liquidambari* B3能使花生产量增加24%[15]；根瘤菌能促进豆科植物对氮的吸收，在地球氮素循环中发挥了重要作用，已作为微生物制剂被广泛应用于促进豆科植物生长[86]；*P. indica*可提高大麦、番茄等作物产量[87−88]。

4 总结与展望

植物内生菌可以直接或间接地改善土壤微生物区系，主要表现在：改变土壤中真菌、放线菌和细菌的种类和数量，提高土壤的微生物量，提高土壤酶的活性。其机制主要有以下几方面：首先，植物内生菌与土壤中的微生物竞争碳、氮源；其次，植物内生菌能够降解土壤凋落物中的木质素和土壤中有机污染物，促进土壤中微生物对碳、氮源的利用，同时也减少了有机污染物、酚酸化感物质对土壤微生物的抑制；再次，植物内生菌能够分泌多种抗菌活性物质，有效抑制土壤中的植物病原菌；最后，植物内生菌还能够促进植物对重金属离子的吸收，减少其对土壤酶以及土壤微生物的抑制。与农药和其他微生物制剂相比，植物内生菌不仅可以抑制植物病害，促进植物生长，提高作物产量，缓解连作障碍，而且不会使病原菌产生耐药性，更不会对环境造成污染。

目前虽已有关于内生菌影响土壤微生物区系的研究，但仍存在着一些尚未解决的问题：第一，对植物内生菌降解大分子物质的机制仍不清楚；第二，没有一个模式菌株能够清晰地阐明内生菌—植物—土壤微生物之间的相互作用机制；第三，关于植物内生菌在土壤中对土壤微生物区系影响的分子机制仍不明确；第四，内生菌虽可改善土壤微生物区系，但在实际应用中仍存在问题，如在土壤中的定殖及其有效作用的发挥会受到生存环境、内生菌自身因素，植物选择性等因素的影响。笔者认为在今后的研究中应该从研究植物—内生菌—土壤微生物之间

相互影响的分子机制以及如何克服内生菌在应用中存在的问题等方面展开研究。

随着世界人口的增长，我们需要越来越多的粮食来应对日益膨胀的人口。不幸的是，由于植物病害和连作障碍导致的粮食损失问题依然严重[89]。土壤微生物区系的恶化是导致植物病原菌增加和连作障碍的主要因素。植物内生菌因与寄主植物在长期共同进化过程中形成密切的相互关系，且生存微环境稳定，已成为化肥、农药和其他微生态制剂的最佳竞争者。它的合理应用将减少化学药剂造成的环境污染，提高农田生态系统的生物多样性，有利于保持生态平衡。研究两者的关系能够为解决一些经济作物中存在的连作障碍及病害防治提供一些新的思路，所以植物内生菌影响土壤微生物区系具有重要的研究价值。

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