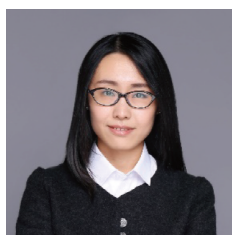


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微生物调控植物次生代谢的研究进展

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摘要: 植物与微生物之间存在复杂的相互作用。从次生代谢的角度而言, 微生物及其代谢物可诱导植物次生代谢重塑, 而植物被调控后分泌的代谢物亦可反向驱动环境中微生物群落的重组。本文综述了微生物调控植物次生代谢的研究进展, 包括: (1) 系统总结了微生物介导的植物次生代谢调控表型; (2) 基于有限的研究探讨了微生物对植物代谢等生理过程的调控机制; (3) 基于代表性研究讨论了植物次生代谢物对微生物群落的反馈调节及生物学意义。现有研究表明, 尽管微生物调控植物次生代谢的表型已被广泛报道与应用, 但关键信号分子的挖掘严重滞后, 表型观测与机制解析的关注重点不一致, 反映植物-微生物互作全局规律的研究尚待加强。最后, 本文对构建“信号分子诱导-植物代谢重塑-微生物组重构-协同反馈调节”全景研究的趋势进行展望, 探讨了本领域拟解决的科学问题、面临的技术瓶颈及潜在的产业化应用前景。

关键词: 植物次生代谢; 微生物; 植物-微生物相互作用; 信号分子; 作用机制

中图分类号: Q946.92; Q948.12+2.3 文献标识码: A

Recent advances in microbial regulation of plant secondary metabolism

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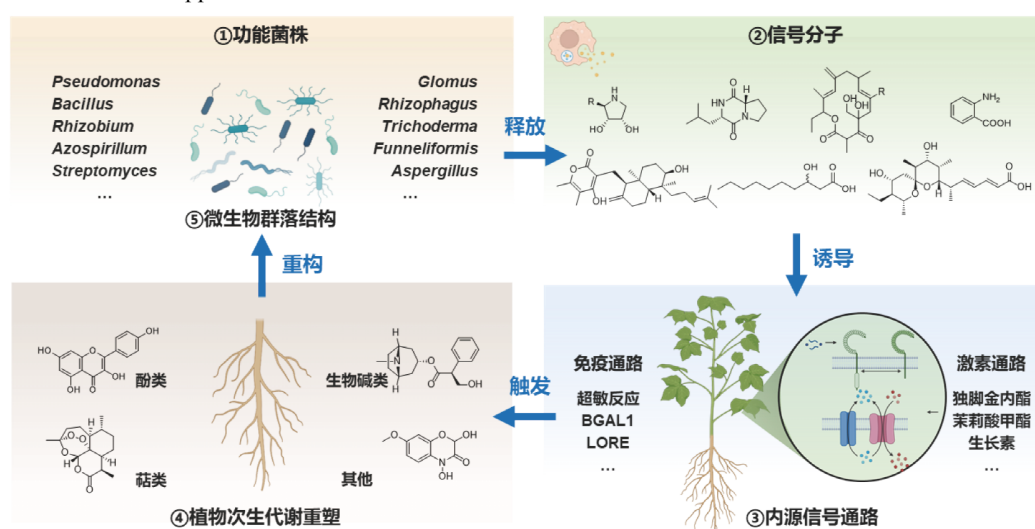
Abstract: Plants and microorganisms engage in intricate interactions. From the perspective of secondary metabolism, microorganisms and their metabolites can induce remodeling of plant secondary metabolism. Conversely, plant-secreted metabolites, modulated by these interactions, can drive restructuring of ambient microbial communities. The complex interactions between microorganisms and plants are ubiquitous throughout the entire plant life cycle, exhibiting extreme dynamism. These interactions profoundly impact plant secondary metabolism and other physiological activities, collaboratively shaping ecosystem dynamics. This review summarizes recent advances in microbial regulation of plant metabolism, covering: (1) a systematic summary of microbial-mediated phenotypes in plant secondary metabolism regulation; (2) an exploration of microbial regulatory mechanisms on plant physiological

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processes, mainly metabolism, based on currently limited studies; (3) a discussion, drawing from representative studies, of feedback regulation by plant secondary metabolites on microbial communities and its biological significance. Key findings of the review indicate: (1) Regulation of plant secondary metabolism by microorganisms and their metabolites is widespread. Functional strains from bacterial genera such as *Pseudomonas*, *Bacillus*, and *Rhizobium*, and fungal genera like *Glomus* and *Rhizopagus*, are most frequently reported for their regulatory effects. (2) The mechanism by which microbial signaling molecules regulate plant metabolism primarily involves interference with plant immune systems and hormone signaling pathways, thereby affecting expression of genes related to secondary metabolite biosynthesis. (3) A continuous interactive cycle based on secondary metabolites exists between plants and microorganisms. This cycle ultimately drives plant metabolic remodeling, alteration of physiological states, and promotes directed restructuring of environmental microbial communities. Despite widespread reporting and application of phenotypes where microorganisms regulate plant secondary metabolism, discovery of key signaling molecules lags significantly. An inconsistency in research focus also exists between phenotypic observation and mechanistic elucidation, highlighting a need to strengthen research on overarching principles governing plant-microbe interactions. Finally, this review anticipates the trend towards constructing a panoramic research framework encompassing "signaling molecule induction-plant metabolic remodeling-microbiome restructuring-synergistic feedback regulation". It further discusses scientific questions to be addressed, technical bottlenecks encountered, and potential industrial applications in this field.



Key words: plant secondary metabolism; microorganisms; plant-microbe interactions; signaling molecule; interaction mechanism

植物生长环境中定殖着数量庞大的微生物群落,二者历经约4.5亿年的协同进化,形成了长期而稳定的共生网络。微生物与植物的相互作用不仅贯穿植物生命周期的始终,更具有高度的动态性,对植物的次生代谢及其他生理活动产生深远影响^[1]。随着近年来该领域研究的快速推进,植物与微生物间的相互作用模式被不断揭示。其中,微生物对植物次生代谢的调控,是该领域普遍且备受关注的互作效应^[2]。

微生物对植物次生代谢的调控是高度复杂的生物学过程。其核心机制可体现为:微生物合成并向环境释放信号分子,并被植物感知;植物在该信号分子的调控下激活体内通路,合成特异的次生代谢物,并将其外排至环境,重塑环境微生物群落的组成。

自2018年以来,已有诸多综述对本领域进行了梳理,探讨环境微生物研究如何揭示“植物-微生物-环境”的复杂互作网络^[3,4]。这些综述大致分为两个方向:一是微生物对植物次生代谢物的调控机制^[5,6];二是植物次生代谢产物的生态与生物学功能^[7,8]。

尽管现有研究已构建了理论框架,但仍未充分建立植物-微生物互作的全链条关系。基于此,本文从植物次生代谢视角出发,重点综述微生物调控植物次生代谢的表型及其分子机制,并进一步探讨其生物学意义。本文系统检索了Web of Science数据库中自1969年以来发表的相关文献,以“microorganism”“plant secondary metabolites”“plant composition”“elicitor”为关键词,共纳入近190项研究(包含综述^[5,6]已汇总的91项研究)。本综述包括

四个部分:(1)微生物介导的植物次生代谢调控表型;(2)微生物调控植物代谢等生理过程的分子机制;(3)植物次生代谢物对微生物群落的反馈调节及生物学意义;(4)总结与展望。

1 微生物介导的植物次生代谢调控表型

微生物普遍参与调控植物次生代谢产物的合成与积累。早在1969年,Libbert等^[9]首次报道了细菌调控玉米、豌豆等的次生代谢。迄今,已有至少157篇文献报道了该类表型。这些研究的形式多样:诱

导因子包括微生物菌株(以下称为“功能菌株”)、微生物提取物及其特定代谢物;接种部位多为根,少数为叶片及种子;培养条件包含土壤栽培、水培及人工培养基体系。代谢产物的表型分析常采用分光光度法、紫外-可见光谱法、色谱/质谱联用法等。本节将从功能菌株(图1)、提取物(图2)及特定代谢物三个层面,系统综述微生物对植物次生代谢的调控表型。其中,针对功能菌株的研究最为广泛,依据结构可将被调控植物成分进一步分为酚类、萜类及生物碱类等^[10]。

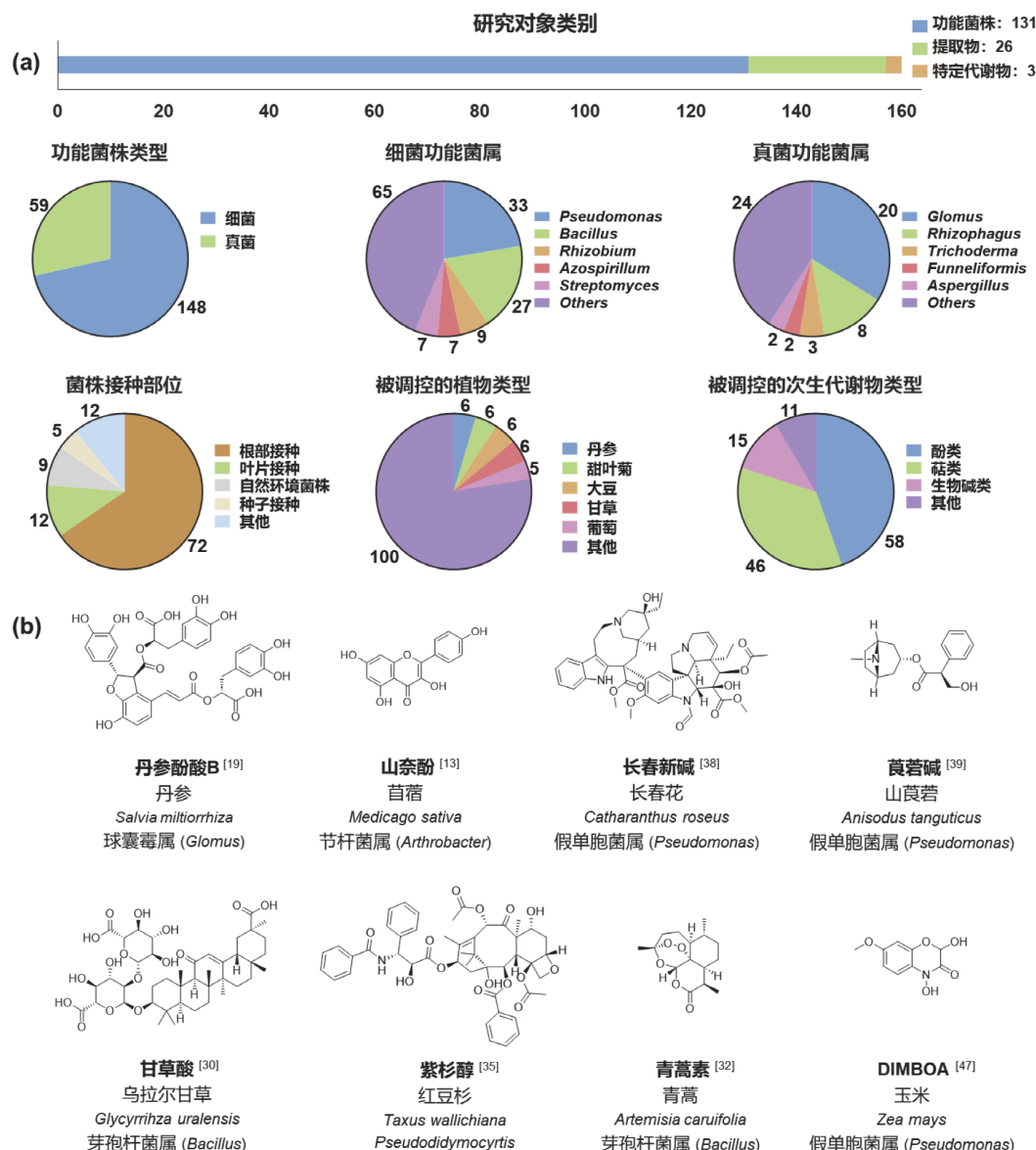


图1 微生物功能菌株对植物次生代谢的影响

(a)微生物调控植物次生代谢的研究对象、研究方法及其结果统计。(b)受微生物正向调控的代表性植物次生代谢物。

Figure 1 Effects of functional microbial strains on plant secondary metabolism

(a) Summary of research subjects, methodologies, and outcomes in studies of microbial regulation of plant secondary metabolism. (b) Representative plant secondary metabolites positively regulated by microorganisms.

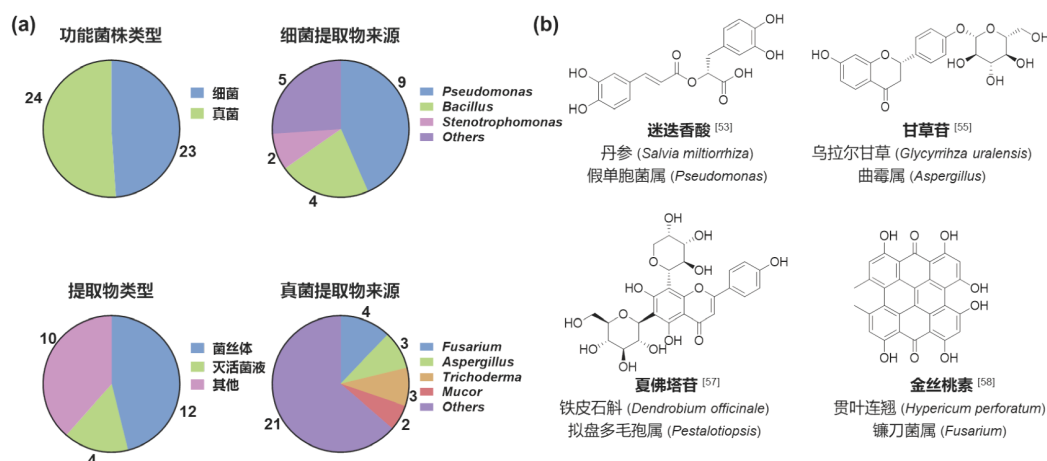


图2 微生物提取物对植物次生代谢的影响

(a)微生物提取物调控植物次生代谢的研究对象、研究方法以及结果统计。(b)受微生物提取物正向调控的代表性植物次生代谢物。

Figure 2 Effects of microbial extracts on plant secondary metabolism

(a) Summary of research subjects and methodologies in studies on the regulation of plant secondary metabolism by microbial extracts. (b) Representative plant secondary metabolites positively regulated by microbial extracts.

1.1 功能菌株介导的植物次生代谢调控表型

1.1.1 功能菌株对植物酚类成分的调控

酚类化合物是以苯环直接连接羟基为核心结构的植物天然产物,经后修饰反应展现出高度的结构多样性,主要包括黄酮、查耳酮、酚酸等^[11]。调控酚类代谢物的细菌种类丰富,包括假单胞菌属(*Pseudomonas*)、芽孢杆菌属(*Bacillus*)、根瘤菌属(*Rhizobium*)、链霉菌属(*Streptomyces*)等。例如,荧光假单胞菌SS101施用于根部,可提升拟南芥根和叶片中总黄酮水平并增强抗病性^[12];敏捷节杆菌UMCV2能诱导山奈酚等黄酮类化合物在苜蓿叶片中的积累^[13];枯草芽孢杆菌Co1-6与多粘类芽孢杆菌Mc5Re-14均可显著提升洋甘菊中芹菜素-7-O-葡萄糖苷的含量^[14];接种固氮螺菌4B或豆科根瘤菌RRE6可能上调水稻根、茎、叶组织的酚酸含量^[15,16];Bois noir植原体感染葡萄叶片可诱导咖啡酸等酚酸类化合物含量升高;解淀粉欧文氏菌SGB 225/12定殖西洋梨叶脉后则诱导叶片绿原酸积累^[17,18]。

真菌定殖亦能显著调控植物酚类代谢,相关研究多聚焦于球囊霉属(*Glomus*)与根孢囊霉属(*Rhizophagus*)。例如,根部接种摩西球囊霉可促进丹参中丹参酚酸B的积累^[19];根孢囊霉属定殖能提升苜蓿、橄榄及甘草等多种植物的酚类水平,其中甜叶菊的总酚类和黄酮类化合物含量较对照组分别提高5.2倍和4.2倍^[20-24]。此外,细菌-真菌复合菌群具

有协同效应,如根瘤菌与丛枝菌根真菌联用可显著提高花生根的酚类化合物总量,且混合菌群效应强于单菌^[25]。综上,目前已有大量研究证实了微生物对植物酚类代谢的广泛调控作用。

1.1.2 功能菌株对植物萜类成分的调控

萜类化合物是以异戊二烯为基本单元构建的天然烃类及其含氧衍生物,是植物中种类最丰富、结构多样性最高的代谢物类群^[11]。细菌调控植物萜类代谢物的研究较多,其中近七成研究聚焦于假单胞菌属(*Pseudomonas*)与芽孢杆菌属(*Bacillus*)^[5,6]。通过根际干预,此类菌株可显著提升植物根、叶及果实中萜类化合物的含量^[26,27]。例如,日本慢生根瘤菌能特异性促进大豆中萜类的合成与积累^[28,29]。在药用植物领域,多种细菌可增强萜类成分的合成或积累。例如,短小芽孢杆菌^[30]与番茄根瘤菌GUH21^[31]均被证实可促进甘草酸的积累;枯草芽孢杆菌、地衣芽孢杆菌、不动杆菌、寡养单胞菌属、伯克霍尔德菌属等多种菌株则能显著提升青蒿素含量^[32-34]。

真菌定殖亦能显著调控植物根系、叶片及果实中的萜类含量。目前研究涉及的真菌类群广泛且分散,主要包括根孢囊霉属(*Rhizophagus*)、球囊霉属(*Glomus*)及梨形孢属(*Serendipita*)等。例如,内生真菌*Pseudodidymocyrtis lobariellae* KL27可有效诱导红豆杉针叶中紫杉醇的合成^[35];而草酸青霉

B4^[36]与根孢囊霉^[37]均可显著提高植物体内青蒿素的积累水平。

1.1.3 功能菌株对植物生物碱类成分的调控

生物碱是一类含氮植物次生代谢产物,其骨架涵盖单环、稠环及大环等多种环状结构。绝大多数生物碱具有手性中心,并以单一对映体形式存在^[11]。在细菌调控植物生物碱类代谢物的报道中,假单胞菌属(*Pseudomonas*)的研究数量最多,其中荧光假单胞菌(*P. fluorescens*)最为集中,其次为寡养单胞菌属(*Stenotrophomonas*)和微球菌属(*Micrococcus*)。这些细菌的调控对象涵盖了多种药用植物与观赏植物。例如,荧光假单胞菌能诱导长春花合成长春新碱^[38],提升山莨菪中莨菪碱的含量^[39],并显著提高鸭嘴花毛状根的喹啉生物碱水平^[40]。松鼠葡萄球菌与微球菌亦可提升长春花叶片的生物碱含量^[41]。值得注意的是,部分菌株存在负向调控效应,如嗜麦芽寡养单胞菌N5.18接种后会显著降低罂粟根、茎部的生物碱含量^[42]。

少数真菌可调控植物生物碱水平。丛枝菌根真菌可通过上调蒜氨酸酶表达,促进大蒜中含氮类成分的积累^[43]。球孢白僵菌AUMC 15401与玫瑰巨孢囊霉可分别调控诱导马铃薯和平滑牧豆树中特定生物碱的合成^[44,45]。此外,真菌还可通过生物转化直接代谢植物成分,改变代谢谱,如聚多曲霉PET-2^[46]能将普洱茶中的咖啡因有效转化为茶碱。

1.1.4 功能菌株对其他类型植物成分的调控

除酚类、萜类、生物碱类外,植物其他次生代谢产物(如多糖、苯并噁嗪等)同样受到微生物调控,目前研究多聚焦于农作物与食用植物。例如,微枝形杆菌等菌群定殖枸杞后,可诱导其果实大量积累多糖类化合物;接种巴西固氮螺菌、脂环固氮螺菌及恶臭假单胞菌等复合菌群^[47-50],则能显著改变玉米体内苯并噁嗪类及其衍生物的含量与组成。

不同微生物对植物次生代谢的调控范围存在显著差异。假单胞菌属(*Pseudomonas*)与球囊霉属(*Glomus*)等表现出广泛的调控活性,可同时影响植物酚类、萜类及生物碱等多种代谢路径;与之相比,慢生根瘤菌属(*Bradyrhizobium*)与巨孢囊霉属(*Gigaspora*)所报道的效应范围则较窄,多集中于特定宿主及特定类群代谢物的诱导。值得注意的是,现有研究形式多样,其中约60%基于田间或土壤培养,38%依托实验室无菌系统,另有2%在非灭菌条

件下开展。不同体系间的研究结果异质,缺乏直接可比性,其效应的重现性仍待进一步验证。以球毛壳菌D38与丹参的互作为例:在液体共培养体系中(18天),该菌可提高丹参酮类成分含量8~14倍;在土壤体系中(6个月),丹参酮类的增幅缩减至1~3倍,而丹参酚酸B含量提升21%^[88]。如何构建简便、高效,且能精准反映土壤真实生境的实验室模型体系,是该领域当前面临的重要挑战。

1.2 微生物提取物介导的植物次生代谢调控表型

探讨微生物提取物对植物次生代谢的影响,是连接“功能菌株”与“活性代谢物”的重要桥梁。微生物提取物的获取途径主要分为两类:一是通过过滤、研磨等物理手段破碎菌体,以提取微生物细胞组分及其胞内代谢物;二是通过萃取、浓缩等化学方法处理培养液,以富集微生物分泌的胞外代谢物。上述提取物常被称为微生物“诱导子”(elicitor),用于处理植物根、叶等部位往往能产生与功能菌株高度相似的调控效应。

微生物提取物调控植物次生代谢的研究主要聚焦于酚类、萜类、生物碱及糖类代谢产物,目前已涵盖21种植物和33个微生物菌属(图2)。早在1984年,研究者用菜豆炭疽菌菌丝体处理菜豆下胚轴后,发现查耳酮合酶mRNA表达量呈时间依赖性上调,160小时后较对照增加29倍^[52]。当前,微生物诱导子对药用植物活性成分含量的提升展现出巨大潜力。例如,假单胞菌属、泛菌属的培养液及毛霉属的菌丝提取物,均能有效提高丹参中丹参酚酸B和迷迭香酸的含量^[53,54];黑曲霉ATCC 16404菌丝体可诱导甘草产生乌拉尔皂苷B、甘草皂苷B2及甘草苷^[55],将其灭活发酵液施用于红豆杉愈伤组织后,紫杉醇产量提升约40%^[56]。此外,拟盘多毛孢属和篮状菌属真菌的培养滤液处理铁皮石斛根际,可促进植株内柚皮素和夏佛塔苷的积累^[57];而镰刀菌属与农杆菌属等菌株的菌丝体则可显著提升贯叶连翘中蒽醌类成分(如金丝桃素)的含量^[58];青霉属、曲霉属及毛霉属等微生物的菌丝体处理长春花悬浮细胞,亦能显著驱动生物碱类成分的合成^[59]。

1.3 微生物信号分子介导的植物次生代谢调控表型

微生物功能菌株及其提取物对植物次生代谢的调控,主要归因于其中含有的活性化合物。它们可作为信号分子被植物识别,并发挥调控作用。然而,目前针对单一信号分子调控植物次生代谢的机制研

究相对匮乏。鲜有研究能够依据功能菌株或提取物的调控表型,成功鉴定出关键信号分子并最终阐明其作用机制。已报道的成功案例包括:番茄根际土壤总菌接种于水培体系的番茄根际,产生的壬二酸(azelaic acid)被其根系吸收并转化为壬二酸糖苷,可调控糖代谢与氧脂素(oxylin),在全株形成系统性代谢重编程^[60]。来自葡萄根际的链霉菌AgN23分泌大环内酯类代谢物galbonolides,可诱导拟南芥根际产生并积累吡啶类植保素camalexin^[61]。丁香假单胞菌DC3000分泌亚胺糖类代谢物glycosyrin,重塑宿主糖相关代谢,改变了半乳糖基甘油、海藻糖等化合物的含量^[62],促进病原菌在烟草叶片中的定殖。木霉T34/T39/SC1在葡萄叶片中释放6-戊基-2H-吡喃-2-酮、2-戊基呋喃等挥发性代谢物,可促使胼胝质(β -1,3-葡聚糖)沉积并提高免疫防御能力^[63]。

由于微生物源单体化合物在农药中应用广泛,它们对植物次生代谢的调控作用也被广泛关注^[64]。例如,来自阿维菌素链霉菌(*Streptomyces avermitilis*)的阿维菌素(ivermectin)是农业领域高效广谱的杀虫剂。该化合物可定向提升芹菜中咖啡酸和木犀草素的水平^[65]。来自春日链霉菌(*Streptomyces kasugaensis*)的抗菌素春雷霉素(kasugamycin)主要用于防治稻瘟病、细菌性角斑病等。该化合物能够迅速诱导槟榔植株内可溶性糖的大量积累,提升植物抗逆水平^[66]。然而,相关的作用机制仍有待进一步阐明。

2 微生物调控植物代谢等生理过程的分子机制

2.1 功能菌株及其提取物调控植物代谢的机制

功能菌株及其提取物调控植物代谢表型的研究已相当丰富,但其作用机制的研究却极为匮乏,目前主要停留在对少数关键基因和蛋白质表达水平的初步表征。例如,豆科根瘤菌定殖豆科植物后,可上调苯丙氨酸解氨酶(PAL)、查耳酮合酶(CHS)等关键生物合成基因的表达,提高植株体内黄酮和查耳酮含量^[67]。类似地,类芽孢杆菌属细菌侵染苜蓿,也可上调黄酮和查耳酮生物合成基因的表达^[68,69]。荧光假单胞菌WCS417r定殖拟南芥后,可显著上调萜烯合酶基因TPS03和TPS04的表达,诱导植株积累(E)- α -香柠檬烯^[70]。含有芽孢杆菌属细菌的黄花蒿内生菌复合菌群可激活WRKY等转录因子,上调3-羟基-3-甲基戊二酰辅酶A还原酶(HMGR)、细胞色

素P450 7AV1(*CYP7AV1*)、青蒿酸合酶(ADS)等青蒿素合成关键基因的表达,同时下调角鲨烯合酶(SQS)等竞争通路基因的表达,引导代谢流向青蒿素合成,显著提升植株的青蒿素含量^[71]。

部分功能菌株已作为微生物农药使用,其抗病、抗逆机制多与调控植物激素代谢有关。例如,微生物菌剂枯草芽孢杆菌在水稻根系的定殖可全面激活水杨酸(*PAD4/EDS1/WRKY62*)、茉莉酸(*WRKY30/WRKY77/JAR1*)及乙烯(*EIN2/EIL1/ERF1*)信号通路^[72],促使宿主植物进入免疫激活状态,显著降低稻瘟病的侵染风险。寡雄腐霉复合菌剂可迅速诱导宿主根际几丁质酶表达并激活水杨酸通路,通过级联放大转录因子WRKY33及病程相关蛋白PR的表达信号,启动植物系统性免疫应答^[73,74]。基于出芽短梗霉的生防产品则通过激活水杨酸途径,逆转病原菌诱导的免疫抑制,抑制病原菌定殖^[75,76]。然而,这些菌株的作用机制研究,仍显著滞后于其表型观察和生产应用。

2.2 微生物信号分子调控植物代谢的机制

目前,通过功能菌株或提取物调控植物代谢表型,进而鉴定相关信号分子并阐明其作用机制的研究仍极为匮乏。尽管如此,上文1.3已综述的可追溯信号分子表明,微生物成分对植物次生代谢的调控展现出系统性特征:其信号可进行长距离传导,通过介导植物免疫通路间接调控次生代谢,并可靶向特异的植物代谢通路(图3)。

根际局部的微生物代谢物可进行长距离传导,诱发植物系统性的代谢重编程。向水培番茄根际局部接种土壤总菌后,壬二酸可被根系吸收,并在番茄中转化为壬二酸糖苷。该衍生物通过长距离运输系统从根际局部转移至全株,调控糖代谢及氧脂素合成途径的相关基因表达。不同功能菌株对番茄根系分泌代谢物的诱导具有高度分类学特异性:假单胞菌目(*Pseudomonadales*)主要诱导阿魏酸己糖(ferulic acid hexoside)分泌,而芽孢杆菌目(*Bacillales*)则主要促进酰基蔗糖(acyl-sucrose)释放。这表明,根际微生物信号分子可借助植物的糖基化修饰与运输机制,实现对其次生代谢的系统性调控^[60]。

多项经典研究揭示了微生物通过信号分子调控植物免疫,驱动代谢重塑的过程。例如,葡萄根系内生链霉菌(*Streptomyces* sp. AgN23)接种于拟南芥根

际后,可通过分泌大环内酯类代谢物galbonolides,抑制植物肌醇磷酸神经酰胺合酶(IPCS),导致神经酰胺前体异常积累,进而激活多条植物防御信号通路,并诱导吡啶类植保素亚麻荠素(camalexin)的生物合成与积累。值得注意的是,积累的亚麻荠素亦能促进链霉菌AgN23在拟南芥根际的有效定殖。这一互惠机制深刻揭示了微生物代谢物galbonolides的双重功能:既能触发宿主植物的免疫防御,又能增强该微生物在生态环境中的适应性^[61]。

丁香假单胞菌番茄致病变种(*Pseudomonas syringae* pv. *tomato* DC3000)接种于烟草叶片后,可通过分泌亚胺糖类代谢物glycosyrin,抑制植物 β -半乳糖苷酶(BGAL1),阻断其介导的宿主鞭毛蛋白加工,从而减少免疫原性多肽的释放,削弱免疫信号通路。此外,抑制BGAL1还影响植物糖蛋白的加工与修饰,并重塑糖代谢,诱导半乳糖基甘油和海藻糖等的异常积累。以上效应共同促进了该致病菌在烟草叶片中的定殖。相关机制揭示了病原菌通过分泌亚胺糖类代谢物,操纵宿主的糖代谢过程,进而实现免疫逃逸并提升自身宿主适应性的策略^[62]。

木霉属真菌(*Trichoderma* T34/T39/SC1)接种于葡萄叶片后,可通过释放挥发性代谢物(6-戊基-2H-吡喃-2-酮和2-戊基呋喃等),上调宿主免疫相关基因表达,促进胼胝质(β -1,3-葡聚糖)在植物细胞壁的沉积。此外,上述挥发性代谢物还对葡萄霜霉病菌具有显著拮抗作用,揭示了有益真菌通过挥发性信号分子激活宿主防御体系并介导生物防治的潜在机制^[63]。

值得一提的是,以上植物次生代谢的变化多数来自代谢组学研究,并非所有途径均出现显著变化,表明微生物信号分子对植物代谢的调控具有特异性。同时,相关研究多涉及信号分子触发的菌株自身反馈调控或菌群重组,反映了复杂的下游相互作用机制。

2.3 微生物信号分子调控植物其他生理过程的机制

虽然针对微生物单体代谢物直接调控植物次生代谢的研究有限,但已有部分研究揭示了其调控植物其他生理过程的机制(图3)。本文对此一并予以综述,以期对相关研究提供思路借鉴。

微生物单体代谢物可靶向调控植物免疫网络。细菌脂多糖的中链脂肪酸代谢物3-羟基癸酸(3-OH-C10:0),能够特异性识别并结合拟南芥受体激酶

LORE的胞外域,触发其酪氨酸磷酸化。该磷酸化过程招募下游激酶PBL34,激发胞内钙信号级联,而上调*FRK1*、*NHL10*等免疫基因的表达。相反,假单胞菌(*Pseudomonas*)能分泌磷酸酶HopAO1逆转LORE的磷酸化水平,抑制该免疫级联反应。因此,在病原菌感染中,3-羟基癸酸驱动的植物免疫激活与细菌的拮抗性抑制机制相互制衡,决定了植物抗性与病原菌定殖的结果^[77,78]。

微生物单体代谢物可通过干预植物激素信号通路,深度参与并重塑宿主的代谢及生理过程。水稻根际微小杆菌(*Exiguobacterium* sp. R2567)分泌的环二肽cyclo(Leu-Pro)特异性结合水稻独脚金内酯(strigolactone, SL)受体OsD14,诱导SL信号阻遏蛋白OsD53降解,激活SL信号转导,在无需改变基因型的情况下,负调控分蘖数,并在室内与田间试验中得到验证^[79]。类似地,病原真菌希金斯刺盘孢(*Colletotrichum higginsianum*)分泌的二萜higginsianin B通过抑制26S蛋白酶体活性,干扰多条激素通路:一是阻碍茉莉酸(jasmonic acid, JA)通路中转录抑制蛋白JAZ的降解,并抑制茉莉酸甲酯(MeJA)向活性形式JA-Ile转化,削弱JA介导的防御;二是干扰生长素(indole-3-acetic acid, IAA)信号转导。同时阻断这些核心激素通路有效压制了植物对病原菌的识别和活性氧等防御反应的激发,促进病原菌定殖并严重干扰了宿主生长发育^[80]。

微生物单体代谢物还可通过阻断特定生物合成途径,提升植物的环境适应性。针对生物胁迫,水稻内生菌瓜类鞘氨醇单胞菌(*Sphingomonas melonis*)产生的邻氨基苯甲酸(anthranilic acid)靶向抑制病原菌毒力调控 σ 因子RpoS。该作用直接阻断了病原菌核心致病物质托酚酮的生物合成途径,从源头削弱了病原菌侵染能力,增强水稻抗病性^[81]。针对非生物胁迫,根际定殖的链霉菌(*Streptomyces*)分泌的聚酮类代谢物pteridic acid H和F在干旱和高盐条件下,显著促进拟南芥根系生长并提升生物量;转录组分析预测,相关作用机制主要涉及胁迫响应、生长素信号转导和光合作用等相关通路的激活,进而增强植物对恶劣环境的耐受性^[82]。

在2.2及2.3中,单一微生物信号分子对植物代谢和生理活动的调控研究主要针对免疫网络、激素信号通路和(植物、微生物的)生物合成途径,研究深度已从宏观表型观察深入到分子调控机制揭示。值得

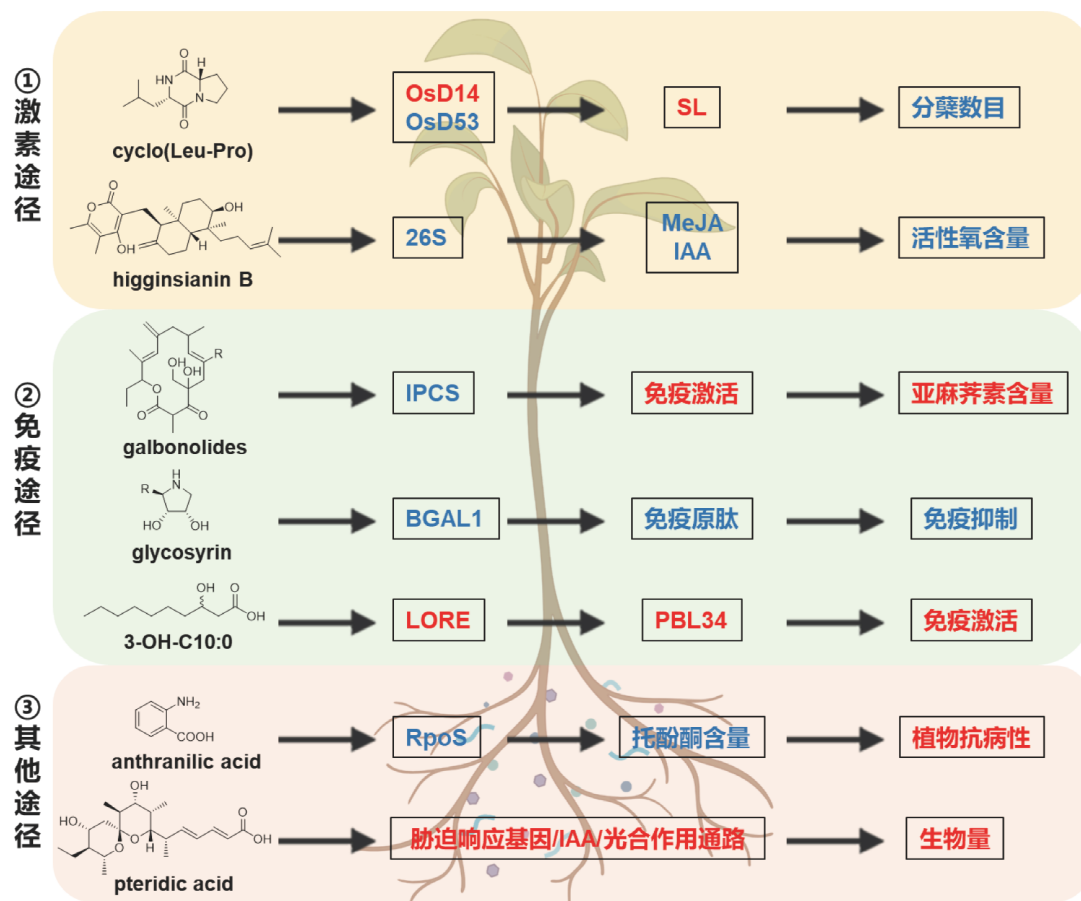


图3 微生物调控植物次生代谢和生理过程的分子机制

红色表示正调控,蓝色表示负调控。OsD14:独脚金内酯受体;OsD53:阻遏蛋白;SL:独脚金内酯;26S:蛋白酶体;MeJA:茉莉酸甲酯;IAA:生长素;IPCS:植物肌醇磷酸神经酰胺合酶;BGAL1: β -半乳糖苷酶;LORE:G型凝集素受体激酶;PBL34:细胞质激酶;RpoS:稳定期 σ 因子。

Figure 3 Microbial regulation of plant secondary metabolites and physiological processes.

Red indicates positive regulation and blue indicates negative regulation. OsD14: rice receptor DWARF14; OsD53: rice repressor protein DWARF53; SL: strigolactone; 26S: 26S proteasome; MeJA: methyl jasmonate; IAA: indole-3-acetic acid; IPCS: inositol phosphorylceramide synthase; BGAL1: β -galactosidase; LORE: lipooligosaccharide-specific reduced elicitation; PBL34: cytoplasmic kinase; RpoS: stationary phase σ factor.

注意的是,针对药用植物次生代谢网络的系统性调控研究仍然缺乏。

3 植物次生代谢物对微生物群落的反馈调节及生物学意义

微生物与植物次生代谢之间存在紧密的双向反馈:微生物可调控植物次生代谢物的合成,而后者又反向重塑环境微生物群落。鉴于该领域研究众多,本文仅聚焦于以微生物调控为切入点,分子机制相对明确的典型案例。

在模式植物领域,拟南芥通过根系特异性分泌的次生代谢物来重塑根际微生态。植物依赖特异性萜类生物合成基因簇向土壤中分泌拟南芥宁素

(thalianin)、拟南芥宁基中链脂肪酸酯(TFAEs)以及拟南芥啉素(arabidin)等三萜类化合物,从而定向提高变形菌门和厚壁菌门的丰度,降低放线菌门占比^[83]。同时,部分微生物具备相应的代谢适应性,如假单胞菌属和土壤杆菌属能够通过表达脂肪酶或乙醇脱氢酶降解或转化这些三萜类物质,进而引发微环境代谢物谱的改变并发生级联效应。再例如,拟南芥在感知丁香假单胞菌DC3000感染时,通过酮脂酰辅酶A脱氢酶与脂肪酸酰胺水解酶,调控体内广谱抗毒素芥酸酰胺(erucamide)的合成与降解动态平衡。芥酸酰胺特异性靶向革兰氏阴性菌III型分泌系统(T3SS)的保守核心蛋白HrcC,通过干扰毒力注射体的组装,有效阻断致病效应蛋白向宿主细胞

的转运。这种“非杀菌型”防御模式在赋予宿主广谱抗性的同时,可显著降低病原菌的进化选择压力,从而规避耐药性的产生^[51]。此外,上文中链霉菌诱导拟南芥分泌的亚麻荠素^[61],也可靶向抑制竞争性菌群的定殖,保障链霉菌自身的定殖优势,实现对根际微生物群落的精准重塑。

在作物领域,甜瓜根系经MATE转运蛋白分泌的葫芦素B(cucurbitacin B),可在根际引发复杂的微生物互作:不仅作为碳源促进肠杆菌属的增殖,被消耗后还解除了对芽孢杆菌属的生长抑制。随后大量富集的芽孢杆菌通过强效拮抗作用,有效抵御了土传病原菌尖孢镰刀菌的侵染,为甜瓜构筑坚固的生物屏障^[84]。类似地,马铃薯幼苗在面临土壤毒性物质香草醛(vanillin)胁迫时,会通过根系释放的川陈皮素(nobiletin)来化解危机。川陈皮素可选择性招募并富集根际有益泛菌MCC16,该菌株可大量合成生长素(IAA)并分泌于根系微环境中,诱导根部应答基因*StARF3*与*StIAA4*的表达,促进不定根的发育以缓解有毒物的胁迫^[85]。

在药用植物领域,次生代谢物介导的根际化学互作则更多地被报道具有负向调控作用。三七根系持续分泌的皂苷类物质不仅抑制被孢霉属(*Mortierella*)等有益菌定殖,更是作为病原菌尖孢镰刀菌(*Fusarium oxysporum*)的碳源,破坏根际微生态平衡并诱导根腐病^[86]。类似地,唐古特大黄的根际互作呈现出高度动态变化:早期通过分泌初级代谢物(有机酸、氨基酸)富集拜叶林克氏菌科(*Beijerinckiaceae*)等有益微生物,助力氮素循环与蒽醌类的积累;在生长后期,其分泌的胺类和苯类等代谢物则反向调控根际微生物群落,抑制有益菌并富集假散囊菌科(*Pseudeurotiaceae*)等病原菌,引发根际微生物群落结构失衡^[87]。阐明药用植物代谢物驱动的根本群落动态变化,对突破中药连作障碍,促进产业可持续发展具有重要意义,是亟待深入探索的研究方向。

4 总结与展望

本综述的主要结论归纳如下。(1)微生物及其代谢物对植物次生代谢的调控具有普遍性。其中,假单胞菌属、芽孢杆菌属、根瘤菌属等细菌,以及球囊霉属、根胞囊霉属等真菌的功能菌株,其调控效应的报道最为频繁。(2)微生物信号分子调控植物代

谢的核心机制,主要涉及对植物免疫系统与激素信号通路的干预,进而影响次生代谢物合成相关基因的表达。(3)植物与微生物间存在基于次生代谢物的紧密双向互作。受微生物诱导的植物次生代谢产物,不仅能调节植物自身生理状态,更可产生强烈的生态反馈效应,驱动环境微生物群落的定向重组。重塑的微生物群落则进一步对植物生长发育产生影响,形成持续互动循环。

推动微生物调控植物次生代谢研究从“现象描述”到“机制阐明”,核心在于揭示植物-微生物相互作用的内在规律及其分子调控网络。我们认为,当前该领域仍面临以下核心科学问题。(1)哪些微生物信号分子驱动植物次生代谢的重塑。在现有研究中,关键信号分子的挖掘严重滞后,在近190项研究(包含综述^[5,6]已汇总的91项研究)中,明确鉴定的关键活性单体的比例不足5%,这主要受限于分离鉴定的技术瓶颈。(2)已报道的代谢调控表型的分子机制是什么。尽管诸多代谢调控现象已被广泛报道,甚至在农业生产中应用,但阐明其分子机理的研究比例却不足3%。凸显出当前研究对“表型观测”与“机制解析”的关注重点存在明显差异:现有机制研究往往聚焦于重要信号通路(如免疫应答),而未能解释表型层面所展现的核心代谢特征及其特异性调控过程。(3)植物-微生物相互作用的全局协同过程与进化意义是什么。植物-微生物互作是一个跨越多维度、涉及多环节的协同过程。然而,当前研究在上游感知(信号分子诱导)、中游响应(植物代谢重塑)与下游反馈(微生物组重构)之间缺乏有机衔接,对长周期的协同反馈调节动态缺乏揭示。由于化学、植物生理学、生态学及微生物学等多学科视角的分化,现有研究成果呈现碎片化倾向,制约了对化学-生态互作全景及其生物学意义的阐释。

针对上述挑战,本领域也亟待在研究范式与技术方法上寻求突破。(1)构建系统化、全景式的研究范式,贯通“信号分子诱导-植物代谢重塑-微生物组重构-协同反馈调节”的完整逻辑闭环。除加强多学科交叉协作外,还应大力发展双向验证策略:既可正向筛选促使植物产生特定代谢物的微生物信号分子,同时又能反向溯源具备活性信号分子产出能力或特定代谢物诱导能力的优势菌株,从而精准揭示关键信号分子及其生物学功能。(2)强化微生物活性代谢物的物质基础研究。针对目前信号分子挖掘

不足、阻碍分子机制研究的现状,亟需引入“活性导向”的分离策略。与天然药物化学等学科深度合作,综合运用高效分离纯化、微量结构解析、生物合成与生物制造等技术,从复杂的微生物代谢物中获得关键活性单体的结构。(3)优化基础研究关键支撑体系。在研究模型方面,构建高通量、模拟真实生境的筛选系统,发展能够反映田间微生态变化的实验室模型;在遗传工具方面,加快推进药用植物等非模式作物的遗传转化体系开发;在数据资源方面,亟需系统积累并建立植物-微生物互作的分子调控网络数据库,为机制阐明提供数据支撑。

微生物对植物次生代谢的调控及其反馈效应的揭示,有望在以下三个领域推动产业化应用:在农林业领域,研究成果可用于开发新型生物制剂与生物农药,降低化学农药依赖,实现绿色、高效抗病与抗逆,助力农业可持续发展。在中药领域,针对中药材有效成分易受环境影响等问题,可利用特异性功能菌株及代谢物诱导剂,精准调控并显著提升药用成分积累,推动中药材绿色栽培。在生物制造领域,面对药品、化妆品等产业对酚类、萜类等高价值天然产物的需求,所阐明的调控机制或发现的活性成分,有望用于强化植物或微生物底盘细胞的生产效率,从而突破传统提取方式的限制,开辟生物制造新途径。

参考文献

- [1] Martin FM, Uroz S, Barker DG. Ancestral alliances: plant mutualistic symbioses with fungi and bacteria. *Science*, 2017, 356: eaad4501.
- [2] Song P, Liu J, Huang P, et al. Diversity and structural analysis of rhizosphere soil microbial communities in wild and cultivated *Rhizoma Atractylodis Macrocephalae* and their effects on the accumulation of active components. *PeerJ*, 2023, 11: e14841.
- [3] Sasse J, Martinoia E, Northen T. Feed your friends: do plant exudates shape the root microbiome? *Trends Plant Sci*, 2018, 23: 25–41.
- [4] Trivedi P, Leach JE, Tringe SG, et al. Plant-microbiome interactions: from community assembly to plant health. *Nat Rev Microbiol*, 2020, 18: 607–21.
- [5] Etalo Desalegn W, Jeon JS, Raaijmakers JM. Modulation of plant chemistry by beneficial root microbiota. *Nat Prod Rep*, 2018, 35: 398–409.
- [6] Lv J, Yang S, Zhou W, et al. Microbial regulation of plant secondary metabolites: impact, mechanisms and prospects. *Microbiol Res*, 2024, 283: 127688.
- [7] Yu J, Tu X, Huang AC. Functions and biosynthesis of plant signaling metabolites mediating plant-microbe interactions. *Nat Prod Rep*, 2022, 39: 1393–422.
- [8] Fan X, Ge AH, Qi S, et al. Root exudates and microbial metabolites: signals and nutrients in plant-microbe interactions. *Sci China Life Sci*, 2025, 68: 2290–302.
- [9] Libbert E, Kaiser W, Kunert R. Interactions between plants and epiphytic bacteria regarding their auxin metabolism VI. The influence of the epiphytic bacteria on the content of extractable auxin in the plant. *Physiol Plant*, 1969, 22: 432–9.
- [10] Wink M. Plant secondary metabolism: diversity, function and its evolution. *Nat Prod Commun*, 2008, 3: 1205–16.
- [11] Al-Khayri JM, Rashmi R, Toppo V, et al. Plant secondary metabolites: the weapons for biotic stress management. *Metabolites*, 2023, 13: 716.
- [12] van de Mortel JE, de Vos RCH, Dekkers E, et al. Metabolic and transcriptomic changes induced in *Arabidopsis* by the rhizobacterium *Pseudomonas fluorescens* SS101. *Plant Physiol*, 2012, 160: 2173–88.
- [13] Flores-Cortez I, Winkler R, Ramírez-Ordorica A, et al. A mass spectrometry-based study shows that volatiles emitted by *Arthrobacter agilis* UMCV2 increase the content of brassinosteroids in *Medicago truncatula* in response to iron deficiency stress. *Molecules*, 2019, 24: 3011.
- [14] Schmidt R, Köberl M, Mostafa A, et al. Effects of bacterial inoculants on the indigenous microbiome and secondary metabolites of chamomile plants. *Front Microbiol*, 2014, 5: 64.
- [15] Chamam A, Sanguin H, Bellvert F, et al. Plant secondary metabolite profiling evidences strain-dependent effect in the *Azospirillum-Oryza sativa* association. *Phytochemistry*, 2013, 87: 65–77.
- [16] Mishra RPN, Singh RK, Jaiswal HK, et al. *Rhizobium*-mediated induction of phenolics and plant growth promotion in rice (*Oryza sativa* L.). *Curr Microbiol*, 2006, 52: 383–9.
- [17] Rusjan D, Halbwirth H, Stich K, et al. Biochemical response of grapevine variety ‘Chardonnay’ (*Vitis vinifera* L.) to infection with grapevine yellows (*Bois noir*). *Eur J Plant Pathol*, 2012, 134: 231–7.
- [18] Vrancken K, Holtappels M, Schoofs H, et al. *Erwinia amylovora* affects the phenylpropanoid-flavonoid pathway in mature leaves of *Pyrus communis* cv. Conférence. *Plant Physiol Biochem*, 2013, 72: 134–44.
- [19] Yang Y, Ou X, Yang G, et al. Arbuscular mycorrhizal fungi regulate the growth and phyto-active compound of

- Salvia miltiorrhiza* seedlings. Appl Sci, 2017, 7: 68.
- [20] Adolfsson L, Nziengui H, Abreu IN, et al. Enhanced secondary- and hormone metabolism in leaves of arbuscular mycorrhizal *Medicago truncatula*. Plant Physiol, 2017, 175: 392–411.
- [21] Mechri B, Tekaya M, Cheheb H, et al. Accumulation of flavonoids and phenolic compounds in olive tree roots in response to mycorrhizal colonization: a possible mechanism for regulation of defense molecules. J Plant Physiol, 2015, 185: 40–3.
- [22] Sarmiento-López LG, López-Meyer M, Sepúlveda-Jiménez G, et al. Arbuscular mycorrhizal symbiosis in *Stevia rebaudiana* increases trichome development, flavonoid and phenolic compound accumulation. Biocatal Agric Biotechnol, 2021, 31: 101889.
- [23] Xie W, Hao Z, Zhou X, et al. Arbuscular mycorrhiza facilitates the accumulation of glycyrrhizin and liquiritin in *Glycyrrhiza uralensis* under drought stress. Mycorrhiza, 2018, 28: 285–300.
- [24] Avio L, Sbrana C, Giovannetti M, et al. Arbuscular mycorrhizal fungi affect total phenolics content and antioxidant activity in leaves of oak leaf lettuce varieties. Sci Hortic, 2017, 224: 265–71.
- [25] Devi MC, Reddy MN. Phenolic acid metabolism of groundnut (*Arachis hypogaea* L.) plants inoculated with VAM fungus and *Rhizobium*. Plant Growth Regul, 2002, 37: 151–6.
- [26] Bharti N, Yadav D, Barnawal D, et al. *Exiguobacterium oxidotolerans*, a halotolerant plant growth promoting rhizobacteria, improves yield and content of secondary metabolites in *Bacopa monnieri* (L.) Pennell under primary and secondary salt stress. World J Microbiol Biotechnol, 2012, 29: 379–87.
- [27] Singh R, Soni SK, Kalra A. Synergy between *Glomus fasciculatum* and a beneficial *Pseudomonas* in reducing root diseases and improving yield and forskolin content in *Coleus forskohlii* Briq. under organic field conditions. Mycorrhiza, 2012, 23: 35–44.
- [28] Couto C, Silva LR, Valentão P, et al. Effects induced by the nodulation with *Bradyrhizobium japonicum* on *Glycine max* (soybean) metabolism and antioxidant potential. Food Chem, 2011, 127: 1487–95.
- [29] Silva LR, Pereira MJ, Azevedo J, et al. Inoculation with *Bradyrhizobium japonicum* enhances the organic and fatty acids content of soybean (*Glycine max* (L.) Merrill) seeds. Food Chem, 2013, 141: 3636–48.
- [30] Xie Z, Chu Y, Zhang W, et al. *Bacillus pumilus* alleviates drought stress and increases metabolite accumulation in *Glycyrrhiza uralensis* Fisch. Environ Exp Bot, 2019, 158: 99–106.
- [31] Liu Z, Ma Y, Lv X, et al. Abiotic factors and endophytes co-regulate flavone and terpenoid glycoside metabolism in *Glycyrrhiza uralensis*. Appl Microbiol Biotechnol, 2023, 107: 2671–88.
- [32] Awasthi A, Bharti N, Nair P, et al. Synergistic effect of *Glomus mosseae* and nitrogen fixing *Bacillus subtilis* strain Daz26 on artemisinin content in *Artemisia annua* L. Appl Soil Ecol, 2011, 49: 125–30.
- [33] Boneca IG, Li J, Zhao GZ, et al. An endophytic *Pseudonocardia* species induces the production of artemisinin in *Artemisia annua*. PLoS One, 2012, 7: e51410.
- [34] Tripathi A, Awasthi A, Singh S, et al. Enhancing artemisinin yields through an ecologically functional community of endophytes in *Artemisia annua*. Ind Crops Prod, 2020, 150: 112375.
- [35] Cao X, Xu L, Wang J, et al. Endophytic fungus *Pseudodidymocyrtis lobariellae* KL27 promotes taxol biosynthesis and accumulation in *Taxus chinensis*. BMC Plant Biol, 2022, 22: 12.
- [36] Zheng LP, Tian H, Yuan YF, et al. The influence of endophytic *Penicillium oxalicum* B4 on growth and artemisinin biosynthesis of in vitro propagated plantlets of *Artemisia annua* L. Plant Growth Regul, 2016, 80: 93–102.
- [37] Mandal S, Upadhyay S, Wajid S, et al. Arbuscular mycorrhiza increase artemisinin accumulation in *Artemisia annua* by higher expression of key biosynthesis genes via enhanced jasmonic acid levels. Mycorrhiza, 2014, 25: 345–57.
- [38] Jaleel CA, Gopi R, Gomathinayagam M, et al. Traditional and non-traditional plant growth regulators alters phytochemical constituents in *Catharanthus roseus*. Process Biochem, 2009, 44: 205–9.
- [39] Ghorbanpour M, Ghafarzadegan R, Khavazi K, et al. Two main tropane alkaloids variations of black henbane (*Hyoscyamus niger*) under PGPRs inoculation and water deficit stress induction at flowering stage. J Med Plants, 2013, 12: 45.
- [40] Singh B, Sahu PM, Aloria M, et al. *Azotobacter chroococcum* and *Pseudomonas putida* enhance pyrroloquinazoline alkaloids accumulation in *Adhatoda vasica* hairy roots by biotization. J Biotechnol, 2022, 353: 51–60.
- [41] Tiwari R, Awasthi A, Mall M, et al. Bacterial endophyte-mediated enhancement of in planta content of key terpenoid indole alkaloids and growth parameters of *Catharanthus roseus*. Ind Crops Prod, 2013, 43: 306–10.
- [42] Bonilla A, Sarria AL, Algar E, et al. Microbe associated

- molecular patterns from rhizosphere bacteria trigger germination and *Papaver somniferum* metabolism under greenhouse conditions. *Plant Physiol Biochem*, 2014, 74: 133–40.
- [43] Borde M, Dudhane M, Jite PK. Role of Bioinoculant (AM Fungi) increasing in growth, flavor content and yield in *Allium sativum* L. under field condition. *Not Bot Horti Agrobot*, 2009, 37: 124–8.
- [44] Salem SH, El-Maraghy SS, Abdel-Mallek AY, et al. GC-MS analysis, cytotoxicity, and molecular docking studies of bioactive alkaloids extracted from tomato leaves inoculated with endophytic fungus *Beauveria* sp. AUMC 15401. *J Food Process Preserv*, 2022, 46: e17039.
- [45] Rojas-Andrade R, Cerda-García-Rojas C, Frías-Hernández J, et al. Changes in the concentration of trigonelline in a semi-arid leguminous plant (*Prosopis laevigata*) induced by an arbuscular mycorrhizal fungus during the presymbiotic phase. *Mycorrhiza*, 2003, 13: 49–52.
- [46] Zhou B, Ma C, Ren X, et al. Production of theophylline via aerobic fermentation of pu-erh tea using tea-derived fungi. *BMC Microbiol*, 2019, 19: 261.
- [47] Couillerot O, Ramírez-Trujillo A, Walker V, et al. Comparison of prominent *Azospirillum* strains in *Azospirillum-Pseudomonas-Glomus* consortia for promotion of maize growth. *Appl Microbiol Biotechnol*, 2012, 97: 4639–49.
- [48] Walker V, Couillerot O, Von Felten A, et al. Variation of secondary metabolite levels in maize seedling roots induced by inoculation with *Azospirillum*, *Pseudomonas* and *Glomus* consortium under field conditions. *Plant Soil*, 2011, 356: 151–63.
- [49] Planchamp C, Glauser G, Mauch-Mani B. Root inoculation with *Pseudomonas putida* KT2440 induces transcriptional and metabolic changes and systemic resistance in maize plants. *Front Plant Sci*, 2015, 5: 719.
- [50] Walker V, Bertrand C, Bellvert F, et al. Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus *Azospirillum*. *New Phytol*, 2010, 189: 494–506.
- [51] Miao P, Wang H, Wang W, et al. A widespread plant defense compound disarms bacterial type III injectisome assembly. *Science*, 2025, 387: eads0377.
- [52] Ryder TB, Cramer CL, Bell JN, et al. Elicitor rapidly induces chalcone synthase mRNA in *Phaseolus vulgaris* cells at the onset of the phytoalexin defense response. *Proc Natl Acad Sci U S A*, 1984, 81: 5724–8.
- [53] Xu W, Jin X, Yang M, et al. Primary and secondary metabolites produced in *Salvia miltiorrhiza* hairy roots by an endophytic fungal elicitor from *Mucor fragilis*. *Plant Physiol Biochem*, 2021, 160: 404–12.
- [54] You H, Yang S, Zhang L, et al. Promotion of phenolic compounds production in *Salvia miltiorrhiza* hairy roots by six strains of rhizosphere bacteria. *Eng Life Sci*, 2018, 18: 160–8.
- [55] Li J, Wang J, Li J, et al. *Aspergillus niger* enhance bioactive compounds biosynthesis as well as expression of functional genes in adventitious roots of *Glycyrrhiza uralensis* fisch. *Appl Biochem Biotechnol*, 2015, 178: 576–93.
- [56] Wang C, Wu J, Mei X. Enhancement of Taxol production and excretion in *Taxus chinensis* cell culture by fungal elicitation and medium renewal. *Appl Microbiol Biotechnol*, 2001, 55: 404–10.
- [57] Zhu B, Wu L, Wan H, et al. Fungal elicitors stimulate biomass and active ingredients accumulation in *Dendrobium catenatum* plantlets. *Biologia*, 2018, 73: 917–26.
- [58] Gadzovska Simic S, Tusevski O, Maury S, et al. Fungal elicitor-mediated enhancement in phenylpropanoid and naphthodianthrone contents of *Hypericum perforatum* L. cell cultures. *Plant Cell Tissue Organ Cult*, 2015, 122: 213–26.
- [59] Zhao J, Zhu WH, Hu Q. Selection of fungal elicitors to increase indole alkaloid accumulation in *Catharanthus roseus* suspension cell culture. *Enzyme Microb Technol*, 2001, 28: 666–72.
- [60] Korenblum E, Dong Y, Szymanski J, et al. Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc Natl Acad Sci U S A*, 2020, 117: 3874–83.
- [61] Nicolle C, Gayraud D, Noel A, et al. Root-associated *Streptomyces* produce galbanolides to modulate plant immunity and promote rhizosphere colonization. *ISME J*, 2024, 18: wrae112.
- [62] Sanguankiatichai N, Chandrasekar B, Sheng Y, et al. Bacterial pathogen deploys the iminosugar glycosyrin to manipulate plant glycobiology. *Science*, 2025, 388: 297–303.
- [63] Lazazzara V, Vicelli B, Bueschl C, et al. *Trichoderma* spp. volatile organic compounds protect grapevine plants by activating defense-related processes against downy mildew. *Physiol Plant*, 2021, 172: 1950–65.
- [64] 张慧, 许宁, 曹丽茹, 等. 我国微生物农药的研发与应用研究进展. *农药学报*, 2023, 25: 769–78.
Zhang H, Xu N, Cao L, et al. Review on research and utilization of microbial pesticides in China. *Chinese Journal of Pesticide Science*, 2023, 25: 769–78.

- [65] 白天,崔新仪,李宁,等.阿维菌素对芹菜中酚类活性成分的影响.新疆环境保护,2022,44:9–14.
- Bai T, Cui X, Li N, et al. Effect of abamectin on phenolic active components in celery. Xinjiang Environmental Protection, 2022, 44: 9–14.
- [66] 吴朝波,任承才,朱明军,等.春雷霉素与松脂酸铜复配防治槟榔叶斑病的效果研究.中国农技推广,2010,37:91–6.
- Wu C, Ren C, Zhu M, et al. Study on the protective effect of kasugamycin combined with copper abietate against leaf spot disease of *Areca catechu*. China Agricultural Technology Extension, 2010, 37: 91–6.
- [67] Recourt K, van Tunen AJ, Mur LA, et al. Activation of flavonoid biosynthesis in roots of *Vicia sativa* subsp. *nigra* plants by inoculation with *Rhizobium leguminosarum* biovar *viciae*. Plant Mol Biol, 1992, 19: 411–20.
- [68] Samain E, van Tuinen D, Jeandet P, et al. Biological control of septoria leaf blotch and growth promotion in wheat by *Paenibacillus* sp. strain B2 and *Curtobacterium plantarum* strain EDS. Biol Control, 2017, 114: 87–96.
- [69] Selim S, Negrel J, Wendehenne D, et al. Stimulation of defense reactions in *Medicago truncatula* by antagonistic lipopeptides from *Paenibacillus* sp. strain B2. Appl Environ Microbiol, 2010, 76: 7420–8.
- [70] Pangesti N, Weldegergis BT, Langendorf B, et al. Rhizobacterial colonization of roots modulates plant volatile emission and enhances the attraction of a parasitoid wasp to host-infested plants. Oecologia, 2015, 178: 1169–80.
- [71] Tripathi A, Pandey P, Tripathi SN, et al. Plant growth-promoting endophytic consortium improved artemisinin biosynthesis via modulating antioxidants, gene expression, and transcriptional profile in *Artemisia annua* (L.) under stressed environments. Plant Stress, 2025, 15: 100757.
- [72] Johnson T, Kemmerer L, Garcia N, et al. *Bacillus subtilis* strain UD1022 as a biocontrol agent against *Magnaporthe oryzae*, the rice blast pathogen. Microbiol Spectrum, 2025, 13: 1–17.
- [73] Xue Y, Li W, Li M, et al. Biological control of a root-knot nematode *Meloidogyne incognita* infection of tomato (*Solanum lycopersicum* L.) by the oomycete biocontrol agent *Pythium oligandrum*. J Fungi, 2024, 10: 265.
- [74] Benhamou N, le Floch G, Vallance J, et al. *Pythium oligandrum*: an example of opportunistic success. Microbiology, 2012, 158: 2679–94.
- [75] Zeng Q, Johnson KB, Mukhtar S, et al. *Aureobasidium pullulans* from the fire blight biocontrol product, blossom protect, induces host resistance in apple flowers. Phytopathology, 2023, 113: 1192–201.
- [76] Caro MDP, Venturuzzi AL, Moschen S, et al. A fungal protease named AsES triggers antiviral immune responses and effectively restricts virus infection in arabidopsis and *Nicotiana benthamiana* plants. Ann Bot, 2022, 129: 593–606.
- [77] Kutschera A, Dawid C, Gisch N, et al. Bacterial medium-chain 3-hydroxy fatty acid metabolites trigger immunity in *Arabidopsis* plants. Science, 2019, 364: 178–81.
- [78] Luo X, Wu W, Liang Y, et al. Tyrosine phosphorylation of the lectin receptor-like kinase LORE regulates plant immunity. EMBO J, 2020, 39: e102856.
- [79] Zhang J, Wang B, Xu H, et al. Root microbiota regulates tiller number in rice. Cell, 2025, 188: 3152–66.e16.
- [80] Dallery JF, Zimmer M, Halder V, et al. Inhibition of jasmonate-mediated plant defences by the fungal metabolite higginsianin B. J Exp Bot, 2020, 71: 2910–21.
- [81] Matsumoto H, Fan X, Wang Y, et al. Bacterial seed endophyte shapes disease resistance in rice. Nat Plants, 2021, 7: 60–72.
- [82] Yang Z, Qiao Y, Konakalla NC, et al. *Streptomyces* alleviate abiotic stress in plant by producing pteridic acids. Nat Commun, 2023, 14: 7398.
- [83] Huang AC, Jiang T, Liu YX, et al. A specialized metabolic network selectively modulates *Arabidopsis* root microbiota. Science, 2019, 364: 546.
- [84] Zhong Y, Xun W, Wang X, et al. Root-secreted bitter triterpene modulates the rhizosphere microbiota to improve plant fitness. Nat Plants, 2022, 8: 887–96.
- [85] Ma H, Ren Z, Luo A, et al. Self-alleviation of continuous-cropping obstacles in potato via root-exudate-driven recruitment of growth-promoting bacteria. Plant Commun, 2025, 6: 101372.
- [86] Liu Y, Lu R, Tian G, et al. Root-secreted saponins weaken soil disease suppression ability by shaping rhizosphere microbial communities in *Panax notoginseng*. Microbiol Res, 2025, 299: 128263.
- [87] Li J, Wang B, Ma H, et al. Root exudates drive plant-microbiome interactions influencing the quality of cultivated *Rheum tanguticum* during different growth development stages. Ind Crops Prod, 2025, 237: 122157.
- [88] Zhai X, Luo D, Li X, et al. Endophyte *Chaetomium globosum* D38 promotes bioactive constituents accumulation and root production in *Salvia miltiorrhiza*. Front Microbiol, 2018, 8: 2694.