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Review 综述

药用植物-微生物互作的化学信号及其作用

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摘　要：药用植物与微生物间存在复杂的相互作用，互作影响着药用植物的生长发育、次生代谢产物的合成、对病原菌的防御及对环境的适应等多个方面。因此，理解作为介导二者建立联系关键纽带的化学信号物质至关重要。本文系统总结了药用植物与微生物互作过程中化学信号的类型及作用机制，分别分析了植物与微生物来源的信号物质对根际微生物群落结构、植物生长及次生代谢产物积累的影响，并探讨了双向信号在共生与竞争互作中的功能差异。尽管目前仍有许多化学信号相关科学问题有待深入研究，但可通过解析已知化学信号及其分子机制，基于“信号-微生物-功能”模式调控植物化学信号或筛选功能性微生物，重塑健康微生物区系，改善根际生态环境，促进药用植物生长，提高药用成分含量，增强对病原菌的抵抗能力。这对提升中药材质量、实现生态种植具有重要意义。

关键词：药用植物；根际微生物；化学信号；次生代谢产物；共生互作

Chemical signals and their roles in medicinal plant-microorganism interactions

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Abstract: Medicinal plants and microorganisms engage in complex, dynamic interactions that profoundly influence plant growth and development, the biosynthesis of secondary metabolites,

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resistance to pathogens, and adaptation to environmental stressors. Therefore, elucidating the chemical signaling molecules that mediate these interactions is of fundamental importance. The review systematically summarizes the types and functional mechanisms of chemical signals involved in medicinal plant-microorganism interactions. It highlights the roles of both plant- and microorganism-derived signaling molecules in shaping the rhizosphere microbial community assembly, regulating plant growth, and modulating the accumulation of bioactive secondary metabolites. In addition, we discuss the functional divergence of bidirectional signaling in both symbiotic and competitive interactions. Although many mechanism aspects of these chemical signals remain to be fully elucidated, current knowledge provides a solid framework for understanding their regulatory roles. With a "signal-microbiome-function" framework, it is possible to manipulate plant chemical signaling or screen functional microbial strains to reconstruct beneficial rhizosphere microbiomes. Such strategies hold potential for improving soil-plant-microorganism interactions, promoting plant growth, enhance the accumulation of medicinal compounds, and strengthen resistance to pathogens. Overall, these insights are of considerable significance for improving the quality of Chinese medicinal materials and promoting the sustainable and ecological cultivation of medicinal plants.

Keywords: medicinal plant; rhizosphere microorganism; chemical signal; secondary metabolites; symbiotic interaction

药用植物作为天然药物的宝库，其药效的物质基础源于植物体内结构多样且活性丰富的化学物质，包括初生代谢产物和次生代谢产物。初生代谢产物一般指碳水化合物、蛋白质、脂类等物质，而次生代谢产物则是以初生代谢产物为前体，在植物不同器官或组织部位产生的、非植物正常生长发育所必需的小分子有机化合物，包括生物碱、黄酮类、酚类等物质[1]。这些物质不仅通过影响植物自身的正常生理功能以增强其对环境的适应性、抵御外界胁迫(如抑制周围杂草生长[2]、防止昆虫啃食[3]等)，还在植物与其他生物(特别是微生物)的互作中扮演重要角色[4]。现代药理学研究表明，药用植物体内合成的次生代谢产物是其发挥药效的物质基础[5]，因其活性多样而被广泛应用于医药学领域。例如，家喻户晓的抗疟药——青蒿素(artemisinin)以及临床上用于治疗癌症的紫杉醇(taxol)，均分别提取自黄花蒿和红豆杉中，属于高效、低毒、广谱的次生代谢产物[6]。为提高药用植物的质量与产量，关注其生长发育过程至关重要，该过程与多种生态因素、生物因素等密切相关。近年来，药用植物与微生物的相互作用受到普遍关注，光、温、土、气等因素直接或间接影响土壤微生物，进而影响该区域所生长药用植物的品质。如本课题组 Zhou 等[7]前期研究表明，不同产区铁皮石斛根际微生物组特征与石斛活性成分累积存在关联，证实了根际微生物群落结构对药用植物次生代谢产物积累的调控作用。因此，深入认识微生物对药用植物生长及次生代谢产物合成与积累的作用具有重要意义。

在药用植物与微生物相互作用的过程中，化学信号在植物-微生物"对话"中发挥着不可忽视的桥梁作用，是二者相互识别的第一步(图 1)。化学物质的产生、释放、检测和反应均属于化学信号的组成环节[8]。药用植物根际的各种过程，如根际效应的构建、根系分泌物的释放、根际微生物群落的组成、菌根的形成以及土壤健康与根际微生态平衡几乎都建立在植物-微生物-化学信号传导的基础之上[9]。

系统概述药用植物-微生物之间的化学信号

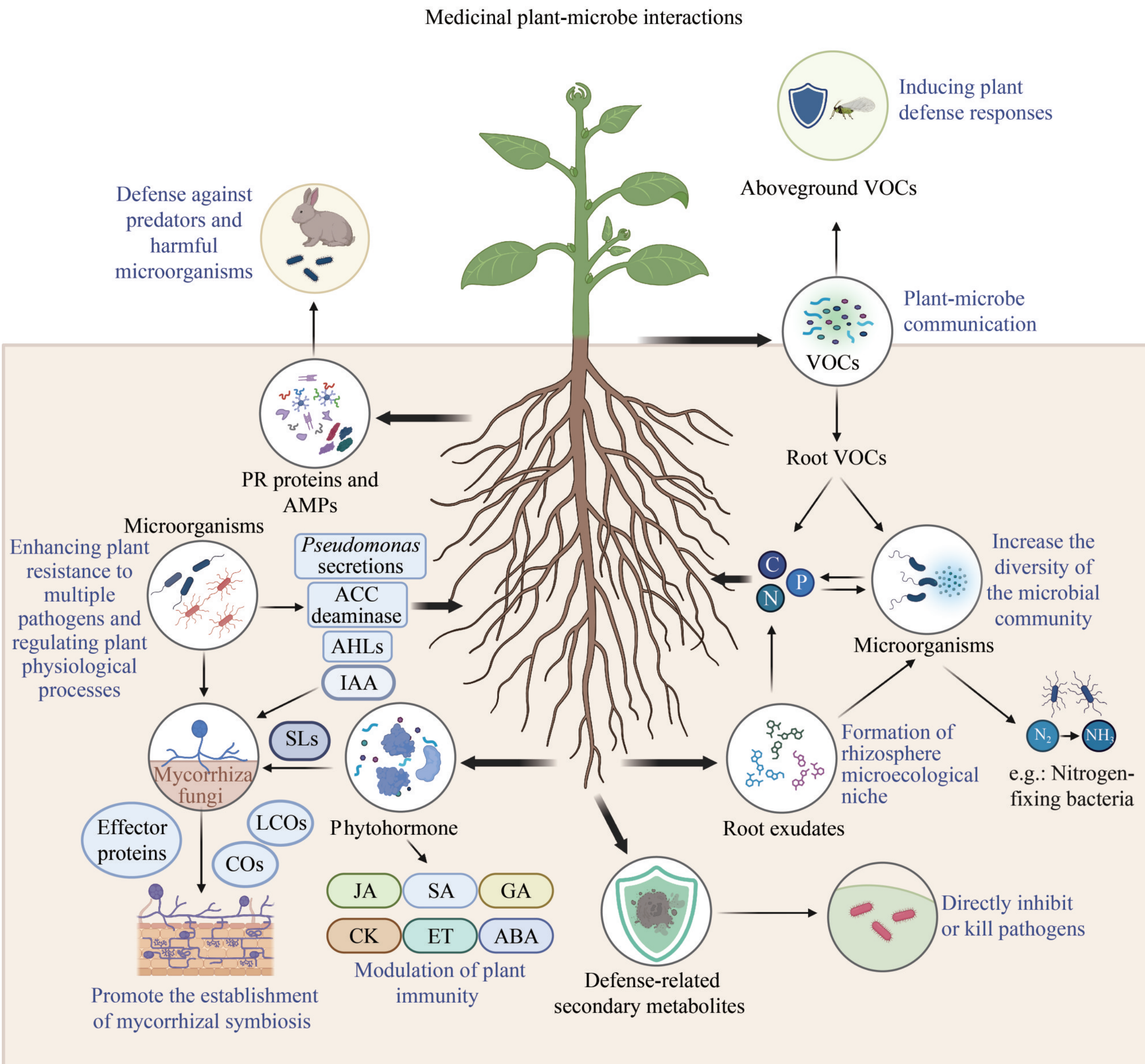

图1　化学信号分子在药用植物-微生物互作关系中的主要作用和体现

Figure 1　Primary roles and manifestations of chemical signaling molecules in medicinal plant-microorganism interactions. Created in BioRender (https://BioRender. com/oo4kznv). VOCs: Volatile organic compounds; PR: Pathogenesis-related; AMPs: Antimicrobial peptides; ACC: 1-aminocyclopropane-1-carboxylic acid; AHLs: *N*-acyl homoserine lactones; IAA: Indole-3-acetic acid; SLs: Strigolactones; LCOs: Lipochitooligosaccharides; COs: Short-chain chitin oligomers; JA: Jasmonic acid; SA: Salicylic acid; GA: Gibberellins; CK: Cytokinins; ET: Ethylene; ABA: Abscisic acid.

传导及相关化合物在二者互作中发挥的不同作用，有助于进一步阐明药用植物生长过程中的各类互作关系，为调控药用植物生长发育及次生代谢产物的合成与积累奠定基础。深入理解这些化学信号及其分子机制对未来更好地开发应用微生物肥料、生物农药，通过调控微生物

群落组成提高中药材质量、实现生态种植具有重要意义。

1 植物来源的化学信号影响微生物的组成、多样性及功能

植物来源的化学信号是连接宿主植物与微生物群落的关键因子，通过介导微生物招募、生态位筛选、维持定殖及功能调控等在植物相关微生物组的组装与稳态维持中发挥核心作用。这些化学信号来源广泛、类型多样，主要包括根系分泌物、挥发性有机化合物(volatile organic compounds, VOCs)以及植物激素等，不同类型信号在作用机制与功能上各具特征(表 1)。

1.1 根系分泌物

根际是指植物根系与土壤及微生物相互作用的区域，包括根系表面和受根系影响的周围土壤[26]，是药用植物与土壤间物质交换的重要场所[27]。根系分泌物(植物生长过程中通过根系主动或被动向生长介质释放的所有物质)含有丰

表1 植物来源化学信号及主要功能

Table 1 Plant-derived chemical signals and their primary functions

Category	Compounds	Functions	References
Root exudates	Phenolic compounds	Antioxidant, antibacterial, and antiviral properties improve plant disease resistance	[10]
	Organic acids	Promote mineral absorption and regulate microbial growth by either inhibiting or promoting it	[11]
	Amino acids	Provide carbon and nitrogen sources that affect the composition of microbial communities	[12]
	Carbohydrates	Enhance the diversity and complexity of microbial communities to support the proliferation of beneficial microorganisms	[13]
Volatile organic compounds (VOCs)	Aboveground VOCs	Attract natural enemies of pests, induce defense responses in neighboring plants, and indirectly influence soil microbial perception as signaling factors	[14]
	Root VOCs	Antibacterial or bacteriostatic agents attract beneficial microorganisms and serve as carbon sources for some of them	[15]
Plant hormones and their analogs	Salicylic acid (SA)	Inhibit pathogen growth and recruit disease-resistant microorganisms	[16]
	Jasmonic acid (JA)	Involved in plant defense and affecting microbial colonization	[17]
	Ethylene (ET)	Involved in plant development, senescence, and stress responses	[18]
	Strigolactones (SLs)	Specifically attract arbuscular mycorrhizal fungi (AMF), induce their spore germination and hyphal branching, and promote the establishment of mycorrhizal symbiosis	[19]
	Cytokinins (CK)	Regulate growth and development; perceive microorganisms	[20]
	Abscisic acid (ABA)	Limit pathogen invasion while enhancing osmotic protection and antioxidant capacity	[21]
	Gibberellins (GA)	Promote growth and development, enhance JA-related defense mechanisms, and restrict pathogen expansion	[22]
Defense-related secondary metabolites	Alkaloids	Directly inhibit or kill pathogens	[23]
Pathogenesis-related (PR) proteins and antimicrobial peptides (AMPs)	PR proteins, serine protease inhibitors	Defensive proteins that inhibit protein digestion in attacking pests	[24]
	AMPs	The plant innate immune system is widely used as a source of diagnostic molecular markers for defense signaling pathways	[25]

富的有机化合物，如酚类物质(酚酸、类黄酮等)、有机酸(柠檬酸、苹果酸、琥珀酸等)、氨基酸(谷氨酸、天冬氨酸等)及糖类(葡萄糖、果糖、蔗糖等)[28]，不仅可作为根际微生物生长代谢的重要碳源和能源底物[29]，选择性招募或排斥特定微生物类群可塑造根际微生态位[30]，甚至通过化感作用抑制竞争植物的生长[31]；还可通过调控植物免疫与抗逆相关过程提高药用植物对生物胁迫的适应能力，从而在一定程度上降低对化肥和农药的依赖。例如，有机酸作为根系分泌物的重要成分之一，可降低土壤有机质的分解速率，调控土壤碳氮矿化过程；还能通过降低根际土壤酸碱度、改变土壤氧化还原条件、影响土壤微生物群落等方式增加土壤中铁、磷及其他微量营养素的有效性[32]。药用植物还可通过释放酚类化合物、非挥发性萜类化合物和含硫化合物，诱导产生对土壤中病原菌和害虫具有显著抑制作用的抗菌微生物，直接抑制其生长[33]。成熟抑制剂(ripening-inhibitor, RIN)是一种调控番茄果实成熟的 MADS-box 转录因子，可通过改变植物根系分泌物(如 3-羟基黄酮等)抑制土壤中植物病原菌茄科罗尔斯通氏菌(*Ralstonia solanacearum*)的积累，并促进富含抗病基因的细菌群落[如链霉菌属(*Streptomyces*)]在根际的聚集，增强植物抗病能力[34]。

此外，根系分泌物在非生物胁迫响应中同样发挥关键作用，可通过内部螯合或清除活性氧(reactive oxygen species, ROS)维持细胞质或液泡中游离金属的无毒水平[35]，建立金属螯合与隔离的防御机制[36]以应对重金属胁迫。根系分泌物中的低分子量有机酸(low molecular weight organic acids, LMWOA)是至少含有 1 个羧基的小分子有机化合物，可活化土壤中无效态磷，提高磷的有效性，是药用植物应对低磷胁迫的重要手段[37]。

1.2 挥发性有机化合物

挥发性有机化合物(volatile organic compounds, VOCs)是具有低分子量(小于 300 Da)和高蒸汽压的有机化合物，种类繁多，包括醇类、醛类、酯类、萜类、硫醇等。药用植物中的 VOCs 是植物通过次生代谢途径产生并向周围释放的一类挥发性非甲烷碳氢化合物，地上部 VOCs 通过花、叶和果实排放至大气中，根系部 VOCs 则通过根系排放至根际[15]。在药用植物中，VOCs 参与多种生态互作，如作为化感物质吸引传粉者、防御草食动物，以及介导植物间、植物-微生物间的通讯[38-39]。植物产生的 VOCs 可被微生物种群用作营养素或信号，而微生物释放的 VOCs 也能直接或间接地激活药用植物的免疫系统，或调节其生长和形态发生[40]。由于其高蒸气压和低沸点，VOCs 易在空气和水中扩散，使这类小分子次生代谢物能够在空气或水膜介质中实现远距离传递[41]，即使不直接接触病原体，也可通过扰乱病原菌膜结构、干扰呼吸代谢、诱导氧化胁迫，或抑制群体感应(quorum sensing, QS)、生物膜形成及毒力基因表达等发挥抗菌作用[42]。单萜、倍半萜等 VOCs，既可通过疏水性作用破坏病原菌细胞膜完整性，又可通过调控微生物基因表达发挥抗菌作用[43]。

1.3 植物激素及其类似物

植物激素是指由植物产生并能被自身感知的化合物，在植物与病原微生物和有益微生物的相互作用以及植物生长发育中起着重要作用[44-45]。其中，水杨酸(salicylic acid, SA)和茉莉酸(jasmonic acid, JA)被认为是植物免疫中的主要激素，而乙烯(ethylene, ET)、独脚金内酯(strigolactones, SLs)、植物细胞分裂素(cytokinins, CK)、脱落酸(abscisic acid, ABA)和赤霉素(gibberellins, GA)等也通过激素间的串扰发挥重要作用[46-47]。当植物遭受病原菌侵染后，SA、JA 和 ET 等信号迅速响应，激活下游转录因子调控萜类合成相关基因的表达[48]，进而调节植物免疫等生理过程。SLs 作为关键分枝因子，能在低磷等养分限制条件下显著增加分泌量，特异性诱导丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)孢子萌发和菌丝分枝，促进 AMF 向

根际趋化以增大与根系的接触概率，既加速了菌根共生的建立，也增强了药用植物对矿质养分的吸收能力。然而，SLs 也可被某些寄生植物[如列当科(Orobanchaceae)独脚金属(*Striga*)植物]识别，诱导其种子萌发[49]。GA 在药用植物与微生物的共生互作中发挥关键调控作用，本课题组 Chen 等[50]提出 GA 是石斛种子共生萌发的关键信号分子之一，并克隆鉴定了铁皮石斛赤霉素 3-氧化酶(gibberellin 3-oxidases, GA3ox)基因[51]，进一步丰富了激素类似物在药用植物-微生物共生互作中的作用机制。此外，本课题组阎波等[52]还系统梳理了植物菌根共生中的激素调控作用，证明了 GA、生长素等多种植物激素在菌根共生建立与维持中的重要地位。

1.4 防御相关次生代谢产物

尽管药用植物次生代谢产物并非植物生长发育所必需，但其在药用植物抵御外界环境胁迫、维持正常生长[43]以及塑造微生物群落结构和调控其代谢活动方面具有重要作用[53]。部分次生代谢产物可作为碳源和能源促进有益微生物的生长[54]，另一些则具有抗菌活性，可抑制特定微生物的生长。人参皂苷可与根际微生物群相互作用[55]并促进益生菌的生长[56]。已有研究表明，人参皂苷可以刺激土壤中伯克霍尔德氏菌属(*Burkholderia*)的生长和生物膜形成，有助于降解自毒物质并拮抗根腐病病原体，从而缓解负向植物-土壤反馈(negative plantsoil feedback, NPSF)[57]。此外，多数生物碱类化合物对真菌也表现出一定的抑制作用[23]。例如，石蒜碱(lycorine, LYC)和水芹碱(narciclasine, NAR)已被证实可抑制水稻稻瘟病菌(*Magnaporthe oryzae*)的生长，并通过影响脂质代谢和黑色素合成等途径发挥抗真菌作用[58]。

1.5 病程相关蛋白和抗菌肽

药用植物为应对各种不利环境而合成了多种病程相关(pathogenesis-related, PR)蛋白和抗菌肽(antimicrobial peptides, AMPs)，如凝集素、核糖体失活蛋白、蛋白酶抑制剂、尿素酶、青蒿素和致孔毒素等，在抵御捕食者和有害微生物方面发挥着关键作用[59]。PR 蛋白由多种蛋白质组成，植物受到病原菌攻击后防御信号通路 SA 和 JA 被激活，诱导 PR 蛋白大量积累，从而最大限度地减少病原菌负载，避免未受感染的植物器官发病[25]。AMPs 是富含半胱氨酸的分子，具有广泛的潜在抗菌活性，包括 PR6 蛋白家族(酶抑制剂)、PR12 蛋白家族(植物防御素)、PR13 蛋白家族(植物硫蛋白)和 PR14 蛋白家族(脂转移蛋白)[60]，其主要靶标为微生物的细胞膜，如植物多肽可破坏其完整性[61]。

2 微生物来源的化学信号对植物的多重影响

微生物来源的化学信号是连接微生物群落与宿主植物互作的重要媒介，通过调控植物生长发育、营养吸收和免疫应答等多种生理过程，在植物适应环境变化及维持健康稳态中发挥重要作用。这些化学信号来源复杂、功能多样，主要包括激素类似物、群体感应信号分子、假单胞菌分泌物和菌根因子等，不同类型信号对植物具有多重影响(表 2)。

2.1 激素类似物

微生物产生的激素类似物，如 1-氨基环丙烷-1-羧酸(1-aminocyclopropane-1-carboxylic acid, ACC)脱氨酶和吲哚-3-乙酸(indole-3-acetic acid, IAA)等是重要的信号分子，能够调节药用植物的生理过程[70-71]。ACC 是植物体内 ET 的直接前体，由 *S*-腺苷甲硫氨酸(*S*-adenosyl-L-methionine, SAM)在 ACC 合成酶催化下生成，随后在 ACC 氧化酶作用下转化为 ET。逆境条件下，药用植物体内 ET 的合成显著增加，ET 胁迫抑制植物生长[72]。然而，部分微生物，特别是植物根际促生菌(plant growth-promoting bacteria, PGPB)能够产生 ACC 脱氨酶分解 ACC，降低植物组织中 ET 水平[62-63]，进而促进植物根

表2 微生物来源化学信号及主要功能

Table 2 Chemical signals derived from microbial sources and their primary functions

Category	Compounds	Functions	References
Hormone analogs	1-aminocyclopropane-1-carboxylic acid (ACC) deaminase	Alleviate the adverse effects of ethylene on plant growth, promote development, and delay the senescence of medicinal plants	[62-63]
	Indole-3-acetic acid (IAA)	Affect the growth and development of medicinal plants and play a key role in plant-microbe communication	[64]
Quorum sensing molecules	*N*-acyl homoserine lactones (AHLs)	Regulate the immunity of medicinal plants to enhance their resistance to various pathogens	[65]
Pseudomonas secretions	Siderophores/antibiotics	Antagonize pathogens	[66]
Mycorrhizal factors	Lipochitooligosaccharides (LCOs)	Recognized by plant root cell receptors, these molecules activate symbiotic signaling pathways and promote the formation of arbuscular mycorrhizal symbiosis	[67]
	Short-chain chitin oligomers (COs)	Act synergistically with LCOs to trigger calcium oscillation signals in plant cells and regulate the expression of genes related to mycorrhizal symbiosis	[68]
	Effector proteins	Interact with host plant transcription factors, inhibit plant defense responses, and promote the establishment of ectomycorrhizal symbiosis	[69]

和茎的生长，并延缓药用植物的衰老。研究表明，接种表达 ACC 脱氨酶的 PGPB 可提高药用植物在盐胁迫和干旱胁迫下的生物量[63]。

IAA 是一种重要的植物生长素，与植物细胞伸长、根系形成和顶端优势等生长发育过程密切相关。多种根际细菌和内生细菌均具有合成 IAA 的能力，主要通过吲哚-3-乙酰胺(indole-3-acetamide, IAM)途径和吲哚-3-丙酮酸(indole-3-pyruvate, IPyA)途径合成，此外还有色胺(tryptamine, TAM)途径、吲哚-3-乙腈(indole-3-acetonitrile, IAN)途径以及色氨酸侧链氧化酶(tryptophan side-chain oxidase, TSO)途径等[73]。合成的 IAA 进入植物根际后可促进 TIR1/AFB 受体复合体对 Aux/IAA 抑制蛋白的识别与降解，解除其对生长素响应因子(auxin response factor, ARF)转录因子的抑制，进而激活一系列生长素响应基因的表达[74]。IAA 不仅影响药用植物的生长发育，还在植物-微生物通讯中发挥关键作用[71]。IAA 促进根系结构形成，不仅提高了水分和矿质养分的吸收效率，也显著增加了根系与 AMF、外生菌根真菌(ectomycorrhizal fungi, ECMF)及其他有益微生物的接触面积，从而促进植物-微生物共生的建立及根际功能微生物的持续富集。同时，产 IAA 细菌可通过时空调节植物生长素库影响植物生长发育，而寄主植物也可积极参与调节细菌的 IAA 生物合成[64]。

2.2 群体感应分子

药用植物生长过程中，微生物群体感应系统持续进行细胞间通讯。群体感应分子 *N*-酰基高丝氨酸内酯(*N*-acyl homoserine lactones, AHLs)是革兰氏阴性菌中最常见的自诱导物[75]，有益微生物可通过 AHLs 触发植物的诱导系统抗性(induced systemic resistance, ISR)，使植物对病原体入侵产生快速、强烈的免疫反应[65]，提高植物对多种病原体的抵抗力。部分 AHLs (如 oxo-C14-HSL 和 oxo-C8-HSL)可被拟南芥识别为激活免疫反应、增强对细菌病原体[如丁香假单胞菌(*Pseudomonas syringae*)]抗性的危险信号[76]。AHLs 还可影响植物体内激素水平，如调节 ISR 通路中的重要信号分子 JA 和 ET 等，从而优化

植物的免疫反应[77]。AHLs 还具有增强植物防御反应的作用，如大蒜来源的群体感应抑制化合物可通过合成 AHLs 类似物抑制铜绿假单胞菌(*Pseudomonas aeruginosa*)的毒性，并阻断黄单胞菌(*Xanthomonas*)的信号接收，有效控制植物病害[78]。也有研究表明，AHLs 可通过激活 *PAL1* 基因促进植物防御物质苯丙素类的合成[79]；而缺乏 AHLs 信号的细菌则会增强植物对蚜虫的抵抗力[80]。

2.3 假单胞菌分泌物

假单胞菌作为一类重要的植物根际促生菌，能够产生多种铁载体(也称为嗜铁素)和抗生素，对药用植物健康具有多重益处[81]。铁是植物生长必需的微量元素[82]，但在土壤中通常以难溶形式存在，难以被植物直接吸收。铁载体是假单胞菌产生的一类小分子物质，能够特异性螯合铁离子，形成可溶性铁-铁载体复合物，提高铁的溶解度和吸收率，从而增强铁的生物有效性[83]。药用植物可利用这些复合物获取铁元素，改善营养状况、促进生长。由于铁是病原菌生长繁殖所必需的元素，铁载体可与病原菌竞争铁资源，抑制其生长，从而减轻病害，因此铁载体还具有拮抗病原菌的作用[66]。例如，荧光假单胞菌产生的铁载体能够有效抑制多种植物病原真菌和细菌的生长[83]。此外，假单胞菌还能产生多种具有抗菌活性的抗生素，如吩嗪、2,4-二乙酰基根皮苷等，可直接抑制植物病原菌的生长繁殖，减轻病害[84]。

3 双向信号

3.1 共生关系的建立(菌根共生)

根际微生物组中某些真菌与药用植物根系可形成共生体，称为药用植物的菌根[85]。菌根真菌的菌丝体既向根周土壤扩展，又与寄主植物组织相连通，一方面从寄主植物中吸收糖类等有机物质作为自身营养，另一方面从土壤中吸收养分和水分供给植物。菌根的存在有利于药用植物扩大根系吸收面积，增强对原根毛吸收范围外元素的吸收能力[86]。菌根类型通常根据真菌在药用植物中的定殖方式分为丛枝菌根(arbuscular mycorrhiza, AM)、外生菌根(ectomycorrhiza, ECM)、类菌根(ericoid mycorrhiza, ERM)和兰花菌根(orchid mycorrhiza, ORM)[87]。研究表明，不同菌根类型对不同药用植物的影响各异，如 AM 可促进墨旱莲地上部分药物活性成分的积累，ECM 可提高油松的抗旱性等[6]。

分布最广的菌根类型是 AM，在药用植物保护中发挥着重要作用，包括改善药用植物营养、损害补偿、争夺定殖位点或光合产物、促进根系和根际微生物种群变化以及激活植物防御机制等[88-89]。在共生关系形成前期，AMF 与植物之间识别与联系的化学信号主要来源于植物根系分泌物中的 SLs 等信号因子，以及 AMF 分泌的结瘤因子(lipochitooligosaccharides, LCOs)和短链几丁质寡聚物(short-chain chitin oligomers, COs)等菌根因子[90]。在植物生长发育过程中，根系分泌 SLs，特异性吸引土壤中的 AMF，诱导其孢子萌发和菌丝分枝，进而增加 AMF 与根系的接触概率[19]。AMF 感知 SLs 后会分泌 LCOs、COs 等信号分子，被植物根细胞表面的 LysM 受体样激酶 3 (LysM receptor-like kinase, LYK3)/结瘤因子感知蛋白(nod factor perception, NFP)类受体识别并激活，随后触发细胞内核周钙离子周期性振荡，通过钙调蛋白互作蛋白(calcium/calmodulin-dependent protein kinase, CCaMK)解码信号[91]，激活下游转录因子(如 RAM1、DELLA)，直接调控菌丝附着体形成、根皮层细胞重编程及丛枝结构发育相关基因的表达，最终形成菌丝侵入植物细胞的共生关系，该过程无需其他辅助信号通路参与[92]。

同时，AMF 也是参与土壤磷活化的重要微生物类群之一[37]。AMF 与细菌共同参与凋落物降解，有助于增强土壤有机碳(soil organic carbon, SOC)的螯合能力并减少氮淋溶[93]；AMF

的存在还可减少养分损失，如降低硝酸盐浸出[94]。此外，根系分泌物中多种次生代谢产物(如脱落酸、茉莉酸、水杨酸、油菜素内酯等)也被发现有助于植物与 AMF 建立共生关系，这些物质可与植物激素产生互作，协同调节植物生长发育及应对各类生物和非生物胁迫[95]。AMF 还可通过增加植物生物量直接影响次生代谢物的产生，或通过刺激次生代谢物生物合成途径间接调控其积累[89]。

另一种被广泛研究的菌根类型是 ECM，目前仅在约 15 种药用植物中发现[96]。外生菌根真菌具有一定的宿主选择性，已知能够影响外生菌根形成的根系分泌物质包括酯类、黄酮类及植物激素[97]。植物根系通过分泌这些物质作为招募 ECMF 的化学信号，ECMF 则分泌 COs，与植物根细胞表面高特异性的几丁质触发子受体激酶(chitin elicitor receptor kinase 1, CERK1)类受体结合并被识别[98]，进而激活钙离子振荡-CCaMK 保守通路。同时，ECMF 分泌效应蛋白(如 MiSSP7)进入植物细胞后与宿主转录因子(如 JAZ)发生互作[99]，启动宿主特异性调控分支通路，抑制植物产生防御反应以清除真菌。此过程还需生长素、茉莉酸等植物激素通路的协同调控[100]。

本课题组 Chen 等[101]通过比较转录组学分析铁皮石斛与 2 种菌根真菌[胶膜菌(*Tulasnella* sp.) S6 和无孢蜡壳菌(*Serendipita* sp.) 12825]共生萌发的分子机制，发现共生萌发显著诱导宿主糖脂代谢、物质转运、激素信号及细胞壁重塑相关基因的表达，并伴随真菌碳水化合物活性酶(carbohydrate-active enzymes, CAZymes)和分泌相关基因的协同响应，表明宿主细胞壁重构与真菌定殖过程是兰科植物共生萌发建立的关键分子基础，为进一步探索植物共生萌发和菌根共生的分子机制提供了重要数据。

3.2 植物与有益/病原微生物互作过程中化学信号的异同

通过对大量研究的总结分析，植物-微生物互作过程中化学信号的差异性主要体现在性质、功能及通路等方面[102-103]。植物与病原菌竞争互作过程中主要涉及植物防御素[104]、病原菌毒素[105]等具有毒性或抑制性的化学信号，驱动植物与病原菌之间的“化学竞争”；而植物与有益微生物的共生互作过程中主要涉及植物根系分泌物、微生物产生的生长素和细胞分裂素等具有营养或促进生长功能的化学信号，促进二者互利互惠共生关系的建立[106]。

在不同的植物-微生物互作过程中，不同化学信号具有多样的功能。在竞争过程中，化学信号的主要功能是促进病原菌侵染和植物防御，病原菌利用化学信号寻找寄主、释放毒素，而植物则利用化学信号识别病原菌、激活防御反应；在共生互作过程中，化学信号的主要功能是促进双方识别、营养交换和协同生长。在信号通路方面，竞争过程中植物的防御反应通常涉及 SA、JA、ET 等信号通路，通过激活这些通路表达防御基因以增强抗病性；而共生互作过程中通常涉及生长素、细胞分裂素等植物激素的调控，通过复杂通路调控根际发育、细胞分裂与分化，提高养分吸收效率，协调植物与共生微生物的生长，建立稳定的共生关系。

植物-微生物互作过程中化学信号种类繁多，信号传递受环境因素(如光、温、水分、养分)的影响，且互作过程均涉及信号识别与响应的共性。因此，无论竞争互作还是共生互作，化学信号均是植物与微生物之间进行识别、通讯和互动的基础。

4 总结与展望

植物与微生物之间的互作关系复杂，化学信号在其中扮演着至关重要的角色。本课题组前期围绕铁皮石斛、天麻等兰科药用植物，在

内生及菌根真菌资源收集与鉴定、菌根共生专一性与植物发育阶段的关系、兰科种子-真菌互作理论、促进种子萌发的分子机制及关键信号分子赤霉素、优势菌群(*Tulasnella*、*Serendipita*)的鉴定等方面取得了系统成果，为理解植物-微生物互作关系提供了重要支撑，因此探究介导二者互作的化学信号具有重要意义。特别是在药用植物中，化学信号的调节直接影响植物健康、生长及药用成分的合成[9]。植物来源的信号(如根系分泌物、挥发性化合物、防御相关次生代谢产物等)能影响根际微生物区系的组成与活性；微生物来源的信号(如激素类似物、群体感应分子、铁载体、抗生素等)则能调节药用植物的生理过程，诱导其产生抗性，增强对病原菌的防御能力；而双向信号能够促进植物与有益微生物的识别与共生，调控根际微生物群落结构与功能，激活植物免疫系统，使植物在受到病原菌侵染时释放化学信号以启动自身免疫反应。

尽管目前仍有许多化学信号及其作用机制有待进一步解析，但已可基于“信号-微生物-功能”模式尝试解决各类土壤健康及植物生长问题。未来可通过调控各类化学信号重塑健康的微生物区系；人为筛选具有降解自毒物质、抑制病原菌等功能的微生物，构建人工微生物群落，实现对根际微生态环境的精准调控；利用合成生物学等手段外源添加或遗传改良，调控植物根系分泌的化学信号，吸引有益微生物、抑制有害微生物；将微生物代谢产生的有益物质(如植物激素、维生素和有机酸等)应用于植物种植生产，促进植物生长并提高抗逆性。这将有助于实现中药材乃至农作物的生态种植，推动微生物肥料及生物农药的开发，同时为提高中药材质量和实现可持续农业生产提供参考。

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