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专论与综述

植物激素调控丛枝菌根发育的作用机制研究进展

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摘　要：丛枝菌根(arbuscular mycorrhiza，AM)是土壤中 AM 真菌和绝大多数维管植物根系长期进化过程中相互识别、相互作用形成的互利共生体。AM 的发育与功能效应依赖 AM 真菌-寄主植物之间精准的“分子对话”，同时受到环境条件特别是土壤养分水平、干旱和盐渍化的制约。植物激素作为低浓度的小分子有机物，是参与调控 AM 共生过程的重要信号分子。其中，主要有 9 种植物激素参与 AM 发育过程且分工各有不同：独脚金内酯(strigolactones，SLs)参与 AM 真菌-寄主植物之间最初的共生识别，脱落酸(abscisic acid，ABA)和油菜素内酯(brassinosteroid，BR)促进前期的菌丝入侵，但水杨酸(salicylic acid，SA)和乙烯(ethylene，ET)抑制前期的菌丝入侵，生长素(auxin，Aux)、ABA 和 BR 促进随后的丛枝形成而 ET 和赤霉素(gibberellin，GA)的作用则相反，茉莉酸(jasmonic acid，JA)对菌丝入侵与丛枝形成均可能存在正调控或负调控作用。目前细胞分裂素(cytokinin，CTK)在 AM 发育中的作用尚不明确。更为复杂的是，通常植物激素信号之间的交叉互作决定 AM 的发育进程。本文针对 AM 发育过程总结了不同植物激素的调控作用特点和不同植物激素信号之间的互作(协同或拮抗)，以及胁迫条件下不同植物激素信号的可能调控机制。深入研究和系统阐明植物激素调控 AM 真菌-寄主植物共生的生理/分子机制，将有助于促进生物共生学理论研究及菌根技术的应用。

关键词：丛枝菌根真菌；共生；互作；信号分子；胁迫

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Mechanisms of phytohormones in regulating arbuscular mycorrhiza development

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Abstract: Arbuscular mycorrhiza (AM) is a symbiont formed by the interaction and mutual recognition of soil-born AM fungi and the roots of most vascular plants in the long-term evolution. The development and function of AM, limited by environmental conditions, especially the soil nutrient level, drought, and salinity, depend on the precise "molecular dialogue" between AM fungi and host plants. Phytohormones are low-molecular-weight organics with low concentration and act as crucial signaling molecules in the regulation of AM symbiosis. There are mainly nine phytohormones participating in regulating AM development with different effects. Strigolactones (SLs) act at the first symbiotic recognition between AM fungi and host plants. At the early stage, abscisic acid (ABA) and brassinosteroid (BR) promote the fungal invasion, whereas salicylic acid (SA) and ethylene (ET) inhibit the fungal invasion. Auxin (Aux), ABA, and BR promote the subsequent arbuscule formation, whereas ET and gibberellin (GA) suppress the arbuscule formation. Jasmonic acid (JA) may have both positive and negative regulating effects on fungal invasion and arbuscule formation. However, the role of cytokinin (CTK) remains unclear in AM development. In addition, the signaling crosstalk among phytohormones normally determines AM development. This review summarized the characteristics of different phytohormones and their associated signaling crosstalk (synergistic or antagonistic) in regulating AM development, and the possible regulation mechanisms of different phytohormone signals involved in AM development under stress conditions. The profound research and systematical illustration of the physiological/molecular mechanisms of phytohormones in regulating the symbiotic relationships between AM fungi and host plants, will help the study on symbiology and the application of mycorrhizal technology.

Keywords: arbuscular mycorrhiza (AM) fungi; symbiosis; interaction; signaling molecules; stress

丛枝菌根(arbuscular mycorrhiza，AM)是土壤中的球囊菌门(*Glomeromycota*)真菌侵染植物根系而形成的互利共生体，存在于 80%以上的陆生维管植物中，是分布最广泛的菌根类型[1]。AM 共生体地理分布的广泛性[2-3]，是植物长期应对陆生生境中养分缺乏等各种逆境不断进化与适应的结果。

AM 共生体构建过程中需要 AM 真菌与植物之间进行精准的"分子对话"[4]。AM 共生体形成的前期，尤其当处于养分缺乏时，植物根系首先在根际产生和分泌独脚金内酯(strigolactones，SLs)，该化合物能有效诱导孢子萌发、菌丝生长与分枝[5]，使菌丝趋向植物根系伸长，提高其接触寄主根系的几率[6]。AM 真菌的相应受体特异性识别 SLs 后即合成并分泌 Myc 因子——脂质几丁寡糖(lipochito-oligosaccharides，LCOs)和短链几丁质寡聚物(chitin oligomers，COs)[7]。潜在的寄主植物通过其受体如 lysin motif (LysM)

受体样激酶[8]识别 Myc 因子，进而激活通用共生信号途径(common symbiosis signaling pathway，CSSP)[9]并诱导根表皮细胞核内 Ca^{2+}峰发生[7,10]。随后 AM 真菌菌丝触及根表皮细胞表面并形成附着胞，数小时之后，表皮细胞内细胞骨架重组装形成侵入前器官(prepenetration apparatus，PPA)的结构，PPA 继而引导 AM 真菌菌丝入侵根皮层细胞[11]，此期间伴随 Ca^{2+}峰频率由高向低的转变[12]。AM 菌丝在皮层细胞间隙伸长扩延，进入皮层细胞的菌丝可以连续地二叉分枝形成丛枝，还有一些真菌菌丝的末端膨大产生泡囊。在特定生境条件下，寄主植物自身生理状况与发育水平可决定 AM 真菌的侵染率与丛枝丰度[13]，以维持最大化的共生效益。因此，寄主植物已分化的根表皮与皮层细胞需要短时间内进行重组装，以利于 AM 真菌菌丝的侵染定殖及丛枝的发育，这一 AM 共生体的构建与维持不仅涉及共生双方发育相关基因的表达变化，也伴随不同植物激素如 SLs、生长素(auxin，Aux)和赤霉素(gibberellin，GA)等信号分子的精细调控[14-15]。植物激素作为信号分子在调控 AM 共生过程中扮演着不可或缺的角色，本文归纳了 AM 发育中(包括胁迫条件下)各种植物激素信号及其互作的调控作用特点，以期为相关研究提供思路和依据。

1 植物激素调控 AM 发育的作用特点

1.1 独脚金内酯(strigolactones，SLs)

AM 共生体的构建起始于植物根系合成与分泌的 SLs[16]。SLs 是一类倍半萜烯内酯，根系分泌的 SLs 浓度与结构特征对 AM 真菌的识别及其菌丝生长、分枝至关重要[16-17]。López-Ráez 等报道异形根孢囊霉(*Rhizophagus irregularis*)侵染早期番茄(*Solanum lycopersicum*)根中 SLs 的合成量显著提高[18]。SLs 以类胡萝卜素为前体，由 β-胡萝卜素异构酶、类胡萝卜素裂解双加氧酶(carotenoid cleavage dioxygenase，CCD)7、CCD8 及细胞色素 P450 单加氧酶等一系列酶参与催化合成[19-20]。SLs 合成缺陷突变体 *CCD7* 或 *CCD8* 根系 AM 真菌侵染率明显下降[21-24]，外源施用 SLs 的类似化合物 GR24 (0.01 μmol/L)能恢复 AM 真菌的侵染率[25]，表明 SLs 在 AM 真菌侵染早期阶段的积极作用。GRAS 蛋白家族的转录因子 NSP1 (nodulation signaling pathway 1)和 NSP2 参与调控 Nod 因子诱导的根瘤共生信号途径[26]，在蒺藜苜蓿(*Medicago truncatula*)和水稻(*Oryza sativa*)中 NSP1 和 NSP2 通过调控 *d27* (*dwarf27*) (编码 β-胡萝卜素异构酶[20])的表达而影响 SLs 的合成，它们的双突变体 *nsp1 nsp2* 中 *d27* 的表达及 AM 真菌侵染率均显著下降[27]，表明 NSP1 和 NSP2 在调控根瘤菌/豆科植物和 AM 共生中发挥双重作用。百脉根(*Lotus japonicus*) *nsp1* 突变体根系的异形根孢囊霉侵染率下降，但外源施用 GR24 (0.1 μmol/L)不能恢复该 AM 真菌的侵染率，表明 NSP1 可能在 AM 真菌侵染早期阶段参与其他途径的调控[28]。蒺藜苜蓿 *nsp2* 突变体根系的异形根孢囊霉侵染率下降约 50%，并且 miR171h 通过负调控 *nsp2* 的表达而控制 AM 真菌的侵染定殖[29]。此外，Kretzschmar 等研究表明，在矮牵牛(*Petunia hybrida*)根系 AM 形成过程中，SLs 由 ABC (ATP-binding cassette)运输蛋白 PDR1 外运至根细胞外，与野生型比较，*pdr1* 突变体根系 AM 真菌菌丝的入侵点与速率显著下降，但菌丝和丛枝的表型正常[30]。

F-box 蛋白 d3 通过 SCF-E3 泛素连接酶复合体泛素化降解靶蛋白，是 SLs 信号识别与转导的重要元件，水稻 *d3* 和豌豆(*Pisum sativum*) *rms4* 是一类 SLs 不敏感性的 F-box 蛋白突变体[31-32]，虽然它们根系的 AM 真菌侵染率也显著下降(表

型与 SLs 合成缺陷突变体相似)，但外源施加 GR24 不能恢复该表型缺陷[25,33-34]。氮或磷素缺乏仍能诱导豌豆 *rms4* 突变体中 SLs 的大量合成，其合成水平与野生型类似，表明 F-box 蛋白介导的 SLs 反应途径在其他方面调控早期 AM 共生过程[32]。有理由推断，SLs 需要被寄主植物感知后通过内源性作用影响 AM 的发育。水稻中另一类 SLs 不敏感性突变体 *d14* 根系的 AM 真菌侵染率却显著高于野生型，表明 d14 也可能间接参与调控 AM 真菌的侵染定殖[31]。SLs 对早期 AM 真菌侵染定殖寄主根系发挥着关键作用，但其在随后的丛枝构建与功能中的作用仍有待进一步研究。

1.2 茉莉酸(jasmonic acid，JA)

研究发现，当植物受病原菌入侵时会产生水杨酸(salicylic acid，SA)以诱导系统获得抗性(systemic acquired resistance，SAR)，而当植物受非病原细菌如根围促生细菌(plant growth-promoting rhizobacteria，PGPR)入侵时将产生 JA 以诱导系统抗性(induced systemic resistance，ISR)[35]。AM 真菌侵染初期将引发寄主的短暂系统性防御反应，称为“菌根诱导抗性”(mycorrhiza-induced resistance，MIR)，而且分别具有 SAR 和 ISR 的部分特性[36]。

JA 及其衍生物茉莉酸甲酯(methyl jasmonate，MeJA)是一类称作氧脂素的多不饱和脂肪酸的氧化代谢产物[37]。AM 真菌侵染寄主根系过程中，参与 JA 合成的丙二烯氧合酶(allene oxide synthase，AOS)和丙二烯氧化环化酶(allene oxide cyclase，AOC)基因在形成丛枝的根皮层细胞中表达上调，引起内源性 JA 水平升高[38-39]。此外，调控 JA 合成的 9-脂氧合酶(9-lipoxygenases，9-LOXs)基因在 AM 真菌侵染的细胞中特异性表达，可能参与调控 AM 真菌菌丝在寄主根细胞中的扩延[40]。Isayenkov 等利用 RNAi 抑制蒺藜苜蓿根细胞 *AOC* 的表达而降低 JA 含量，导致根内根孢囊霉(*Rhizophagus intraradices*)的侵染定殖过程推迟和丛枝丰度减少，但丛枝结构仍然保持完好[39]。同样地，番茄 JA 合成缺陷突变体 *spr-2* 和 *def-1* 根系异形根孢囊霉侵染程度降低，但丛枝丰度无变化[40]。Tejeda-Sartorius 等研究发现，番茄 *spr-2* 根系聚生根孢囊霉(*Rhizophagus fasciculatus*)的侵染频率、程度及丛枝丰度均下降，同时伴随蔗糖合成酶 *Sus3* 和细胞壁转化酶 *Lin6* 的转录水平下调，外源叶施 MeJA (5 μmol/L)能恢复该缺陷表型和上调 *Sus3* 和 *Lin6* 的转录水平，JA 可能通过提高蔗糖水解及碳源向 AM 真菌转运，从而促进 AM 共生构建[41]。与之相反，番茄 JA 不敏感突变体 *jai-1* (JA 受体复合体组分)根系根内根孢囊霉的侵染频度、程度及丛枝丰度均显著升高，并且对野生型外源叶施 MeJA (5 μmol/L)能降低根系根内根孢囊霉的侵染程度和丛枝丰度[42]。Gutjahr 等研究发现，水稻 JA 合成缺陷突变体 *cpm2* 和野生型根系异形根孢囊霉的侵染定殖无显著差异，但外源根施 JA (50 μmol/L)抑制野生型根系异形根孢囊霉的侵染定殖，同时诱导防御基因 *PR4* (pathogenesis related protein gene 4)的表达上调[43]。由此推断，JA 信号在 AM 真菌侵染寄主根系的不同阶段可能发挥正、负或不显著的调控作用。

事实上，外源施用 JA 或 MeJA 对 AM 发育的影响与寄主或 AM 真菌的种类、JA 浓度与施用方式及寄主植物组织中 JA 的时空分布等有关[44]。例如，外源叶施低浓度(5 μmol/L) JA 能增强球囊霉(*Glomus* sp.)对大蒜(*Allium sativum*)根系的侵染及丛枝形成[45]，而外源叶施不同浓度(0.05、0.5 或 5 mmol/L) JA 均抑制摩西斗管囊霉(*Funneliformis mosseae*)对旱金莲(*Tropaeolum majus*)、番木瓜(*Carica papaya*)和黄瓜(*Cucumis*

sativus)根系的侵染[46]。高磷[(约 75 kg-P/(hm^2·a)]水平下，外源根施 0.5 mmol/L MeJA 提高了黄瓜根系根内根孢囊霉的侵染率与丛枝丰度，而无论高磷或低磷[(约 25 kg-P/(hm^2·a)]水平下根施 5 mmol/L MeJA 均降低根内根孢囊霉的侵染率与丛枝丰度[47]。

1.3 水杨酸(salicylic acid，SA)

在侵染早期，AM 真菌菌丝入侵寄主根表皮层形成附着胞时能诱导根中 SA 的合成瞬间增加[48]，并伴随防御相关基因的短暂上调表达[49]。烟草(*Nicotiana tabacum*)通过转基因 *NahG* (编码 SA 羟化酶，降低 SA 含量)促进根内根孢囊霉或摩西斗管囊霉的侵染，与之相反，烟草转基因 *CSA* (编码 SA 合成酶，提高 SA 含量)可以抑制它们的侵染，但转基因植株根系的最终侵染率与丛枝丰度和野生型一样，表明 SA 能延缓 AM 真菌的侵染进度，但不影响其侵染势[50]。外源根施不同浓度(0.5、1.0 或 1.5 mmol/L) SA 不影响摩西斗管囊霉在水稻根表皮的附着胞形成，但短暂延迟了其入侵寄主根皮层的起始时间[48]。可见，SA 在 AM 真菌侵染寄主根系早期起抑制作用，而在侵染后期的作用却不显著。

1.4 生长素(auxin，Aux)

AM 真菌侵染早期诱导寄主根中吲哚乙酸(indole-3-acetic acid，IAA)[51-54]或吲哚丁酸(indole-3-butyric acid，IBA)[55]的合成增加，并且外源施用生长素合成化合物或生长素运输抑制剂三碘苯甲酸(tri-iodo-benzoic acid，TIBA)提高了寄主根系 AM 真菌的侵染率[56]。此外，外源施用生长素受体结合竞争性抑制剂对氯苯氧异丁酸(p-chlorophenoxyisobutyric acid，PCIB) (10 mmol/L)降低枸橘(*Poncirus trifoliata*)根系变形球囊霉(*Glomus versiforme*)的侵染率和侵入点数[57]。由此推测，生长素可能通过诱导寄主植物根系侧根分枝或增强 AM 真菌菌丝生长而促进 AM 真菌的早期侵染定殖。

Hanlon 和 Coenen 对番茄生长素不敏感突变体 *dgt* (编码生长素信号转导所需的亲环蛋白 LeCYP1)和生长素运输超活性突变体 *pct* (超表达生长素外运体 PIN1)幼苗接种根内根孢囊霉发现，与野生型相比其侵染率均下降了约 50%，但根内菌丝、丛枝及泡囊发育正常，表明生长素参与调控 AM 真菌的早期侵染定殖[58]。Etemadi 等证实，外源施加低浓度(10^{-4} μmol/L)的生长素类似化合物刺激异形根孢囊霉在番茄、蒺藜苜蓿和水稻根系的侵染定殖，特别是丛枝的形成，并且生长素响应的启动子 *DR5-GUS* 融合基因在形成丛枝的根皮层细胞中特异性表达，过表达 miR393 可抑制生长素受体基因 *TIR1*/*AFB* (*transport inhibitor response1*/*auxin-related F box*)的表达及丛枝形成[59]；Liao 等也发现，番茄根中一些外源生长素响应的 *GH* (*Gretchen Hagen*)基因受异形根孢囊霉侵染的诱导表达，其中 *GH3.4* 在含丛枝的根皮层细胞中特异性表达[60]，表明生长素信号途径也可能参与调控丛枝的发育。丛枝发育过程中，根皮层细胞发生极化、细胞骨架进行重组装形成包围丛枝的围丛枝膜域[61]，TIR1/AFB 依赖性的生长素信号途径可能诱导根皮层细胞再极化与细胞骨架重组[62-64]，进而有利于丛枝形成。

此外，豌豆生长素合成缺陷突变体 *bsh* 根系根内根孢囊霉的侵染率显著降低，但根内菌丝和丛枝的表型与野生型相似；此突变体中合成 SLs 的关键基因 *CCD8* 的表达下调，同时根系 SLs 的分泌量减少，外源施加 GR24 (0.02 μmol/L)可以部分恢复该 AM 真菌的侵染率，表明生长素可能通过调控 SLs 的合成水平而介导 AM 真菌的早期侵染定殖[65]。利用 RNAi 沉默 *IAA27* 表达后，番茄根系异形根孢囊霉的侵染率下降，推测 IAA27 可能是 ARF (auxin response factor)

的负调控因子，通过提高 *NSP1* 和参与 SLs 合成的 *d27* 的表达而促进 AM 真菌入侵[66]。

1.5 赤霉素(gibberellin，GA)

AM 真菌侵染诱导寄主植物根中一些与 GA 合成相关基因如 GA3-β-双加氧酶和 GA20-氧化酶的表达上调[67-68]。Shaul-Keinan 等发现，根内根孢囊霉侵染的烟草根中活性 GA 浓度显著增加[69]。豌豆 GA 合成缺陷突变体 *na-1* 根皮层中根内根孢囊霉的丛枝丰度比野生型提高约 40%，对 *na-1* 外源施用 GA_3 使该 AM 真菌的丛枝丰度降低，类似于野生型[70]。外源施用 GA_3 或 GA 合成抑制剂调环酸钙(prohexadione calcium，PrCa)能分别抑制或促进番茄根皮层中异形根孢囊霉的丛枝发育与形成[71-72]。由此可见，GA 对丛枝形成具有负调控作用。此外，外源低浓度(1 μmol/L) GA_3 处理下豌豆根系摩西斗管囊霉的侵染频率与程度下降且无丛枝形成，高浓度(10 μmol/L) GA_3 处理下完全未出现菌丝侵染与丛枝[73]。GRAS 蛋白家族的 DELLA 转录因子负调控 GA 信号的转导，DELLA 与 GA 的受体蛋白 GID1 (gibberellin insensitive dwarf 1)互作，经泛素化途径降解后而激活 GA 信号途径[74]。水稻 DELLA 突变体 *slr1*[75]、番茄 DELLA 突变体 *procera*[71-72]和豌豆 DELLA 双突变体 *la cry-s*[70]根系 AM 真菌的根内菌丝数量和丛枝丰度均显著下降。蒺藜苜蓿基因组存在 3 个 DELLA 基因，其 DELLA 双突变体 *della1*/*della2* 根系变形球囊霉的丛枝丰度显著下降，但根内菌丝数量无变化，可推测其 DELLA 三突变体的根内菌丝分枝可能也会被抑制[76]。这些研究表明，GA 信号通过 DELLA 介导 AM 真菌菌丝在根外皮层的定殖与内皮层的丛枝发育。

DELLA 与 GRAS 蛋白 DIP1 (DELLA interacting protein 1)互作，同时 DIP1 又与 RAM1 (required for arbuscular mycorrhization 1)互作，进而促进 AM 共生相关基因的表达及丛枝发育[75]。钙离子/钙调素依赖性蛋白激酶(calcium/calmodulin-dependent protein kinase，CCaMK)与转录因子 CYCLOPS (结合于 RAM1 启动子区的 AMCYC 元件)互作并磷酸化后者，激活 RAM1 的转录表达；同时，DELLA 也与 CYCLOPS 互作，增强其对 RAM1 的转录激活，从而诱导丛枝的发育与形成[77]。DELLA 的过表达(35S 启动子驱动的 *della1-Δ18* 表达)能恢复 *cyclosps* 突变体的丛枝表型缺陷，表明 DELLA 也可能与其他转录因子如 NSP2 互作，进而调控 AM 共生或丛枝发育[76-77]。虽然外源施用 GA_3 抑制异形根孢囊霉对百脉根根系的入侵和 AM 共生信号途径中 RAM1 和 RAM2 的表达，但阻止内源性 GA 合成或其信号途径也能抑制 AM 共生所需 SbtM1 (arbuscular mycorrhiza-induced subtilisin-like serine protease1)的表达及根内菌丝的分枝[78]，表明 GA 信号对丛枝的发育与形成或许也存在积极作用。另外，DELLA、NSP1 与调控丛枝消解的 MYB1 互作，诱导编码几丁质酶、脂肪酶和蛋白酶等水解酶基因的表达和丛枝消解过程[79-80]。

Seto 等[81]和 Nakamura 等[82]发现，水稻中 GA 信号的负调控蛋白 DELLA (由 *slr1* 编码)与 SLs 信号受体 d14 互作而进一步影响 SLs 的信号转导。Ito 等的研究表明，水稻中 GA 信号可以抑制根系 SLs 的合成与分泌[83]。Wu 等发现，番茄 SLs 合成缺陷突变体 *SL-ORT1* 根中 GA_3 含量显著升高而叶片中 GA_3 和 GA_9 含量显著下降[84]，因此，GA 与 SLs 信号协作是否调控寄主植物根系 AM 真菌的早期侵染定殖值得进一步研究。

1.6 细胞分裂素(cytokinin，CTK)

根内根孢囊霉侵染诱导烟草根中 CTK 的合成水平显著升高[69]，表明 CTK 可能参与调控

AM 发育过程。然而，外源叶施激动素(500 μmol/L)不影响明根孢囊霉(*Rhizophagus clarus*)对绿豆(*Vigna radiata*)根系的侵染定殖[85]，但外源叶施 6-苄氨基嘌呤(5 mg/L)降低了石榴(*Punica granatum*)根系异形根孢囊霉的侵染率[86]。蒺藜苜蓿 CTK 不敏感突变体 *cre1*[87]根系球状巨孢囊霉(*Gigaspora margarita*)的侵染频率、程度及丛枝丰度与野生型相似[88]，暗示 CRE1 依赖的 CTK 信号途径对 AM 共生是非必需的。烟草通过转基因 *CKX2* (编码 CTK 氧化酶，降低内源 CTK 含量)提高根系根内根孢囊霉的侵染率[89]，但却抑制异形根孢囊霉的菌丝侵染与丛枝形成[90]。豌豆突变体 *E151* (内源 CTK 含量升高)根系异形根孢囊霉的菌丝数量与丛枝丰度均显著升高[91]。总之，CTK 对不同 AM 真菌侵染与丛枝发育的作用存在不确定性，有待开展广泛且深入的研究。

1.7 乙烯(ethylene，ET)

外源 ET 抑制 AM 真菌在不同寄主植物根系的侵染定殖并具有剂量效应，对豌豆外源施加 5.5 μL/L ET 降低了聚丛根孢囊霉(*Rhizophagus aggregatus*)的根内菌丝数量和丛枝丰度[92]，对韭葱(*Allium porrum*)外源施加 0.6 μL/L ET 降低了聚丛根孢囊霉的根内菌丝数量和丛枝丰度，而 0.3 μL/L ET 对侵染水平无显著影响[93]。番茄 ET 超表达突变体 *epi* 根系明根孢囊霉的侵染率下降[94-96]，而低敏感突变体 *Nr* 根系明根孢囊霉的侵染率下降[94]或升高[95]，蒺藜苜蓿 ET 不敏感突变体 *sickle* 根系变形球囊霉或根内根孢囊霉的侵染率升高[97]。外源施加 ET 合成抑制剂氨基乙氧基乙烯甘氨酸(aminoethoxyvinyl glycine，AVG) (10 μmol/L)能恢复 *epi* 根系明根孢囊霉的侵染率[96]。类似地，De Los Santos 等发现番茄 *epi* 突变体根系根内根孢囊霉或异形根孢囊霉的侵染程度与丛枝丰度下降，但成熟抑制突变体 *rin* (RIN 属 MADS-box 转录因子)根系 AM 真菌的侵染程度与丛枝丰度显著提高，暗示 ET 受 RIN 介导的信号途径可以负调控 AM 发育[98-99]。

1.8 脱落酸(abscisic acid，ABA)

AM 真菌侵染诱导寄主根中 ABA 的合成增加[54,100]，外源根施低浓度(5 μmol/L) ABA 促进异形根孢囊霉对蒺藜苜蓿根系的侵染定殖，但高浓度(50 μmol/L) ABA 的作用却相反[101]，表明 ABA 对 AM 发育具有重要作用且存在剂量效应。然而，外源根施高浓度(50 μmol/L) ABA 提高了番茄根系根内根孢囊霉的侵染频率、强度及丛枝丰度[102]，表明同一剂量的 ABA 对不同寄主植物根系 AM 发育的效应也可能不同。番茄 ABA 合成缺陷突变体 *sitiens* 根系根内根孢囊霉的侵染频率、强度及丛枝丰度显著下降，并伴随 ET 含量的显著升高，外源根施 ABA (50 μmol/L)能抑制 *sitiens* 根中 ET 的合成量，并一定程度上恢复该 AM 真菌的侵染频率与强度[102]。番茄突变体 *sitiens* (ABA 合成下降，ET 合成升高)根皮层中 AM 共生磷转运体 *PT4* 的表达下调，异形根孢囊霉的丛枝发育受抑制，这与外源根施 ABA 合成抑制剂 Na_2WO_4 对野生型的丛枝发育效应一致，但番茄 ABA 突变体 *notabilis* (ABA 合成正常，ET 合成升高)根系异形根孢囊霉的侵染程度下降而丛枝发育正常[103]。外源施加 AVG (50 μmol/L)能恢复 *sitiens* 根系异形根孢囊霉的侵染频率与强度，若同时再施加 ABA (50 μmol/L)则能恢复其丛枝丰度[104]。这些研究表明，ABA 不仅直接正向调控丛枝的形成，也可能通过拮抗 ET 信号途径而提高 AM 真菌的侵染频率/强度。Charpentier 等发现，ABA 信号可能是被其受体复合物亚基 PP2AB′1 识别，利用 RNAi 抑制 *PP2AB′1* 表达后，蒺藜苜蓿根系异形根孢囊霉的侵染率下降约 50%，丛枝和泡囊形成减少，并伴随 *PT4* 转录水平的下降，表明 ABA 信号经

PP2AB′1 介导促进 AM 真菌入侵与丛枝发育[101]。

此外，番茄 ABA 合成缺陷突变体(*notabilis*、*sitiens* 和 *flacca*)根系 *CCD7* 和 *CCD8* 的表达水平下调，SLs 的分泌量减少了 40%−52%[105]，表明内源性 ABA 可能通过增强 SLs 的合成而促进 AM 真菌的生长分枝与侵染定殖。另一方面，SLs 也可能影响 ABA 的合成，例如，番茄 SLs 合成缺陷突变体 *SL-ORT1* 根和叶片中的 ABA 水平显著下降[84]，突变体 *CCD8* 叶片中的 ABA、JA 和 SA 水平都显著下降[106]。Martín-Rodríguez 等还发现，ABA 通过拮抗 GA 的合成而抑制 DELLA 降解，从而维持番茄根系异形根孢囊霉的丛枝正常发育[72]。

1.9 油菜素内脂(brassinosteroid，BR)

BR 是一类甾体类化合物，主要通过增强植物细胞的伸长与分裂而促进维管组织的发育及茎的伸长[107]。外源叶施表油菜素内酯(5 μmol/L)提高摩西斗管囊霉对小麦(*Triticum aestivum*)根系的侵染率[108]，表明 BR 可能正调控 AM 发育过程。虽然豌豆 BR 合成缺陷突变体 *lkb* 根中 BR 含量较野生型具有一定程度下降，但此突变体和野生型根系根内根孢囊霉的侵染率与丛枝丰度无显著差别[70]。BR 合成极度缺陷突变体(BR 含量极少)如豌豆 *lk*[109]、番茄 d^x[110]和水稻 *brd2-1*[111]根系 AM 真菌的侵染率与丛枝形成被显著抑制。由此可见，BR 含量必须低于一定阈值才能负调控 AM 共生过程。豌豆突变体 *lk* 中 ET 的合成量增加[112]，但豌豆 BR 合成缺陷和 ET 不敏感双突变体 *lk ein2* 根系异形根孢囊霉的丛枝表型与突变体 *lk* 相似，表明 BR 对丛枝发育过程的影响不依赖于 ET[109]。Bitterlich 等研究表明，BR 可能通过提高丛枝周膜上蔗糖转运体 SUT2 活性与糖运输至丛枝，进而促进丛枝发育[110-111]，关于 BR 在 AM 真菌菌丝入侵与丛枝形成、丛枝养分交换及与其他植物激素互作中发挥的具体作用有待深入研究。

植物激素合成或感知产生改变的突变体与转基因植物的菌根表型见表 1。

2 植物激素信号途径及其互作介导 AM 发育的作用机制

有些植物激素调控 AM 真菌-寄主植物的共生识别，有些则参与调控菌丝在胞间或胞内的延伸、根细胞形态的变化、丛枝构建及丛枝中的养分转运，还有的在 AM 发育的不同阶段发挥作用(图 1)。植物根系分泌的 SLs 启动 AM 真菌的共生识别及菌丝生长分枝，ABA 和 BR 正调控早期阶段 AM 真菌的菌丝入侵，但 SA 和 ET 负调控早期阶段 AM 真菌的菌丝入侵，随后，生长素、ABA 和 BR 正调控丛枝的发育与功能运作，而 ET、GA 抑制丛枝发育，GA 信号的负调控因子 DELLA 对促进丛枝发育则起关键作用，同时也参与 MYB1 调控的丛枝消解过程。JA 对 AM 真菌菌丝入侵与丛枝发育均可能具有正或负调控作用。

植物激素信号途径之间的交叉互作也影响 AM 发育过程(图 1)。生长素或 ABA 正调控 SLs 信号促进 AM 真菌的生长分枝与早期侵染定殖，而 GA 负调控 SLs 信号抑制 AM 真菌的生长分枝与早期侵染定殖，ABA 负调控 ET、GA 信号而分别促进 AM 真菌侵染根外皮层和内皮层的丛枝形成。JA 和 BR 也与糖分子信号互作来精细调控 AM 共生构建过程[41,110-111]。Tanaka 等最近还发现，在培养基中添加豆蔻酸钾和蛋白胨条件下，联合施用 GR24 (0.1 μmol/L)和 MeJA (1 μmol/L)能诱导纯培养的明根孢囊霉 HR1 产生大量具有侵染能力的次生孢子[113]。由此可见，SLs 和其他植物激素合成、分布和活性的时空变化介导着 AM 发育的复杂网络。

表1 植物激素合成或感知产生改变的突变体与转基因植物的菌根表型

Table 1 Mutants and transgenic plants altered in hormone biosynthesis or perception and the corresponding mycorrhizal phenotypes

Hormone	Plant species	Mutant/transgenic	Hormonal alteration	Arbuscular mycorrhizal (AM) fungal isolate	AM phenotype	References
Strigolactones (SLs)	*Solanum lycopersicum*	*CCD7*-antisense	SLs deficiency	*Rhizophagus intraradices*	Decreased mycorrhization	[21-22]
	S. lycopersicum	*CCD8*-RNAi		*R. intraradices*	Decreased mycorrhization	[23]
	Oryza sativa	*d17* (*CCD7*)		*R. intraradices*	Decreased mycorrhization	[24]
	O. sativa	*d10* (*CCD8*)		*R. intraradices*	Decreased mycorrhization	[24]
	Pisum sativum	*rms1* (*CCD8*)		*R. intraradices*	Decreased mycorrhization	[32]
	O. sativa	*d3* (*dwarf3*)	SLs insensitivity	*R. intraradices* or *Gigaspora margarita*	Decreased mycorrhization	[31]
	O. sativa	*d14*		*R. intraradices* or *G. margarita*	Increased mycorrhization	[31]
	P. sativum	*rms4*		*R. intraradices*	Decreased mycorrhization	[32]
Jasmonic acid (JA)	*Medicago truncatula*	*AOC1*-antisense	JA deficiency	*R. intraradices*	Delayed mycorrhizal colonization	[39]
	S. lycopersicum	*spr-2*, *def-1*		*R. irregularis*	Decreased mycorrhizal colonization	[40]
	S. lycopersicum	*spr-2*		*R. fasciculatus*	Decreased mycorrhization	[41]
	O. sativa	*cpm2* (*coleoptile photomorphogenesis 2*)		*R. irregularis*	No change	[43]
	S. lycopersicum	*jai-1*	JA insensitivity	*R. intraradices*	Increased mycorrhization	[42]
Salicylic acid (SA)	*Nicotiana tabacum*	*NahG*	SA deficiency	*R. intraradices* or *Funneliformis mosseae*	Accelerated mycorrhizal colonization	[50]
		CSA	Constitutive SA biosynthesis	*R. intraradices* or *F. mosseae*	Retarded mycorrhizal colonization	[50]
Auxin (Aux)	*P. sativum*	*bsh* (*bushy*)	Auxin deficiency	*R. intraradices*	Decreased mycorrhizal colonization	[65]
	S. lycopersicum	*dgt* (*diageotropica*)	Auxin insensitivity	*R. intraradices*	Decreased mycorrhizal colonization	[58]
		pct (*polycotyledon*)	Hyperactive polar auxin transport	*R. intraradices*	Decreased mycorrhizal colonization	[58]
	S. lycopersicum, *M. truncatula* and *O. sativa*	miR393-overexpressing	Lower sensitivity to auxin	*R. irregularis*	Decreased mycorrhizal colonization and arbuscule abundance	[59]
	S. lycopersicum	*IAA27*-RNAi	High sensitivity to auxin	*R. irregularis*	Decreased mycorrhizal colonization	[66]
Gibberellin (GA)	*P. sativum*	*na-1*	GA deficiency	*R. intraradices*	Increased mycorrhizal colonization and arbuscule abundance	[70]

(待续)

(续表 1)

	S. lycopersicum	*procera*	Constitutive GA response (DELLA deficient)	*R. irregularis*	Decreased mycorrhizal colonization and arbuscule abundance	[71-72]
	P. sativum	*la cry-s*	DELLA deficiency	*R. intraradices*	Decreased mycorrhizal colonization and arbuscule abundance	[70]
	O. sativa	*slr1* (*slender rice1*)		*R. irregularis*	Decreased mycorrhizal colonization and arbuscule abundance	[75]
	M. truncatula	*della1*/*della2*		*Glomus versiforme*	Less arbuscules	[76]
Cytokinin (CTK)	*M. truncatula*	*cre1* (*cytokinin response 1*)	CTK signaling	*G. margarita*	No change	[88]
	N. tabacum	*35S:CKX2*	CTK deficiency	*R. intraradices*	Increased mycorrhizal colonization	[89]
	N. tabacum	*35S:CKX1*, *35S:CKX2*		*R. irregularis*	Decreased mycorrhizal colonization and arbuscule abundance	[90]
	P. sativum	*E151*	High CTK production	*R. irregularis*	Increased mycorrhizal colonization and arbuscule abundance	[91]
Ethylene (ET)	*S. lycopersicum*	*epi* (*epinastic*)	High ET production	*R. clarus*	Decreased mycorrhization	[94-96]
	S. lycopersicum	*epi*		*R. intraradices*	Decreased mycorrhization	[98]
	S. lycopersicum	*epi*		*R. irregularis*	Decreased mycorrhization	[99]
	S. lycopersicum	*Nr* (*Never ripe*)	Low ET sensitivity	*R. clarus*	Decreased mycorrhization	[94]
	S. lycopersicum	*Nr*		*R. clarus*	Increased mycorrhization	[95]
	M. truncatula	*sickle*	ET insensitivity	*G. versiforme* or *R. intraradices*	Increased mycorrhizal infection	[97]
	S. lycopersicum	*rin* (*ripenenig-inhibitor*)		*R. intraradices*	Increased mycorrhization	[98]
				R. irregularis		[99]
Abscisic acid (ABA)	*Lycopersicon esculentum*	*sitiens*	Deficient in ABA, but increased in ET	*R.intraradices*	Decreased mycorrhizal colonization and arbuscule abundance	[102]
	S. lycopersicum	*sitiens*		*R. irregularis*	Decreased mycorrhizal colonization and arbuscule abundance	[103-104]
	S. lycopersicum	*notabilis*	Normal in ABA, but enhanced in ET	*R. irregularis*	Decreased mycorrhizal intensity	[103]
	M. truncatula	*PP2AB'1*	ABA signaling	*R. irregularis*	Decreased mycorrhizal colonization	[101]
Brassinosteroid (BR)	*P. sativum*	*lkb*	BR deficiency	*R. intraradices*	No change	[70]
	P. sativum	*lk*		*R. irregularis*	Decreased mycorrhization	[109]
	S. lycopersicum	d^x (*DWARF*)		*R. irregularis*	Decreased mycorrhization	[110]
	O. sativa	*brd2-1*		*R. irregularis*	Decreased mycorrhization	[111]

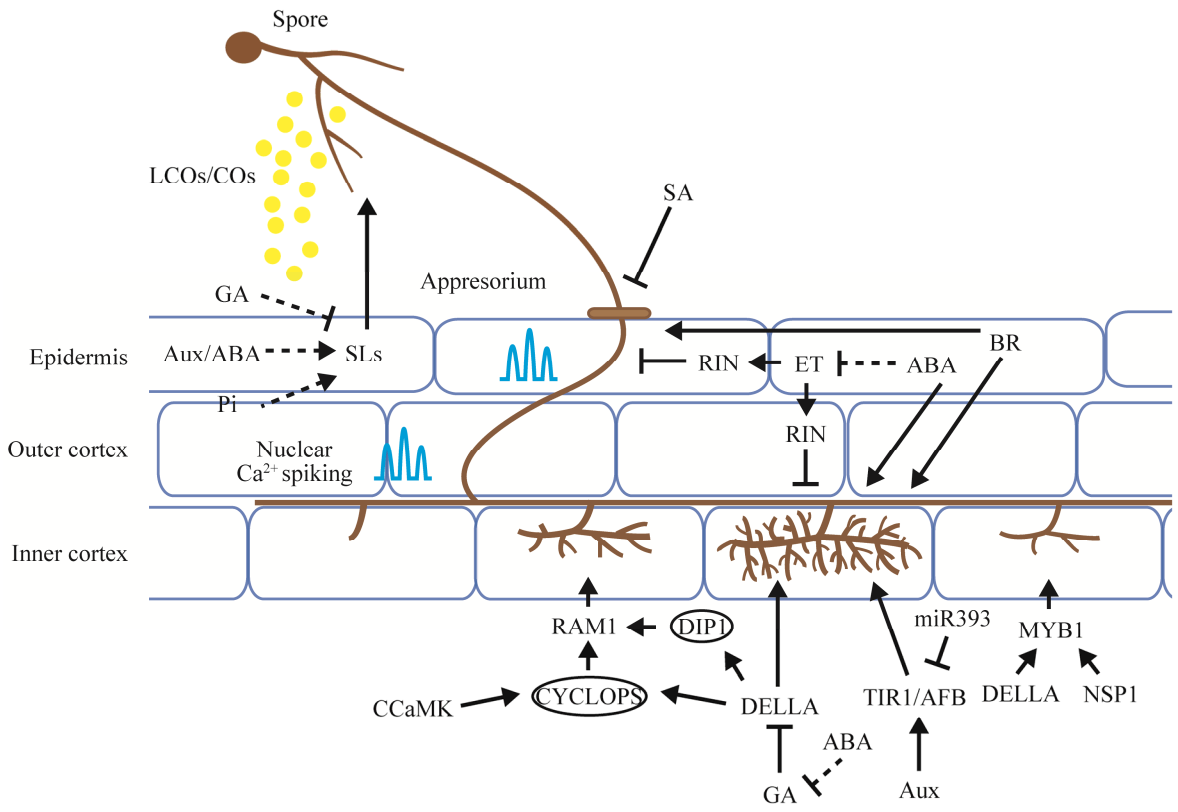

图 1　植物激素及其互作在丛枝菌根不同发育阶段的调控作用　LCOs：脂质几丁寡糖；COs：几丁质寡聚物；SLs：独脚金内酯；JA：茉莉酸；SA：水杨酸；Aux：生长素；GA：赤霉素；CTK：细胞分裂素；ET：乙烯；ABA：脱落酸；BR：油菜素内酯；Pi：磷；CCaMK：钙离子/钙调素依赖性蛋白激酶

Figure 1　The role of different phytohormones and their possible signaling interactions at different stages of arbuscular mycorrhizal (AM) development. LCOs: Lipochito-oligosaccharides; COs: Chitin oligomers; SLs: Strigolactones; JA: Jasmonic acid; SA: Salicylic acid; Aux: Auxin; GA: Gibberellin; CTK: Cytokinin; ET: Ethylene; ABA: Abscisic acid; BR: Brassinosteroid; Pi: Phosphate; CCaMK: Calcium/calmodulin-dependent protein kinase.

3　胁迫对植物激素信号传递及 AM 发育的影响

寄主植物-AM 真菌之间的共生受环境条件的制约，环境因素胁迫下，寄主植物激素合成与分泌的变化会影响 AM 发育。磷素缺乏条件下，植物会增强 SLs 合成和分泌[114-116] (图 1)，促进 AM 共生体形成，以帮助自身从土壤中获取养分。还有研究报道，磷缺乏能刺激寄主植物根系 SLs 的合成增加而 CTK 的合成减少，从而诱导 AM 真菌菌丝的生长分枝及侵染定殖[89,117]。然而氮素对 SLs 合成的影响取决于植物种类，氮缺乏使高粱(*Sorghum bicolor*)根系 SLs 的分泌增加[116]，但对红花苜蓿(*Trifolium pratense*)却无影响[115]。Yoneyama 等研究发现，氮缺乏可能通过改变植物地上部磷含量而影响其根系 SLs 的合成[118]。当丛枝发育成熟和 AM 共生体建立后，SLs 的合成会显著减少[18]，这可能是由于寄主体内营养水平的提高或内在调节机制防止 AM 真菌的过度定殖。例如，Floss 等的研

究表明，丛枝发育成熟后，由共同体界面转运的磷能使植物体内磷水平升高，可能诱导 GA 合成增强并导致 DELLA 的降解，对丛枝发育形成负反馈调控[76]。高磷水平(100 μL/L)下，异形根孢囊霉在番茄野生型和突变体 *rin* 根系的侵染水平(侵染率、程度和丛枝丰度)下降，而在突变体 *epi* 根系的侵染水平却无变化，外源根施乙烯利(40 μmol/L)可提高异形根孢囊霉对野生型的侵染水平[99]，表明 ET 信号途径拮抗高磷水平对 AM 发育的抑制作用。干旱抑制莴苣(*Lactuca sativa*)或番茄根中 SLs 的合成[119]，盐胁迫抑制莴苣根中 SLs 的合成[120]，然而干旱或盐胁迫下接种 AM 真菌的寄主根中 SLs 与 ABA 含量之间存在正相关关系[119-120]，表明 SLs 与 ABA 可能通过协作来提高 AM 真菌对寄主根系的侵染与丛枝形成及寄主抗逆性。此外，机械损伤和病原菌侵染也可能引发植物激素的合成与信号转导，从而影响 AM 发育。例如，蒺藜苜蓿叶片反复损伤诱导叶片和根中 *AOC* 和细胞壁转化酶基因 *INV* 的转录表达显著升高，提高了根系根内根孢囊霉的侵染率与丛枝丰度[121]；用感染力弱的灰葡萄孢菌(*Botrytis cinerea*)菌株侵染番茄叶片可诱导其体内产生 JA，寄主的地上生长未受影响，但根系 AM 真菌的产孢量提高约 60%[122]。

4 展望

植物激素往往是通过协同或拮抗作用参与植物的生长发育与抗逆，以及 AM 共生关系的建立与维持[14-15]。利用质谱分析表明，纯培养的异形根孢囊霉孢子萌发时可产生 CTK、IAA 和 GA[123]，但由于 AM 真菌源的激素合成及信号传递突变体难以获得，因而无法直接证明 AM 发育中激素的合成及作用是否也部分决定于 AM 真菌。植物受到外界非生物或生物胁迫的刺激引起激素和活性氧、活性氮等信号分子合成的变化，激素被其受体感知激发由不同转录调控因子参与的信号途径网络[124]。AM 真菌开始侵染寄主根系时，其分泌的 COs 不仅激活 AM 共生信号途径，同时也抑制微生物关联分子模式(microbe-associated molecular pattern，MAMP)引发的免疫防御反应，而且 Myc 因子受体 MYR1 和 MAMP 受体 EBiP 通过竞争结合 CERK1 启动共生或防御信号途径[125]。如同植物-病原菌互作一样，菌根真菌也能通过分泌效应分子的策略干扰寄主的防御反应，从而有利于自身入侵。例如，根内根孢囊霉分泌的 SP7 抑制调控乙烯信号途径转录因子 ERF19 (ethylene response factor 19)的表达，从而增强对寄主根系的侵染定殖[126]。为阐明激素介导的级联网络如何协调植物的生长与防御反应来促进 AM 真菌共生而抑制病原菌寄生，未来可利用组学和基因编辑等分子生物学手段进行系统研究。

AM 真菌从外界吸取氮、磷等养分转运至丛枝共生体界面，依赖与植物“交换”获取糖类和脂肪酸而完成生活史，根皮层细胞中发育成熟的丛枝维持 1−3 d 后便逐渐消亡，同时新的丛枝又开始侵染定殖[127]。RAM1 和 RAM2 在丛枝发育时起关键作用[128-129]，Myc 因子诱导 *RAM1*、*RAM2* 和 *PT4* 的上调表达[130]，并且 RAM1 激活脂肪酸途径中的关键酶 *RAM2* 或脂肪酸转运体 *STR/STR2* 的转录表达[131]。AP2/EREBP 蛋白家族的转录因子 WRI5a (其诱导表达也依赖于 RAM1)能与 *STR* 启动子区元件和 *PT4* 互作而调控丛枝中脂肪酸和磷的双向交换运输[130]。丛枝消解时 MYB1 与 GRAS 蛋白家族的转录因子 DELLA 和 NSP1 发生互作[80]。然而，不同激素、转录调控因子及其互作在丛枝养分交换和丛枝寿命或周转中的潜在作用尚待进一步探索。

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