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AHLs 介导的群体感应和群体淬灭对植物-根际微生物相互作用的影响*

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摘　要: 根际是由植物根系和土壤微生物之间相互作用形成的一种特殊环境, 根际微生物群落的宏基因组是植物微生物组的重要组成部分。植物与根际微生物之间的相互作用是一个复杂的过程。在根际环境中, 微生物群落利用复杂的种内和种间信号传导机制招募特定的微生物, 协调并控制混合群落的行为, 从而影响植物的生长发育和健康。根际微生物能够自发产生、释放特定的信号分子, 并能感知其浓度变化, 从而调节微生物的群体行为, 这一调控系统称为群体感应 (quorum sensing, QS)。QS 系统的特征是合成和释放特定的信号分子。根际土壤细菌中存在多种 QS 信号分子, 如 *N*-酰基高丝氨酸内酯 (AHLs)、二酮哌嗪、扩散信号因子、次生代谢物、植物激素类分子等。AHLs 作为细菌中被广泛研究的 QS 信号分子, 在植物与根际微生物的相互作用中发挥重要作用。本文综述了 AHLs 介导的群体感应机制, 并讨论了 AHLs 在植物与根际微生物相互作用中的调节作用, 包括 AHLs 对植物的生长发育、逆境耐受性和抗病性等方面的有益影响, 以及 AHLs 介导的 QS 系统调控导致的根际致病菌对植物的有害影响, 同时还探讨了基于 AHLs 的群体淬灭对植物-根际微生物相互作用的影响, 以期为植物健康与农业生产提供新的思路和方法, 推动可持续农业的发展。

关键词: 根际微生物; *N*-酰基高丝氨酸内酯 (AHLs); 群体感应; 群体淬灭; 植物健康

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Effects of quorum sensing and quorum quenching mediated by AHLs on plant-rhizosphere microbial interactions*

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Abstract: The rhizosphere is a unique environment that arises from the interaction between plant roots and soil microorganisms. The metagenome of the microbial community in the rhizosphere plays a crucial role in shaping the plant microbiome. The interaction between plants and rhizosphere microorganisms is a complex process. In the rhizosphere environment, the microbial community recruits specific microorganisms through intricate signaling mechanisms within and between species. This coordination and control of the mixed community ultimately impacts the growth, development and health of plants. From an academic perspective, rhizosphere signaling mechanisms can be categorized into three primary types. Firstly, plants transmit signals to microorganisms by secreting low molecular weight molecules. Secondly, there is inter- and intraspecific microbial signaling. Lastly, microorganisms transmit signals to plants through compounds they produce. Rhizosphere microbes utilize quorum sensing (QS) to autonomously generate and release distinct signaling molecules, enabling them to detect variations in their concentrations and thereby regulate microbial quorum behavior. QS is a bacterial intercellular communication mechanism that regulates the expression of numerous bacterial genes, which are involved in various plant-microbe interactions. These interactions encompass functions such as biofilm formation, nitrogen fixation, hydrolysis, enzyme and extracellular polysaccharide synthesis, toxin production, cell movement, and intercellular connectivity. QS systems are characterized by the synthesis and release of specific signaling molecules. This process is crucial in rhizosphere communication as it enables the transmission of inter- and intraspecific information through the necessary signaling molecules. Due to the high density and diversity of rhizosphere bacteria, the rhizosphere may facilitate the transmission of QS signals. Additionally, these signaling molecules aid in the colonization of plant root surfaces or other rhizosphere-related areas by rhizosphere bacteria through gene expression mediated by QS. Recent research has revealed the presence of *N*-acyl-homoserine lactones (AHLs), diketopiperazines, diffusible signaling factor, secondary metabolites, phytohormonelike molecules and other QS signaling molecules in rhizosphere soil bacteria. AHLs are the most extensively studied quorum sensing signaling molecules in bacteria. They not only mediate bacterial quorum sensing, but also have a significant impact on the interaction between plants and rhizosphere microorganisms. This includes the colonization of rhizosphere microorganisms, the maintenance of soil ecosystems and the effects on plant growth. An in-depth understanding of the quorum sensing mechanism mediated by AHLs holds significant importance in promoting agricultural production, enhancing plant health, and fostering sustainable development. This article presents a review of the quorum sensing mechanism mediated by AHLs and discusses the regulatory role of AHLs in the interaction between plants and rhizosphere microorganisms. It explores the beneficial effects of AHLs on plant growth and development, stress tolerance and disease resistance, as well as the harmful effects of rhizosphere pathogenic bacteria on plants due to AHLs-mediated regulation of the QS system. Additionally, the article explores the impact of AHLs-based quorum quenching on plant-rhizosphere microbial interactions, aiming to provide valuable insights for plant health and agricultural production. The article also proposes new ideas and methods to promote the development of sustainable agriculture.

Keywords: Rhizosphere microorganisms; *N*-acyl-homoserine lactones (AHLs); Quorum sensing; Quorum quenching; Plant health

根际是由植物根系和土壤微生物之间相互作用形成的一种特殊环境。根际土壤对植物体来说是一个重要的生境, 根际微生物群落的宏基因组是植物微生物组的重要组成部分[1-3]。不同的植物-微生物相互作用会导致根际微生物种群的组成发生变化[4-5]。根际微生物群落非常丰富和复杂, 存在种内和种间的信号传导。这些复杂的信号机制在根际微生物群落的形成中起着关键作用, 通过种间或种内通信招募特定的微生物, 以调控微生物群落的行为。一般来说, 根际信号机制可分为 3 种主要类型: 1) 植物通过分泌低分子量分子向微生物传递信号; 2) 微生物信号在种间和种内的传递; 3) 微生物通过其产生的化合物向植物传递信号[6-7]。根际微生物群落通过产生调节其基因表达的信号分子来相互作用。微生物的种间或种内交流是在群体感应 (quorum sensing, QS) 机制的调节下发生的, 而这种机制取决于细胞密度[7]。群体感应是根际微生物交流的重要方式, 它通过提供必要的信号分子来传递种间和种内的信息, 从而协调和控制混合群落的行为[8]。

QS 是指细菌通过自发产生并释放特定信号分子, 并感知其浓度变化, 从而调节微生物的群体行为[9]。这是一种依赖于细菌种群密度的细胞间通信机制。Fuqua 等[9] 提出了 QS 的概念, 并认为大多数微生物都具有这种现象。在正常情况下, 每个细菌会分泌低水平的 QS 信号分子, 随着细菌密度的增加, QS 信号分子的积累达到一定浓度, 可以激活相关基因表达。QS 激活了数百种细菌基因的表达, 其中的许多基因在植物与微生物的相互作用中发挥着重要作用, 这些功能包括生物膜形成、固氮、水解酶、胞外多糖和毒素合成、细胞运动和细胞间相互连接等[10]。QS 最早在费氏弧菌 (*Vibrio fischeri*) 中被发现, 这是一种定殖在夏威夷短尾鱿鱼 (*Euprymna scolopes*) 上的革兰氏阴性菌[11]。QS 系统的特征是合成和释放特定的信号分子。根际具有高密度且多样的细菌, 因此有利于 QS 信号分子的传递。同时, QS 信号分子可以促进根际细菌在植物根系表面或根际定殖[12]。

目前已经在土壤细菌中发现了多种 QS 网络, 这些网络包括许多信号分子, 如 *N*-酰基高丝氨酸内酯 (AHLs)、二酮哌嗪、扩散信号因子、次生代谢物、植物激素类分子和其他小型有机化合物[13]。在根际环境中, 微生物之间通过 QS 系统进行信号传递和交流非常普遍[14-15]。细菌中受 QS 调控的细胞过程多种多样, 细菌-宿主之间的相互作用无论是共生关系还是致病关系, QS 调控的过程对细菌-宿主相互作用通常都非常重要。QS 能够促进生物适应环境的能力, 成为全球基因调控网络的重要组成部分[16]。

AHLs 作为被广泛研究的 QS 信号分子, 不仅介导细菌 QS, 而且还在植物与根际微生物的相互作用中扮演重要角色[17-18]。深入了解 AHLs 介导的 QS 机制对于推动农业生产、促进植物健康和实现可持续发展具有重要意义。本文综述了 AHLs 介导的 QS 机制, 并讨论其在植物与根际微生物相互作用中的调节作用, 包括 AHLs 对植物的生长发育、逆境耐受性和抗病性等方面的有益影响, AHLs 介导的 QS 系统调控所导致的根际致病菌对植物的有害影响, 以及基于 AHLs 介导的群体淬灭 (QQ) 对植物和根际微生物的影响。本研究旨在深入了解这一领域的机制和应用前景, 以期为植物健康与农业生产提供新的思路与方法, 推动可持续农业的发展。

1　AHLs 介导的群体感应机制

AHLs 作为革兰氏阴性菌中常见的 QS 信号分子, 由内酯环和酰基侧链组成, 它们的合成和传导由特定的酶和受体完成, 并且很容易从细胞释放到环境中, 当其浓度达到一定水平时, 细菌群体内的细菌能感知到信号分子的存在并做出相应反应, 从而调控群体行为[19-26]。不同的细菌合成不同类型的 AHLs, 其作用特异性由 *N*-酰基的碳链长度或 3-碳位置的取代基的差异决定[27]。LuxI 是一类可催化合成自诱导物质的胞内蛋白酶, 其通过催化载体蛋白的酰基侧链与 S-腺苷甲硫氨酸上的高丝氨酸结合, 生成 AHLs。AHLs 中, 短 CH 链具有亲水性, 而长 CH 链具有疏水性[28-29]。AHLs 能够自由进出细胞, 随着细菌密度的增加, 当细菌在细胞外环境中分泌的 AHLs 积累到一定浓度时, 可与同源的 LuxR 型受体蛋白结合, 形成调控基因表达的复合物, 从而激活 QS 调控的靶基因, 进而促进转录[30-33]。每个 LuxR 蛋白只与其特定的 AHLs 自诱导分子结合, 因为它们具有特异选择性。AHLs 介导的 QS 调节了许多基因的表达, 这些基因负责生物膜的形成、生物发光、色素的产生、致病性、铁载体的产生、质粒结合转移、抗生素和抗真菌化合物的产生和聚集[34]。AHLs 介导的 QS 很可能发生在数千种不同的细菌种类中[35]。

2　AHLs 介导的群体感应对植物的有益影响

AHLs 对植物的生长发育、逆境耐受性和抗病性等具有重要影响。AHLs 由根际微生物合成, 能够进一步诱导植物根系中的特定反应, 进而影响植物与根际微生物的相互作用。前人研究表明, 根际土壤的可培养细菌中, 能够产生 AHLs 的细菌占比达 10%~20%, 这表明产生 AHLs 的细菌在植物生长过程中占据重要地位[36-39]。AHLs 介导的 QS 在植物-微生物相互作用和根际细菌的运动和定殖中起着重要作用[40-41]。植物相关细菌利用 QS 系统感知生态位, 适应环境压力并分布种群, 从而影响宿主植物的生长和健康[42-43]。研究表明, AHLs 可以促进植物的生长和根系发育, 提高植物的适应能力和耐受性, 通过调节植物的免疫反应和信号传导通路, 增强植物对病原菌的抵抗能力[7]。

2.1　AHLs 对植物生长和发育的影响

AHLs 不仅可以调节细菌种群中各种细胞过程, 还能够提高植物的生长和光合活性, 调节营养物质的同化, 诱导植物内源激素平衡发生改变, 并增强宿主植物的防御能力[44-47]。研究表明, 短链 AHLs 通常影响植物生长, 长链 AHLs 可以增强植物抗性[48-50]。当前研究表明, 多种 AHLs 和分泌 AHLs 的根际细菌对植物的生长发育和抗性存在影响 (表 1)。Mathesius 等[52] 首次开展了关于细菌 AHLs 对植物生长影响的研究, 并发现用两种 AHLs [*N*-(3-氧代十二烷酰基)-L-高丝氨酸内酯 (3-oxo-C12-HSL) 和 *N*-(3-氧代十六烷酰基)-L-高丝氨酸内酯 (3-oxo-C16-HSL)] 处理模式豆科植物蒺藜苜蓿 (*Medicago truncatula*) 根系后, 参与氧化应激、类黄酮和植物激素代谢等过程的 150 多个蛋白表达水平发生了显著改变。随后, 在拟南芥 (*Arabidopsis thaliana*) 中也发现了类似的效应。使用 *N*-(3-氧代辛酰基)-L-高丝氨酸内酯 (3-oxo-C8-HSL) 处理拟南芥幼苗会改变植物参与各种生理活动的蛋白质积累水平, 包括碳代谢、蛋白质生物合成、保护反应和对不利环境因素的抗性[46,79]。有研究表明, *N*-丁酰基-L-高丝氨酸内酯 (C4-HSL) 作为 QS 信号分子, 可以诱导拟南芥根细胞内钙离子浓度升高[51]。据报道, C4-HSL 和 *N*-己酰基-L-高丝氨酸内酯 (C6-HSL) 能够促进拟南芥根系的生长[50]。*N*-(3-氧代己酰基)-L-高丝氨酸内酯 (3-oxo-C6-HSL) 和 3-oxo-C8-

表 1 不同类型 *N*-酰基高丝氨酸内酯 (AHLs) 和分泌 AHLs 的根际细菌对植物的影响

Table 1 The effects of different types of *N*-acyl-homoserine lactones (AHLs) and AHLs-producing rhizosphere bacteria on plants

相关植物 Associated plant	AHLs/分泌AHLs的细菌 AHLs/AHLs-secreting bacteria	主要影响 Major effect	参考文献 Reference
拟南芥 *Arabidopsis thaliana*	3-oxo-C6-HSL	增强拟南芥的耐盐性 Enhance salt tolerance in *A. thaliana*	[47]
	3-oxo-C6-HSL, 3-oxo-C8-HSL	激发*GCR1*/*GPA1*基因, 促进根系生长 Stimulate the *GCR1*/*GPA1* genes, promote root growth	[48]
	C6-HSL	改变植物激素平衡 Change the balance of phytohormone	[50]
	C4-HSL	诱导根细胞细胞内钙离子升高 Induce intracellular calcium elevation in root cells	[51]
蒺藜苜蓿 *Medicago truncatula*	3-oxo-C12-HSL, 3-oxo-C16:1-HSL	诱导生长素反应蛋白和类黄酮合成蛋白, 分泌群体感应拟态物质 Induce auxin-responsive and flavonoid synthesis proteins, secrete mimetics of quorum sensing	[52]
	3-oxo-C14-HSL	增加根系结瘤数量 Increase the number of nodules formed on root systems	[53]
番茄 *Solanum lycopersicum*	AHL/液化沙雷氏菌 MG1和恶臭假单胞菌 IsoF AHL/*Serratia liquefaciens* MG1 and *Pseudomonas putida* IsoF	增加植物系统抗性, 增加水杨酸含量, 诱导防御基因的表达发生变化 Increase systemic resistance of plants, increase salicylic acid content, induce changes in the expression of defense genes	[54]
	AHL/恶臭假单胞菌 AHL/*P. putida*	促进细胞间的有效交流 Promote efficient communication between the cells	[55]
	3-oxo-C12-HSL, 3-oxo-C14-HSL/禾谷伯克霍尔德菌 M12和M14 3-oxo-C12-HSL, 3-oxo-C14-HSL/*Burkholderia graminis* M12 and M14	促进植物生长, 诱导抗盐胁迫 Promote plant growth, induce protection against salt stress	[56]
	3-oxo-C14-HSL	保护番茄免受晚疫病 Protect *S. lycopersicum* from late blight disease	[57]
	3-oxo-C6-HSL, 3-oxo-C8-HSL, 3-oxo-C12-HSL, 3-oxo-C14-HSL	促进植物生长, 诱导对植物病原体的抗性 Promote plant growth, induce resistance to plant pathogens	[58]
小麦 *Triticum aestivum*	3-oxo-C6-HSL	增强小麦的耐盐性 Enhance salt tolerance in *T. aestivum*	[47]
	AHL/恶臭假单胞菌 AHL/*P. putida*	促进细胞间的有效交流 Promote efficient communication between the cells	[55]
	AHL/致黄假单胞菌 AHL/*Pseudomonas aureofaciens*	AHL介导的交流 AHL-mediated communication	[59]
	C4-HSL	提高植物对真菌病原体的防御能力 Improve plant defense against the fungal pathogens	[60]
油菜 *Brassica napus*	C4-HSL, C6-HSL, 3-oxo-C6-HSL/普城沙雷氏菌 HRO-C48 C4-HSL, C6-HSL, 3-oxo-C6-HSL/*Serratia plymuthica* HRO-C48	降低大丽轮枝菌对作物的致病性, 保护作物免受黄萎病的危害, 诱导产生抗真菌挥发物和水解酶 Reduce the pathogenicity of *Verticillium dahliae* to crops, protect crops against *Verticillium* wilt, and induce the production of antifungal volatiles and hydrolytic enzymes	[61-62]
黄瓜 *Cucumis sativus*	C6-HSL, 3-oxo-C10-HSL	促进主根伸长, 促进植物生长 Promote primary root elongation, enhance plant growth	[63]
	3-oxo-C14-HSL	增强植株对病原体的防御能力 Enhance the plant’s defense against pathogens	[63]
鹰嘴豆 *Cicer arietinum*	C4-HSL	提高植物的生长能力和植物对真菌病原体的防御能力 Improve the plant growth and plant defense against the fungal pathogens	[60]
大麦 *Hordeum vulgare*	3-OH-C10-HSL/食酸菌 N35 3-OH-C10-HSL/*Acidovorax radicis* N35	诱导有益菌根际定植, 提高幼苗防御能力 Induce beneficial mycorrhizal colonization, improve seedling defense	[64]
燕麦 *Avena sativa*	AHL/变形菌门 AHL/Proteobacteria	控制细胞外酶活性 Control extracellular enzyme activity	[65]
玉米 *Zea mays*	C4-HSL, C6-HSL, 3-oxo-C6-HSL/绿针假单胞菌 449 C4-HSL, C6-HSL, 3-oxo-C6-HSL/*Pseudomonas chlororaphis* 449	对植物病原真菌具有拮抗活性 Antagonistic activity against phytopathogenic fungi	[66]
芝麻 *Sesamum indicum*	C6-HSL, C8-HSL/沙雷氏菌属 GS2 C6-HSL, C8-HSL/*Serratia glossinae* GS2	形成生物膜, 促进植物生长 Form biofilms, promote plant growth	[67]
水稻 *Oryza sativa*	C4-HSL/气单胞菌属, 肠杆菌属, 肺炎克雷伯菌, 考氏科萨克氏菌, 水性鞘氨醇单胞菌, 斯惠假单胞菌和*Providentia rettigeri* C4-HSL/*Aeromonas* sp., *Enterobacter* sp., *Klebsiella pneumoniae*, *Kosakonia cowanii*, *Sphingomonas aquatilis*, *Pseudomonas sihuiensis* and *Providentia rettigeri*	形成生物膜 Form biofilms	[68]
千年芋 *Xanthosoma sagittifolium*	AHL/假单胞菌 CMR12a AHL/*Pseudomonas* CMR12a	对群结腐霉(*Pythium myriotylum*)具有拮抗活性 Antagonistic activity against *P. myriotylum*	[69]

续表 1

相关植物 Associated plant	AHLs/分泌AHLs的细菌 AHLs/AHLs-secreting bacteria	主要影响 Major effect	参考文献 Reference
绿豆 *Vigna radiata*	3-oxo-C10-HSL	促进根系分枝, 改变根系结构 Promote root formation, change the root architecture	[70]
菜豆 *Phaseolus vulgaris*	3O-C7-HSL, 3OH-C7-HSL/苍白杆菌属 Pv2Z2 3O-C7-HSL, 3OH-C7-HSL/*Ochrobactrum* sp. Pv2Z2	促进植物生长和生物降解潜力 Promote plant growth and biodegradation potential	[71]
马铃薯 *Solanum tuberosum*	3-oxo-C6-HSL, 3-oxo-C8-HSL/欧文氏菌 3-oxo-C6-HSL, 3-oxo-C8-HSL/*Erwinia carotovora*	抑制毒力因子 Inhibit virulence factor	[72]
烟草 *Nicotiana tabacum*	C4-HSL, C8-HSL, 3-oxo-C6-HSL/粘质沙雷氏菌 C4-HSL, C8-HSL, 3-oxo-C6-HSL/*Serratia marcescens*	诱导植物系统抗性 Induce systemic resistance (ISR)	[73]
地黄 *Rehmannia glutinosa*	AHL/假单胞菌属, 肠杆菌属 AHL/*Pseudomonas*, *Enterobacteriaceae*	对植物病原体具有拮抗活性, 引起地黄组培苗枯萎病 Antagonistic activity against plant pathogen, cause severe wilt disease in the tissue culture seedlings of *R. glutinosa*	[74]
人参 *Panax ginseng*	C8-HSL, C10-HSL, C12-HSL	改变土壤微生物群落结构 Alter the soil microbial community structure	[75]
碱蓬 *Suaeda glauca* 芦苇 *Phragmites australis*	C6-HSL, C8-HSL/红细菌目 C6-HSL, C8-HSL/Rhodobacterales	形成生物膜, 降解二甲基巯基丙酸内盐和油 Form bioflms, degrade Dimethylsulfoniopropionate and oil	[76]
洋葱 *Allium cepa*	C6-HSL, 3-oxo-C6-HSL/菠萝泛菌 SK-1 C6-HSL, 3-oxo-C6-HSL/*Pantoea ananatis* SK-1	引起洋葱中心腐烂病 Cause center rot disease of *A. cepa*	[77]
太子参 *Pseudostellaria heterophylla*	AHL/粘质沙雷氏菌 AHL/*S. marcescens*	导致太子参枯萎病 Cause *P. heterophylla* wilt disease	[78]

HSL 通过 G 蛋白偶联受体间接诱导了拟南芥根系的显著伸长[48]。前人研究发现, 短链 (如 C6-HSL) 和中链 [如 *N*-(3-氧代癸酰基)-L-高丝氨酸内酯 (3-oxo-C10-HSL)] AHLs 可以分别促进黄瓜 (*Cucumis sativus*) 初生根的伸长和根结构的修饰, 进而促进了植物的生长[63]。对大麦 (*Hordeum vulgare*) 进行 *N*-癸酰基-L-高丝氨酸内酯 (C10-HSL) 处理后, 植株体内抗氧化酶和解毒酶的活性增强[80]。Rankl 等[81] 研究了 C6-HSL、*N*-辛酰-L-高丝氨酸内酯 (C8-HSL) 和 *N*-十二烷酰-L-高丝氨酸内酯 (C12-HSL) 对大麦生长和根系发育的影响, 结果显示仅在特定浓度下, C6-HSL 和 C8-HSL 处理可以刺激根细胞对 K^+的吸收, 但是 C12-HSL 在所有测试浓度下均能够诱导根细胞对 K^+的吸收, 这表明 AHLs 能够促进植物生长和侧根形成。C6-HSL 处理冬小麦 (*Triticum aestivum*) 种子可以促进植株生长和产量增加, 该结果在田间具有潜在的应用价值。此外, C6-HSL 作为一种新的诱导剂, 能够提高谷物对非生物胁迫的抵抗能力[82]。通过苜蓿中华根瘤菌 (*Sinorhizobium meliloti*) 合成的 *N*-(3-氧代十四烷酰基)-L-高丝氨酸内酯 (3-oxo-C14-HSL) 能够刺激蒺藜苜蓿形成根瘤, 但未发现其他 AHLs (如 C4-HSL、C10-HSL 和 3-oxo-C12-HSL) 存在该效应[53]。He 等[76] 发现能够产生 AHLs 信号分子的 QS 细菌广泛分布于沿海湿地植物碱蓬 (*Suaeda glauca*) 和芦苇 (*Phragmites australis*) 的根际土壤和根组织中, 且部分 QS 菌可以促进生物膜的形成、降解二甲基巯基丙酸内盐 (DMSP) 和油, 进而促进碱蓬和芦苇的生长, 以上可以为保护沿海湿地生态系统提供重要的参考。

2.2　AHLs 对植物逆境胁迫的影响

AHLs 还可以提高植物的抗胁迫能力, 增强其自身的防御能力。据报道, AHLs 可以缓解拟南芥幼苗受到的盐胁迫, 降低拟南芥丙二醛 (MDA) 含量, 增加抗氧化酶活性, 并促进与保护作用、光合作用、信号传导和细胞壁生物合成相关的 97 种蛋白质的积累, 表明植物对盐胁迫的耐受性与蛋白质数量和功能的变化密切相关[46]。接种产生 AHLs 的禾谷伯克霍尔德菌 M12 和 M14 (*Burkholderia graminis* M12 和 M14) 对野生型番茄 (*Lycopersicum esculentum*) 植株的盐胁迫具有显著的保护作用, 表达 *Yen*I (短链 AHL 生产者) 和 *Las*I (长链 AHL 生产者) 的转基因番茄植株对盐胁迫的耐受性增加[56]。Zhao 等[47] 发现用 3-oxo-C6-HSL 处理植物根部可以增强拟南芥和小麦的耐盐性。在盐胁迫条件下, 3-oxo-C6-HSL 显著改善了拟南芥和小麦的根长、芽长和鲜重的生长抑制表型, 使叶绿素和脯氨酸含量增加, MDA 和 Na^+含量以及 Na^+和 K^+的比值降低。分子实验分析显示, 在

盐胁迫条件下, 3-oxo-C6-HSL 显著上调拟南芥的盐响应基因表达, 包括脱落酸依赖与脱落酸非依赖的渗透胁迫响应基因和离子稳态调控基因[47]。以上这些结果表明, AHLs 能够增强植物的耐逆境胁迫能力。

2.3 AHLs 对植物抗病的影响

AHLs 除了促进植物生长发育和提高逆境耐受性外, 还可以增强植物的抗病性。根际受 AHLs 介导的 QS 调控驱动对植物病原体的抑制, 可作为替代化学物质的生物防治剂[83]。Schikora 等[84] 研究结果表明, 经过 3-oxo-C14-HSL 处理后, 拟南芥对病原菌的抗性明显增强。Schuhegger 等[54] 在番茄根部接种产生 AHLs 的菌株液化沙雷氏菌 MG1 (*Serratia liquefaciens* MG1) 和恶臭假单胞菌 IsoF (*Pseudomonas putida* IsoF) 后, 增强了番茄植株对病原体交链格孢 (*Alternaria alternata*) 的系统抗性。从油菜 (*Brassica napus*) 根际分离的普城沙雷氏菌 HRO-C48 (*Serratia plymuthica* HRO-C48) 是由 AHLs 介导的 QS 调控, 可以诱导大豆 (*Glycine max*) 和番茄植株对灰霉病的抗性[85]。为了更好地研究根际情况, Shrestha 等[58] 分析了植物与多个 AHLs 信号分子 (3-oxo-C6-HSL、3-oxo-C8-HSL、3-oxo-C12-HSL 和 3-oxo-C14-HSL) 之间的相互作用, 结果显示不同 AHLs 的组合增强了番茄对病原菌丁香假单胞菌 (*Pseudomonas syringae*) 的抗性, 这表明诱导抗性是 AHLs 多重感应的结果。Gahoi 等[60] 开发了一种轻质纳米复合生物肥料 (NCB), 该肥料由 C4-HSL 包覆的铁碳纳米纤维和固定在活性炭珠中的细菌混合物组成, 并发现在鹰嘴豆 (*Cicer arietinum*) 和小麦种植过程中添加 NCB 后, 植物的生物量、根长、叶绿素和蛋白质含量均显著增加。此外, 将植物培养在 NCB 中 21 d 后, 鹰嘴豆和小麦分别对枯萎病和根腐病表现出显著的抗性潜力。这些结果表明该材料在促进植物生长活性和防治常见真菌病害方面具有良好的适用性[60]。另外, Ibal 等[75] 发现 C8-HSL、C10-HSL 和 C12-HSL 的添加均能促进盆栽人参 (*Panax ginseng*) 的生长和发育, 提高植物的生物量, 并改变土壤根际微生物群落的组成, 其中 C10-HSL 的处理效果最佳, 这为解决连作人参生长不良和易受病害影响等问题提供了参考。De Maeyer 等[69] 从千年芋 (*Xanthosoma sagittifolium*) 根际分离的假单胞菌 CMR12a (*Pseudomonas* CMR12a), 对千年芋根腐病病原体群结腐霉 (*Pythium myriotylum*) 具有拮抗作用。外源信号分子 3-oxo-C14-HSL 添加至黄瓜幼苗水培液中, 能够增强黄瓜对病原菌古巴假霜霉菌 (*Pseudoperonospora cubensis*) 和细菌性叶斑病菌 (*Pseudomonas syringae* pv. *lachrymans*) 的防御反应[63]。由此可见, AHLs 能够增强植物对病原菌的抵抗能力, 而这种影响是通过调节植物的免疫反应和信号传导通路实现的。

3 AHLs 介导的群体感应与植物病原菌互作

对土壤根际细菌的研究显示, QS 是根际细菌的主要特征之一[86]。植物和其他微生物群落也可以通过 QS 的信号分子直接或间接地改变根际细菌的作用[87]。由 AHLs 介导的植物相关细菌的通信在病原体和宿主植物之间的相互作用中至关重要。一旦根际细菌感知到信号分子, 通信和相互作用随之展开[88]。许多广泛存在于土壤和根际环境中的细菌可以利用 QS 系统感知信号分子来影响植物[36-37]。近年来的研究还显示, 许多致病菌利用 QS 引起植物病害[40,89-90]。表 1 中列出了 AHLs 介导的群体感应与植物病害的相关例子。AHLs 介导的 QS 调节了根际和植物致病菌之间的多种行为[91]。黑腐果胶杆菌 (*Pectobacterium atrosepticum*) 和胡萝卜果胶杆菌 (*Pectobacterium carotovorum*) 是引起马铃薯 (*Solanum tuberosum*) 黑胫病和胡萝卜 (*Daucus carota*)、甜瓜 (*Cucumis melo*) 软腐病的植物致病菌。果胶杆菌属 (*Pectobacterium*) 的毒力因子受 AHL 依赖的 QS 系统控制, 其主要信号分子为 3-oxo-C6-HSL 或 C8-HSL[40,92]。据报道, 植物病原体菠萝泛菌 (*Pantoea ananatis*) 通过 QS 产生的 C6-HSL 和 3-oxo-C6-HSL 可以引起洋葱 (*Allium cepa*) 中心腐烂病[77]。研究表明, 太子参 (*Pseudostellaria heterophylla*) 连作障碍导致根际 QS 菌的数量显著增加, 这些菌均为粘质沙雷氏菌 (*Serratia marcescens*), 将其接种到太子参根部, 会引起太子参幼苗枯萎病的发生[78]。随后, Li 等[74] 探讨了 AHLs 介导的 QS 细菌动态与地黄 (*Rehmannia glutinosa*) 再植病害的关系, 研究结果显示, 重茬发病土壤中的 QS 菌主要为肠杆菌属 (*Enterobacteriaceae* sp.), 并且对地黄组培苗具有较强的致病性。由此可见, AHLs 介导的 QS 系统通过调控根际微生物数量和动态, 在植物-根际微生物相互作用中对植物产生不利的影响。

4 AHLs 介导的群体淬灭对植物-根际微生物相互作用的影响

有效抑制病原菌的 QS 和干扰 QS 系统的过程被称为群体淬灭 (QQ), 这种作用是一种可以有效防治微生物病害且不易引发抗药性的方法, 因此可以作为控制植物致病菌的一种潜在策略[93-98]。近年来, 对

QQ 的研究引起了越来越多学者的高度重视。QQ 通过抑制或干扰细胞间的 QS 系统, 阻断细胞间的“信息交流”, 从而抑制病原菌的 QS 现象。开发针对 QS 信号通路相关蛋白或其分泌的信号小分子物质的抑制剂, 即群体感应抑制剂 (QSI), 可以实现 QQ, 为定向分子调控植物根际病原菌群体提供了有效途径。微生物可以通过产生降解酶或信号分子的结构类似物来减轻 QS 细菌的致病性[89]。

4.1　QQ 细菌通过酶降解实现群体淬灭

许多天然来源的 QSI 已经被广泛报道, 其中最有效的是细菌源的酶促 QSI。QQ 系统的作用是抑制 AHLs 合成, 与 AHLs 结合受体蛋白竞争, 从而减少受 QS 控制的基因表达[99-101]。不同类型的 AHL 降解酶, 即 QQ 酶, 已被描述为能够影响 QS 信号分子[102]。根据 QQ 酶的作用机制, 可将其分为 3 种主要类型: AHL 内酯酶、AHL 酰化酶、AHL 氧化酶和还原酶[103]。AHL 内酯酶属于金属-β-内酰胺酶家族, 编码具有内酯酶活性的 aiiA 蛋白, 是从芽孢杆菌 240B1(*Bacillus* sp. 240B1) 中首次分离得到的, 该蛋白通过水解打开内酯环, 使 AHL 信号分子失活[93]。此外, 农杆菌属 (*Agrobacterium*)、节杆菌属 (*Arthobacter*)、芽孢杆菌属 (*Bacillus*) 和克雷伯氏菌属 (*Klebsiella*) 的细菌可以通过水解内酯环产生内酯酶来降解 AHL 信号分子[104-106]。Shevate 等[107] 采集了 36 种不同植物的根际土壤, 根际分离菌株中阿氏芽孢杆菌 J1D (*Priestia aryabhattai* J1D) 和蜡样芽孢杆菌 G (*Bacillus cereus* G) 产生 AHL 内酯酶作为 QQ 分子, QQ 分子水解 AHL 信号分子 C6-HSL, 从而阻断 QS 系统。此外, 在罗尔斯通氏菌 XJ12B (*Ralstonia* sp. XJ12B) 中发现一种具有酰化酶活性的酶, 它可以水解 AHL 中的酰胺键, 释放高丝氨酸内酯和脂肪酸[103]。链霉菌属 (*Streptomyces*) 的细菌可以产生 AHL 酰化酶, 通过裂解分子的酰基侧链来使 AHL 信号分子失活[95]。也有研究表明, 农杆菌属 (*Agrobacterium*) 和假单胞菌属 (*Pseudomonas*) 细菌能够产生不同类型的 AHL 自诱导物, 通过内酯酶或酰化酶降解 AHL 信号分子[108-109]。另一方面, AHL 氧化酶和还原酶通过修饰酰基链使 AHL 失活[103]。土壤、根际和其他来源的一些细菌能够产生 AHL 酰化酶、AHL 内酯酶或氧化还原酶使 AHL 信号分子降解[110-112]。有研究表明, 固氮共生细菌 *Ensifer* sp. NGR234 具有多个 *N*-酰基高丝氨酸内酯的群体淬灭位点[113]。

4.2　植物分泌 AHL 拟态物质实现群体淬灭

据报道, 植物具有降解 AHLs 的酶促机制[114-115]。植物根系能产生 QS 信号拟态物质, 导致 QQ[116]。植物代谢物与 AHL 受体相互作用, 激活靶基因表达, 并通过与受体蛋白相互作用来取代 AHLs[117]。植物源 AHL 拟态物质是一种安全有效的 QS 抑制物质来源, 因此备受关注[118-119]。有研究发现水稻 (*Oryza sativa*)、大豆和番茄等作物能够分泌 AHL 拟态物质[117,120-121]。AHL 拟态物质在植物和致病微生物相互作用中发挥重要作用。此外, 在不同植物中发现的黄烷酮柚皮素、圣草酚、花旗松素、山奈酚、槲皮素和芹菜素也表现出 QS 拟态物质的活性[122-123]。植物根际细菌分泌的 QS 信号分子激活了 AHL 拟态物质的合成[124]。在水稻和菜豆 (*Phaseolus vulgaris*) 中检测到了 AHL 拟态物质, 这些物质可以特异性改变两种 QS 细菌费氏中华根瘤菌 SMH12 (*Sinorhizobium fredii* SMH12) 和菠萝泛菌 AMG501 (*Pantoea ananatis* AMG501) 的生物膜形成, 这说明植物能够通过增强或抑制细菌的 QS 系统影响细菌的生长[125]。AHL 类似物己内酯刺激了能够降解 AHLs 的红平红球菌 (*Rhodococcus erythropolis*) 种群, 并将其定殖在植物根际[126]。此外, 红平红球菌可以保护作物免受植物病原体果胶杆菌的侵害[127]。

4.3　AHLs 介导的群体淬灭对植物-根际土壤微生物相互作用的影响

在根际中, 能够降解 AHLs 的细菌 (即 QQ 细菌) 可被应用于防治产生 AHLs 的植物致病菌。许多从土壤和根际中分离出的革兰氏阴性菌和革兰氏阳性菌都具有 AHLs 降解活性[128]。植物根际 QS 化合物的降解是最常见的生物防治方式, 可以有效防止病原体的出现, 并改良根际土壤[129]。QQ 细菌广泛存在于土壤和根际环境中 (表 2), 其种群数量的失衡可能是影响植物生长的关键[137]。此前有报道称, 许多根际细菌的 aiiA 内酯酶基因具有 QQ 活性, 且内酯酶基因对 AHLs 的水解特性对植物病原体具有生物防治作用[135]。据报道, 革兰氏阳性芽孢杆菌属细菌可分泌大量的 AHL 内酯酶 (如 AiiA), 从而减弱植物病原体欧文氏菌 (*Erwinia carotovora*) 的毒性[93]。Park 等[131] 将苏云金芽孢杆菌 (*Bacillus thuringiensis*) 添加至辣椒 (*Capsicum annuum*) 根际, 并对辣椒根际的苏云金芽孢杆菌种群动态进行评价, 发现其能保护植物免受欧文氏菌所引起的根腐病的影响。D’Angelo-Picard 等[36-37] 研究了土壤和烟草根际土壤中 AHLs 降解细菌的数量, 结果表明有 5%~10% 的细菌具有降解 AHLs 的能力。Mahmoudi 等[130] 则研究了马铃薯根际土壤中使 AHL 信号分子失活的细菌的多样

表 2　植物根际土壤或土壤中存在的群体淬灭细菌及作用

Table 2　The quorum-quenching bacteria and their effects present in the plant rhizosphere soil or soil

相关植物或土壤来源 Associated plants or soil source	群体淬灭细菌 Quorum quenching bacteria	主要作用 Major effect	参考文献 Reference
烟草 *Nicotiana tabacum*	芽孢杆菌、变形杆菌、鞘氨醇单胞菌和博斯氏菌 *Bacillus*, *Proteobacteria*, *Sphingomonas*, *Bosea*	降解 AHLs Degrade AHLs	[37]
地黄 *Rehmannia glutinosa*	不动杆菌属 *Acinetobacter* sp.	破坏有益菌的群体感应系统 Disrupt the quorum sensing system of the beneficial bacteria	[74]
太子参 *Pseudostellaria heterophylla*	苏云金芽孢杆菌 *Bacillus thuringiensis*	缓解由粘质沙雷氏菌引起的枯萎病 Alleviate wilt disease caused by *Serratia marcescens*	[78]
马铃薯 *Solanum tuberosum*	红平红球菌 *Rhodococcus erythropolis*	保护马铃薯免受果胶杆菌属(*Pectobacterium*)细菌的侵害 Protect *S. tuberosum* against the pathogen *Pectobacterium*	[126]
	短小芽孢杆菌、荧光假单胞菌、假单胞菌属 *Bacillus pumilus*, *Pseudomonas fluorescens*, *Pseudomonas*	对软腐病原体具有生物防治活性 Have a biocontrol activity against soft-rot pathogens	[128]
	芽孢杆菌属 EM84 *Bacillus* EM84	抑制病原菌生长, 降低马铃薯块茎中黑腐果胶杆菌 SM1 (*Pectobacterium atrosepticum* SM1)的致病性 Inhibit growth of pathogen, reduce the pathogenicity of *P. atrosepticum* SM1 in *S. tuberosum* tubers	[130]
辣椒 *Capsicum annuum*	苏云金芽孢杆菌 *B. thuringiensis*	保护植物免受由欧文氏菌(*Erwinia carotovora*)所造成的根腐病的侵害 Protect the plant from root rot caused by *E. carotovora*	[131]
黄瓜 *Cucumis sativus*	不动杆菌属 C1010 *Acinetobacter* sp. C1010	降解AHLs, 减轻由欧文氏菌引起的软腐病 Degrade AHLs, attenuate soft rot symptom caused by *E. carotovora*	[132]
生姜 *Zingiber officinale*	不动杆菌 GG2、克雷伯氏菌 Se14 *Acinetobacter* GG2, *Klebsiella* Se14	降低植物病原体中毒力因子的产生 Attenuate virulence factor production in plant pathogens	[133]
胡萝卜、马铃薯和黄瓜 *Daucus carota*, *Solanum tuberosum* and *Cucumis sativus*	蜡样芽孢杆菌 RC1 *Bacillus cereus* RC1	缓解由河生肠杆菌(*Lelliottia amnigena*)引起的软腐病 Alleviate soft rot caused by *L. amnigena*	[134]
印度36种不同植物根际土壤 Rhizosphere soil of 36 different plant species in India	阿氏芽孢杆菌 J1D、蜡样芽孢杆菌 G *Priestia aryabhattai* J1D, *B. cereus* G	水解AHL信号分子, 阻断群体感应系统 Hydrolyse AHL signalling molecules, and block the quorum sensing system	[107]
泰国不同省份的根际土壤 Rhizosphere soils in different provinces of Thailand	链霉菌 *Streptomyces*	抑制马铃薯软腐病 Inhibit soft rot of *S. tuberosum*	[135]
农业污染土壤 Agricultural contaminated soil	不动杆菌属 XN-10 *Acinetobacter* sp. XN-10	降低胡萝卜果胶杆菌(*Pectobacterium carotovorum*)的致病性 Attenuate the pathogenicity of *P. carotovorum*	[136]

性, 并分离出了 18 株 AHLs 降解菌株, 为芽孢杆菌属、节杆菌属、中慢生根瘤菌属 (*Mesorhizobium*)、假单胞菌属和链霉菌属。这些菌株能够降解由黑腐果胶杆菌 (*Pectobacterium atrosepticum*) SM1 产生的 AHLs。在淬灭试验中, 芽孢杆菌 EM84 显著降低了马铃薯块茎中黑腐果胶杆菌 SM1 的致病性[130]。前人很多研究揭示了不动杆菌属 (*Acinetobacter* sp.) 的 AHLs 降解活性[132-133]。最近的研究表明, 巴西固氮螺 (*Azospirillum brasilense*) Az39 能够降解未取代的 C4-C12 以及被羟基或酮基取代的 AHLs[138]。可以推测, 这种 AHL 降解活性支持了巴西固氮螺菌 Az39 在根系定殖中的竞争力, 并可能有助于控制具有 AHL 活性的植物病原体。因此, 通过中断根际群落内的 QS 通信, 包括竞争的根际细菌和植物病原体, 可以通过植物促生长细菌 (如巴西固氮螺菌 Az39) 来支持植物生长刺激活性。Li 等[74] 研究表明地黄连作下根际土壤中淬灭油菜假单胞菌的特异性 QQ 菌的种类和数量均发生显著变化, 在重茬土壤和重茬病土中的数量都远高于头茬土壤, 并且主要以不动杆菌属为主, 进一步研究还发现筛选的 QQ 菌对地黄组培苗有较强的致病性。Zhang 等[78] 从太子参根际土壤中分离出 1 株 QQ 菌株, 鉴定为苏云金芽孢杆菌, 它分泌内酯酶降解 QS 信号分子, 可缓解太子参枯萎病。Chankhamhaengdecha 等[135] 从泰国不同地区的根际土壤中分离得到链霉菌, 该菌株能够裂解 AHL 底物中酰基侧链的酰胺键, 有效抑制了由胡萝卜果胶杆菌引起的马铃薯软腐病。Kachhadia 等[134] 从根际土壤中分离的蜡样芽孢杆菌 RC1 的提取物能缓解胡萝

卜、马铃薯和黄瓜中由河生肠杆菌 (*Lelliottia amnigena*) 引起的软腐病, 该研究有助于利用细菌的代谢物来控制病原体, 同时降低病原体的致病性。

综上所述, QQ 可被视为一种新的生物防治策略, 用于防治植物病原体[116]。然而, 在产生 AHLs 的菌株中, 也发现了 AHL 失活酶, 它们很可能利用这些酶来调节自身的 QS 系统[91]。因此, QQ 策略也可能阻止植物根际有益菌的 QS 调节功能[129]。

5　总结与展望

根际微生物形成了一个复杂结构的动态群落。植物与根际微生物互作中, AHLs 介导的根际微生物群体感应是一个重要过程, 对植物健康具有不可忽视的作用。AHLs 在植物和根际微生物中起到十分重要的作用, 这些化合物在研究保护机制和诱导遗传抗性方面具有潜在的应用价值。因此, 本文综述了 AHLs 介导的群体感应机制, 以及 AHLs 介导的群体感应对植物和根际微生物相互作用的调控作用, 并探讨了基于 AHLs 的群体淬灭对植物和根际微生物的影响。AHLs 介导的群体感应调控了根际微生物的定殖、土壤生态系统的维持以及植物的生长发育和抗病性。深入了解 AHLs 介导的群体感应机制对于促进农业生产、提高植物健康和推动可持续发展具有重要意义。与此同时, 基于 AHLs 的群体淬灭为改良 QS 系统活性提供了新的见解, 这有助于更好地了解 QS 分子和 QQ 过程, 推动开发新的农业策略。通过开发 AHL 化合物和传递 AHL 信号分子的有益细菌, 可以促进植物生长和胁迫耐受性, 同时对抗植物病原体。借助基于群体淬灭的 QS 抑制剂, 还能积极开发针对植物病原菌的农药替代品, 减少对农药的依赖。因此, 利用这些知识开发新型的生物农药和植物保护措施, 有助于提高农作物产量和品质, 并为植物健康与农业生产提供新的思路和方法, 从而推动可持续农业的发展。

尽管 AHLs 介导的群体感应在植物根际微生物互作中的作用已经得到初步认识, 但由于根际和植物微生物群落之间的复杂关联以及各种协同或抑制的相互作用, 仍存在许多未解决的问题。因此, 未来的研究应重点关注 AHLs 的合成和感应机制及其调控网络的探索。目前, 已经测序的根际细菌基因组数量仍然较少。更深入地了解根际的宏基因组学, 将有助于进一步了解根际细菌与宿主植物之间的相互作用。通过运用系统生物学方法和多组学技术, 可以深入了解植物-根际微生物相互作用的网络系统和机制。此外, 基于 AHLs 的群体感应和群体淬灭的生态意义有待进一步探索。

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