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Research Progress in Stress Resistance of Plants Mediated by Endophytic Bacteria

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Abstract

Endophytic bacteria have significantly effects on the plant growth and development in adverse environments by promoting plant growth, improving plant nutrient uptake, decreasing plant pathogens infection, affecting plant enzyme and metabolic products activities and enhancing plant stress resistance. The paper reviewed the recent studies on the diversity of stress-resistant endophytic bacteria. In addition, the effects of the functional endophytic bacteria on the plant stress-resistance were analyzed and the mechanisms involved were elucidated. This study provides new idea and foundation that the application of endophytic bacteria improving stress resistance of plants.

Keywords

Endophytic Bacteria, Stress Resistance, Mechanism

植物内生细菌介导的植物抗逆性研究进展

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摘　要

内生细菌对植物生长发育具有重要影响，在恶劣环境中，可促进植物生长、改善植物营养吸收、降低病原菌侵染、影响酶及代谢产物活性，增强植物抗逆性。本文通过结合近年来有关具胁迫功能内生细菌多样性研究进展，分析了不同功能内生细菌在植物胁迫效应上的影响；阐述了功能内生细菌调控植物抗逆性的机制。旨在为进一步利用内生细菌调控植物抗逆性提供思路和依据。

关键词

内生细菌，抗逆性，机制

1. 引言

植物是一个复杂的微生态系统，栖居着不同的微生物类群，且在长期演化过程中建立了紧密的互惠共生关系[1] [2]；在植物生长阶段，某些微生物可促进植物生长，提高抗逆性，进而提高其对环境变化的适应能力[3]，这为相关微生物在农业可持续发展及环境友好型社会建立中的开发利用开辟了一条新途径。内生微生物是植物相关微生物类群中最为特殊的一类，由于其具有相对稳定的生长环境，不易受外界环境变化的影响，且易获得有机物质[4]，因此可对植物产生更稳定的影响[5]。近几十年来，关于菌根真菌[6] [7] [8]和根瘤菌科固氮内生菌[9] [10]及内生真菌[11] [12] [13] [14]在宿主植物上的作用已于植物有大量研究和总结；而关内生细菌与宿主植物间的促生策略及生态机制的研究相对较少。

植物内生细菌是指定殖在植物组织内部，能从表面灭菌的植物组织分离获得，而不引起任何负面特征的细菌群体[15] [16]。内生细菌分布在地球上几乎每一种植物中，并能从根部、叶部和茎部，甚至花、果实及种子中分离获得[17]。内生细菌与植物在长期共同进化中已成为植物微生态系统的天然组分，可促进植物对恶劣环境的适应，加强系统生态平衡；其定殖植物体后，可赋予宿主植物生态优势，提高植物适合度，包括增加营养吸收、促进生长和发育、赋予胁迫耐性和病虫害抗性等[18]-[23]。本文旨在归纳植物内生菌对宿主植物抗逆性的影响及其所涉及的胁迫抗性机制，为深入了解内生细菌与植物抗逆性关系提供理论依据。

2. 具抗逆功能内生细菌的分布

表 1 归纳了当前已发表的定殖植物体后具有显著抗逆效应的内生细菌、抗逆类型及宿主植物等。基于表 1 阐述了内生细菌的胁迫抗性和涉及的相互作用机制。结果表明具有抗逆功能的内生细菌主要分布于游动放线菌属(*Actinoplanes*)、棍状杆菌属(*Clavibacter*)、微杆菌属(*Microbacterium*)、节杆菌属(*Arthrobacter*)、库克氏菌属(*Kocuria*)、小单孢菌属(*Micromonospora*)、血杆菌属(*Sanguibacter*)、链霉菌菌属(*Streptomyces*)、芽孢杆菌属(*Bacillus*)、梭菌属(*Clostridium*)、假单胞菌属(*Pseudomonas*)、肠杆菌属(*Enterobacter*)、伯克霍尔德氏菌属(*Burkholderia*)、甲基杆菌属(*Methylobacterium*)、沙雷氏菌属(*Serratia*)、克雷伯氏菌属(*Klebsiella*)、不动细菌属(*Acinetobacter*)、鞘氨醇单胞菌属(*Sphingomonas*)、丛毛单胞菌属

(*Comamonas*)、*Herbaspirillum* 属、嗜麦芽寡食单胞菌属(*Stenotrophomonas*)、泛菌属(*Pantoea*)、青枯雷尔氏菌属(*Ralstonia*)、拉恩菌属(*Rahnella*)、*Naxibacter* 属和 *Variovorax* 属等 26 个属。其中芽孢杆菌属、假单胞菌属、肠杆菌属和伯克霍尔德氏菌属为优势类群，这些内生细菌大多是土壤细菌属的普通成员[17]。

Table 1. Stress resistance of plants mediated by endophytic bacteria
表 1. 内生细菌介导的植物胁迫抗逆性

门 Phylum	内生细菌 Endophytic bacteria	来源 Source	抗逆性 Activity of Stress-resistant	实验植物 Experimental plant	参考文献 Reference
Actinobacteria	*Actinoplanes campanulatus* #2	黄瓜	抗病性	黄瓜	[24]
	*Clavibacter*sp. Enf 12	高山离子芥	耐冷性	高山离子芥	[25]
	Microbacteriumesteraromaticum TP 3	万寿菊	抗线虫	马铃薯	[26]
	Microbacterium sp. G16	油菜	铅	油菜	[27]
	Arthrobacter sp. EZB 4	辣椒	抗旱性	辣椒	[28]
	Kocuriavarians TE4	万寿菊	抗线虫	马铃薯	[26]
	Micromonosporachalcea#8	黄瓜	抗病性	黄瓜	[24]
	Sanguibacter sp. s_d 2	烟草	镉	烟草	[29]
	Streptomyces coelicolor DE 07	Phog	耐旱性	小麦	[30]
	Streptomyces olivaceus DE 10	Phog	耐旱性	小麦	[30]
	Streptomyces geysiriensis DE 27	Bajra	耐旱性	小麦	[30]
	Streptomyces spiralis #17	黄瓜	抗病性	黄瓜	[24]
Firmicutes	*Bacillus* sp. Em 7	小麦	抗病性	油菜	[31]
	Bacillus subtilis BS-2	辣椒	抗病性	荔枝	[32]
	Bacillus subtilis ERD 4	小麦	抗病性	小麦	[33]
	Bacillus subtilis YS-45	柑橘	抗病性	油菜	[34]
	Bacillus subtilis BS-315	苹果	抗病性	苹果	[35]
	Bacillus subtilis EBS 05	樟树	抗病性	烟草	[36]
	Bacillus amyloliquefaciens TB 2	烟草	抗病性	荔枝	[32]
	Bacillus sp. SE 48	翅碱蓬	耐盐性	小麦	[37]
	Bacillus sp. Q2BG1	鸭跖草	铅	油菜	[38]
	Bacillus sp. N 1	龙葵	镉	龙葵	[39]
	Bacillus megaterium N 4	龙葵	镉	龙葵	[39]
	Bacillus megaterum SaN1	东南景天	镉	油菜	[40]
	Bacillus megaterium JL 35	海州香薷	铜	油菜/玉米	[41]
	Bacillus megaterium Kp 5	海滨锦葵	耐盐性	小麦	[42]
	Bacillus sp. TL 2	茶树	氯氰菊酯	茶树	[43]
	Bacillus thuringiensis GDB-1	樟子松	铅、镍、锌、铜	*Alnus firma*	[44]
	Bacillus cereus Kp 120	海滨锦葵	耐盐性	小麦	[42]
	Bacillus sp. EC 4, EC 13	黄瓜	抗病性	茄子	[45]
	Bacillus sp. EZB 8	辣椒	抗旱性	辣椒	[46]
	Bacillus sp. SENDO 6	仙人掌	耐瘠性	仙人掌	[47]
	Clostridium sp. Kas 201-1	芒	耐盐性	芒	[48]
	Pseudomonas putida VM 1450	杂交杨树	2,4-二氯苯氧乙酸	豌豆	[49]

Continued

Proteobacteria	*Pseudomonas putida* Q2EJ2	大豆	铅	油菜	[38]
	Pseudomonas putida W619-TCE	杂交杨树	三氯乙烯	杂交杨树	[50]
	Pseudomonas putida IMBG 294	马铃薯	抗病性	马铃薯	[51]
	Pseudomonas sp. VM 1468	杂交杨树	甲苯	黄花羽扇豆	[52]
	Pseudomonas sp. G 10	油菜	铅	油菜	[27]
	Pseudomonas oryzihabitans LP 11	碱蓬	抗盐性	碱蓬、黄瓜	[53]
	Pseudomonas thivervalensis Y1 3-9	石香薷	铜	油菜	[38]
	Pseudomonas sp. EB 9, EB 67	茄子	抗病性	茄子	[45]
	Pseudomonas sp. SENDO 2	仙人掌	耐瘠性	仙人掌	[47]
	Pseudomonas pseudoalcaligenes Sal 35	海蓬子	耐盐性	海蓬子	[54]
	Enterobacter sp. 7J2	野蒜	菲	小麦	[55]
	Enterobacter sp. 12J1	野蒜	芘	小麦	[27]
	Enterobacter sp. HA02	棉花	抗病性	棉花	[56]
	Enterobacter sp. MB-1-6-6	水稻	抗病性	水稻	[57]
	Enterobacter sp. N 2	龙葵	镉	龙葵	[39]
	Enterobacter sacchari G 1	茶树	铝	茶树	[58]
	Enterobacter sp. B 901-2	水稻	耐盐性	芒	[48]
	Enterobacter sp. EB 44, EB 89	茄子	抗病性	茄子	[45]
	Burkholderia sp. CBMB 40	水稻	镍和镉	番茄	[59]
	Burkholderia sp. GL 12	海州香薷	铜	油菜/玉米	[41]
	Burkholderia phytofirmans PsJN	葡萄	耐冷性	葡萄	[60]
	Burkholderiapyrrocinia JK-SH007	杨树	抗病性	杨树	[61]
	Burkholderia cepacia G 3	茶树	铝	茶树	[58]
	Burkholderia seminalis G 4	茶树	铝	茶树	[58]
	Methylobacteriumpopuli BJ 001	杂交杨树	TNT, RDX, HMX	杂交杨树	[62]
	Methylobacteriumoryzae CBMB 20	水稻	镍和镉	番茄	[63]
	Serratia marcescens SRM	西葫芦	耐冷性	小麦	[64]
	Serratia nematodiphila LRE 07	龙葵	镉	龙葵	[65]
	Serratia plymuthica 3Re4-18	马铃薯	抗病性	马铃薯	[66]
	Klebsiella pneumonia Kp 342	玉米	耐贫瘠	特伦顿小麦	[67]
	Acinetobacter baylyi Q2BJ2	鸭跖草	铅	油菜	[38]
	Acinetobacter sp. SENDO 1	仙人掌	耐瘠性	仙人掌	[47]
	Sphingomonas sp. SaMR 12	东南景天	锌和镉	东南景天	[68]
	Sphingomonas sp. YM 22	鸭跖草	铜	油菜/玉米	[41]
	Comamonas sp. KD2, KD7, PD1	白三叶草	三呋喃	白三叶草	[69]
	Herbaspirillum sp. YM 23	鸭跖草	铜	油菜/玉米	[41]
	Stenotrophomonas sp. MB-1-6-5	水稻	抗病性	水稻	[57]
	Pantoea agglomerans Jp3-3	小飞蓬	铜	油菜	[38]
	Ralstonia sp. JL22-2	鬼针草	铜	油菜	[38]
	Rahnella sp. JN 6	毛竹	锌、镉、铅	油菜	[70]
	Naxibacter sp. Pn 2	看麦娘	菲	黑麦草	[71]
	Variovorax sp. SaNR 1	东南景天	锌和镉	东南景天	[68]

3. 内生细菌对植物抗逆性的影响

3.1. 内生细菌对植物抗旱性的影响

在非生物胁迫因子中，干旱胁迫是阻碍植物生长最为广泛的限制因子，研究表明在干旱和半干旱地区农作物接种土著有益微生物可显著增强农作物耐旱性[72]。Yandigeri 等从印度拉贾斯坦邦干旱区 5 种植物中分离、筛选出 *Streptomyces coelicolor* DE 07、*S.olivaceus* DE10 和 *S. geysiriensis* DE27 等 3 株耐旱内生放线菌，其定殖小麦(*Triticum aestivum*)后在干旱胁迫条件下可显著增强小麦幼苗活力，提高耐旱性。[30]在渗透胁迫条件下，辣椒(*Capsicum annuum*)通过接种内生细菌 *Arthrobacter* sp. EZB4 和 *Bacillus* sp. EZB 8，可显著降低干旱胁迫诱导基因 CaACCO (编码 ACC 氧化酶)和 CaLTPI (编码脂质转移蛋白)的上调($P < 0.05$)，并增加脯氨酸含量，从而提高辣椒耐渗透胁迫能力[28]。

3.2. 内生细菌对植物抗盐性的影响

众多研究表明，不同宿主植物通过接种内生有益细菌可显著缓解盐分胁迫的负向效应。Ozawa 等[54]研究表明盐生植物盐角草(*Salicornia europaea*)通过接种内生细菌 *Pseudomonas pseudoalcaligenes* Sal 35 可显著提高幼苗生长的盐浓度，而且相比对照植物，接种内生细菌的盐角草茎具有更高的总氮、叶绿素、Na^+和 K^+含量。盐敏感类型芒草(*Miscantbus sinensis*)通过接种内生细菌 *Clostridium* sp. Kas 201-1 和 *Enterobacter* sp. B901-2 可缓解盐分胁迫产生的种群扰动，提高耐盐性[48]。滕松山(2011) [53]在盐生植物碱蓬(*Suaeda glauca*)中分离获得一株内生细菌 *Pseudomonas oryzihabitans* LP11，其能够定殖碱蓬和黄瓜(*Cucumis sativus*)幼苗，且在盐分胁迫条件下可提高种子萌发率，增加植物叶绿素、可溶性糖及脯氨酸含量，促进植物根长、叶长、株高及鲜重增加，提高抗盐性。研究表明，分离自盐生植物海滨锦葵(*Kosteletzkya virginica*)的内生细菌 *Bacilluscereus* Kp120 和 *Bacillus megaterium* Kp5 能显著提高盐胁迫下小麦幼苗的干物质重和叶绿素含量，并能提高植物保护酶活性，进而缓解盐分胁迫对植物危害[42]。

3.3. 内生细菌对植物耐冷性的影响

低温也是许多物种生长发育、地理分布和农作物产量的主要限制因子[74] [75]；研究发现相比冷敏感植物，耐冷植物具有更高的抗氧化酶活性，表明抗氧化酶活性与植物耐冷性密切相关[76]。丁硕(2011) [77]通过对高山离子芥(*Chorispora bungeana*)及相关内生细菌协同抗寒性分析，表明内生细菌 *Clavibacter* sp. Enf 12 可显著降低冷诱导产生的电解质渗透及脂质过氧化反应，增加植株抗氧化酶活性和脯氨酸含量，从而提高植物耐冷性。内生细菌 *Serratia marcescens* SRM 在 4℃低温条件下仍具有相当稳定的促生属性，其定殖小麦后可显著改善小麦营养吸收状况，提高小麦生物量，增强耐寒性[64]。低温胁迫条件下接种内生细菌 *Burkholderia phytofirmans* PsJN 也可显著增加葡萄(*Vitis vinifera*)的根长及生物量，提高其耐冷性[78]。

3.4. 内生细菌对植物耐瘠性的影响

内生细菌可促进不利环境条件下植物的萌发及种群建立[78]。Puente 等(2009) [47]研究表明内生细菌 *Bacillus* sp. SENDO 6、*Acinetobacter* sp. SENDO1 和 *Pseudomonas* sp. SENDO 2 在岩生植物武伦柱(*Pachycereus pringlei*)的幼苗形态建成及生长发育过程中扮演了重要角色，可协助其生长于裸露岩石；实验室分析表明缺乏内生细菌的幼苗表现更小，其在干重、根长和苗高上差异显著。接种内生细菌 *Klebsiella pneumonia* Kp342，可缓解特伦顿小麦在氮肥缺乏情况下的氮缺失症状，显著增加根、茎干重、提高叶绿素水平[67]。类似的是，固氮内生菌也可缓解甘薯(*Ipomoea batatas*)在氮贫瘠土壤上生长的不利影响[79]。Dalton 等(2004) [80]研究表明，生长于营养贫乏沙丘上的草本栖居有大量 *Pseudomonas*、*Stenotrophomonas* 和 *Burkholderia* 属菌株，分析表明 *Burkholderia* 属内生细菌有助于沙丘草本吸收、利用氮。

3.5. 内生细菌对植物抗病性的影响

世界农业每年因病原菌感染面临巨大损失，而利用微生物控制疾病发生是最有希望的防治策略之一。众多研究表明，内生细菌可通过拮抗、生态位竞争及诱导植物防御反应等手段帮助宿主植物远离有害微生物[17] [73]。Ramesh 等(2009) [45]从茄子(*Solanum melongena*)、黄瓜和花生(*Arachis hypogaea*)中分离获得 *Pseudomonas* sp. EB 9、EB67，*Enterobacter* sp. EB 44、EB 89 和 *Bacillus* sp. EC 4、EC13 等内生细菌菌株，能够产生抗生素 2, 4-二乙酰基间苯三酚(DAPG)，可抑制病原菌生长；温室试验中通过接种茄子，发现能够显著降低茄青枯菌(*Ralstonia solanacearum*)的发病率，改善幼苗生长。内生细菌 *Bacillus subtilis* EDR4 接种小麦后可降低小麦全蚀病(*Gaeumannomyces graminsis*)对小麦生长的影响，进而增加其植株高度、每穗种子数及千粒重，增强抗病性[33]。温室实验中，分离自黄瓜根部的 *Actinoplanes campanulatus*、*Micromonospora chalcea* 和 *Streptomyces spiralis* 可拮抗瓜果腐霉(*Pythium aphanidermatum*)引起的腐霉病，保护黄瓜幼苗和成株[24]。龙良鲲(2003) [81]研究表明，内生细菌 *Bacillus subtilis* 01-144 能够定殖番茄根茎内，进而与青枯病菌竞争生态位点，可有效抑制番茄青枯病发生。内生细菌 *Bacillus subtilis* EBS05 可使烟草获得对烟草花叶病毒(TMV)的系统抗性，其对 TMV 具有稳定抑制活性，防治效果达 67.38% [36]。

3.6. 内生细菌对植物抗虫性的影响

研究表明，内生菌在植物耐虫性上具有正向作用[82] [83]；Kloepper 等(1991) [84]进一步指出农作物相关的一些根际及内生细菌拥有拮抗植物病原线虫的能力。目前，对于害虫防治研究最多的是重组内生细菌 *Clavibacterxyli* subsp. *cynodontis*，其能够表达源于 *Bacillus thuringiensis* 的 *cryIA* 基因，生成内毒素拮抗欧洲玉米螟(*Ostrinia nubilalis*) [17]。接种分离自线虫拮抗植物万寿菊(*Tageteserecta*)和孔雀草(*Tagetes patula*)的内生细菌 *Microbacteriumesteraromaticum* TP3 和 *Kocuria varians* TE4 可降低马铃薯(*Solanum tuberosum*)根区根腐线虫(*Pratylenchus penetrans*)的群体密度，从而维持马铃薯产量稳定[26]。

3.7. 内生细菌对植物抗重金属毒害的影响

重金属在土壤中具有低迁移率特性[86] [87]，不易被植物吸收利用，从而严重阻碍了植物修复进程；而内生细菌可提高重金属溶解态含量，改善根际重金属生物利用度[88] [89]。Sheng 等(2008) [27]研究报道，分离自油菜(*Brassica campestris*)的内生细菌 *Pseudomonas fluorescens* G10 和 *Microbacterium* sp. G16 具有溶解铅的潜力，可提高土壤中水溶性铅含量，从而提高植物修复效率。内生细菌 *Rahnella* sp. JN6 高耐镉(Cd)、锌(Zn)和铅(Pb)胁迫，具有活化土壤中碳酸镉、碳酸铅和磷酸锌能力，其定殖油菜后可促进油菜生长，提高油菜对 Cd、Pb、Zn 的吸收[70]。此外，研究也发现内生细菌还能分泌多种有机配位体与体内重金属结合，改变重金属的存在形态，促进重金属在植物组织器官间转运，从而增强重金属在植物组织中的利用。接种内生细菌 *Methylobacterium oryzae* CBMB 20 和 *Burkholderia* sp. CBMB 40 可促进重金属离子镍(Ni)和镉在番茄(*Solanum lycopersicum*)茎叶内的转运，提高番茄茎叶中重金属含量[59]。万勇(2012) [90]从龙葵(*Solanum nigrum*)根部分离到一株内生细菌 *Serratia nematodiphila* LRE07，具有多重重金属耐性，接种龙葵后能提高植物重金属抗性，显著增加植株分蘖数和叶片数，从而使单株植物重金属镉提取量增加，提高植物修复效率。

3.8. 内生细菌对植物耐有机污染物的影响

研究表明，内生细菌与植物相互作用能够增强植物对除草剂、甲苯等有机污染物的修复能力，减轻有机污染物对植物毒害作用[49] [52]。Germaine 等(2006) [49]研究表明豌豆(*Pisumsativum*)接种内生细菌 *Pseudomonas putida* VM1450 能有效降解杀虫剂 2,4-二氯苯氧乙酸(2,4-D)对植株造成的危害，在高水平

2,4-二氯苯氧乙酸胁迫下可维持其根部系统正常发育，增加植物生物量。刘爽(2012) [71]从多环芳烃(PAHs)污染区看麦娘(*Alopecurus aequalis*)植株中分离获得一株高效降解菲的内生细菌 *Naxibacter* sp. Pn 2，其能成功定殖黑麦草，促进黑麦草吸收环境中的菲，去除率为 89.09%。在 400 mg/L 三氯乙烯(TCE)胁迫条件下，接种内生细菌 *Pseudomonas putida* W619-TCE 于白杨(*Populus alba*)插条，可显著降低其根和叶中的 TCE 含量，减缓其对植物的毒性[50]。

4. 内生细菌提高植物抗逆性的机制

4.1. 内生细菌改善植物生长环境

最近研究表明，内生细菌与其宿主植物交互协同作用可改善植物生长环境，促使植物生长及种群建立。Puente 等(2009) [47]研究表明，内生细菌与岩生植物武伦柱相互作用利于其定殖裸露岩石和生长，内生细菌主要通过释放大量必须养分满足幼苗在岩石上的生长、发育，进而利于土壤母质形成。某些内生细菌具有代谢多样性，可通过特殊代谢途径降解环境中有毒组分，如：三氯乙烯[91]，2,4-二氯苯氧乙酸[49]，2,4,6-三硝基甲苯(TNT) [52]和菲[71]等，从而降低其对植物毒性，提高植物耐受性。此外，部分内生细菌也能通过直接拮抗或生态位竞争等手段保护宿主植物远离有害微生物[81]和病原线虫[26]的侵害，改善植物生长条件，提高植物病虫害耐受性。

4.2. 内生细菌改变植物形态结构

植物相关微生物在其根部形态建成过程中扮演了重要角色，能促进根部生长[92]和生物量提高及侧根和根毛形成[93] [94] [95] [96]，进而增加根系总吸收面积，利于植物在水分和营养上的吸收。内生细菌 *Pseudomonas putida* VM 1450 侵染豌豆幼苗后利于其根系统在胁迫条件下维持正常形态构成，避免根端膨大和胼胝质形成[49]。内生细菌侵染也能促使植物在胁迫条件下增加根长及生物量，从而提高植物耐旱性[73]、耐寒性[64] [74]及重金属耐性[41]等。叶片叶绿素含量是植物光合活性的基础，是植物光合最关键因子之一，通常作为植物胁迫程度的指标参数[97]，而研究表明内生细菌侵染通常能够增加宿主植物叶片数、叶长及叶绿素 a、叶绿素 b、类胡箩卜素含量等，从而提高植物耐盐性[42] [54] [53]、重金属耐性[65]和耐贫瘠性[67]等。在细胞水平，生防内生细菌定殖植物体也可诱导植物细胞壁改变，如：形成胼胝质和酚类化合物，从而限制病原菌侵染，提高植物抗病性[98] [99]。

4.3. 内生细菌改善植物养分吸收利用

内生细菌和植物相互作用，可协助植物建立内生态恢复系统[100]，促进植物根部发育、增加植物营养吸收或改善营养元素利用等手段增强植物利用土壤养分能力[101]，提高环境胁迫耐性。内生固氮细菌 *K. pneumonia* Kp342 侵染农作物后能够缓解其氮缺失症状[67]，增加农作物产量[102]。内生细菌 *S. marcescens* SRM 侵染小麦后能显著促进小麦根生长，改善小麦幼苗的营养吸收能力，增加氮、磷、钾吸收量，增强小麦耐冷性[64]。在盐分胁迫条件下，内生细菌也可增强植物液泡膜 Na^+/K^+逆向转运蛋白活性，显著缓解因 Na^+累积而引起的 K^+降低，从增强耐盐性[54]，但对 Mg^{2+}和 Ca^{2+}等二价金属离子含量的减少没有显著影响。重金属胁迫条件下，部分内生细菌即能通过促进植物生长，提高宿主植物对土壤重金属离子的吸收[70]，也可通过改变土壤重金属离子生物利用度，提高重金属离子在茎叶中转移速率[27] [89] [103]，增强植物重金属抗性；此外内生细菌也能通过吸收微量元素锌和铁，减缓重金属胁迫诱导的植物体金属离子变化，增强重金属抗性[104]。

4.4. 内生细菌改善植物酶活性和次生代谢产物产生

众多研究表明，内生细菌对维持植物细胞膜结构完整性和稳定性发挥了重要作用，可显著提高植物

抗氧化酶活性和脯氨酸含量，从而提高植物抗寒性[25]、抗病性[32]和重金属耐性[41]；另外，某些内生菌还可通过表面吸附和积累等手段将重金属转运到其细胞内，降低重金属对植物的伤害[105]。植物体内的水解酶类与植物抗病性密切相关，研究表明内生细菌也能通过产生多种水解酶类，如纤维素酶、几丁质酶、葡聚糖酶、果胶酶、蛋白酶等，提高植物抗病性[24] [32]。内生细菌侵染植物后也能通过部分次生代谢产物，增强植物抗逆性，如产生 DAPG 等抗生素类物质[45]和酚类物质[106]等提高抗病性；产生 *δ*-内毒素，提高抗虫性[107] [108]或增加脯氨酸和碳水化合物含量，提高耐冷性[60]。众多研究表明，假单胞菌属、肠杆菌属、葡萄球菌属、固氮菌属(*Azotobacter*)和固氮螺菌属(*Azospirillum*)细菌具有产玉米素和细胞分裂素能力，可影响植物生长发育[85] [110]。Idris 等(2004) [111]研究表明，相比根际细菌，内生细菌在调节植物荷尔蒙水平方面具有更为重要作用。尤其是产 ACC 脱氨酶活性的内生细菌，在胁迫水平下可降低胁迫诱导产生的乙烯水平，从而提高植物抗逆性[59] [63]。

4.5. 内生细菌诱导植物抗逆基因表达

最近众多研究表明，有益细菌接种可改变植物相关基因表达[69] [112]。Chi 等(2010) [113]利用蛋白质组法也证明植物在内生菌存在条件下，相关 *Rubisaco* 活性蛋白、丙酮酸正磷酸激酶、核酸编码蛋白及叶绿体营养吸收的相关基因上调，从而刺激植物光合系统活性。周蕊(2013) [36]研究表明，内生细菌 *Bacillus subtilis* EBS05 的代谢活性物质 *Surfactin* A 是 EBS05 发挥生防作用的关键因子，可诱导植物 SA 信号传导途径相关的 *NPR*1、*PR*1*a* 和 *PR*1*b* 基因持续超量表达及 JA/ET 信号传导途径的 PDF1.2 基因瞬时超量表达，其存在 SA 信号传导途径与 JA/ET 信号传导途径间的交叉协同作用，从而使内生细菌 EBS05 对烟草花叶病毒具有稳定抑制活性。CaACCO 基因[114]和 CaLTPI 基因[115]能被干旱、高盐、低温等胁迫条件下被强烈诱导，可分别在番茄和辣椒中转录激活下游信号通路从而提高其抗逆性。研究表明，45% PEG 6000 适度渗透胁迫条件下，辣椒接种内生细菌 *Arthrobacter* sp. EZB4 或 *Bacillus* sp. EZB 8，可显著降低胁迫诱导基因 CaACCO、CaLTPI 的上调，进而提高耐旱性[28]。

5. 展望及存在问题

前期人们主要通过植物基因工程技术来改善植物生长和农作产量及品质提高，但随着“农业可持续发展”及“环境友好型社会”概念的提出，急需开发一种新技术去应对环境变化带来的各种危害。综上所述，内生细菌作为植物微生态系统的天然组分，具有促进植物生长，增加植物营养吸收，抑制植物病原菌生长，提高植物环境胁迫耐性的特性。因此，内生细菌在改良植物胁迫抗性上具有重要应用价值，是未来开发利用的重要方向。

尽管内生细菌在植物生长发育和植物健康上具有重要作用，但多重因素限制了内生细菌的开发利用，其仍需大量且深入的研究。首先，植物－内生细菌有益特性具有专一性，其在一个宿主植物上的有益效应，不易移植到别的宿主植物上，这种特性的深度理解能够帮助我们应用专一菌株接种提高产量。其次，内生细菌赋予宿主植物的有益特性可能是细菌众多促生属性互作的共同结果，其每一次互作都是独特的，没有简单规程可理解其有益效应的产生。第三，截至目前，在实验室或温室水平获得了大量具有促生属性的内生细菌，但其在大田条件下难以表现出始终如一的促生属性，其定植水平及促生效应可能受到宿主植物、相关微生物和环境条件的协同调节，仍然缺乏足够认知。第四，目前关于植物内生细菌多样性和物种组成的理解已取得巨大进步，但植物－内生细菌相互作用的准确机制阐述尚不明确，利用新的方法和技术如蛋白质组学、转录组学和代谢组学研究植物－内生菌群体的相互作用值得深入。第五，地球环境组成具有极端复杂多样性，依据“生境适应性共生”理论，我们有必要继续筛选不同环境、不同植物的内生细菌物种，扩大内生细菌物种多样性，建立内生细菌－植物－逆境数据库。

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