

链霉菌的功能及其在农业上的应用

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摘要: 链霉菌是自然界中大量存在的一类微生物, 具有多种多样的功能, 其基内菌丝多核有间隔, 气生菌丝上附着孢子链, 从孢子萌发到孢子释放完成整个生命周期。链霉菌以菌丝体的形式定殖于多种植物体的根、茎、叶等部位而发挥功能, 能分泌多种具有促进植物生长与生物防治功能的代谢物。对近几年链霉菌在提升植物营养吸收、促进植物生长、增强植物应对逆境能力、改善土壤结构、恢复污染水体等方面的研究进行了综述, 并对今后链霉菌的研究方向和应用前景进行了展望。

关键词: 链霉菌; 生长; 生物防治; 菌肥

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Function of *Streptomyces* and Their Application in Agriculture

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Abstract: *Streptomyces* widely exist in nature with various functions. Their basal hyphae are multi-nucleated with septa, and spore chains are attached to aerial hyphae. The life cycle is completed from spore germination to spore release. *Streptomyces* are able to colonize the roots, stems, leaves and other parts of plants. They secrete various metabolites which play important roles in plant growth promotion and biological control. The functions of *Streptomyces* mainly focused on the enhancement of plant nutrient uptake, promotion of plant growth, and increase of the ability of plants coping with biotic and abiotic stresses were reviewed. The future research directions and application were also prospected.

Key words: *Streptomyces*; Growth; Biological control; Bacterial fertilizer

链霉菌是一类革兰氏阳性菌, 19 世纪末, 研究者从土壤中分离出大量好气腐生菌, 1943 年将这类菌归为链霉菌属(*Streptomyces* sp.)^[1]。链霉菌属于原核生物界、放线菌目(Actinobacteriales)、链霉菌科(Streptomycetaceae)。链霉菌是放线菌目中最大的一个属, 包含 1 000 多种菌。链霉菌从孢子萌发到孢子释放完成整个生长周期。孢子在固体培养基上萌发, 逐步产生基内菌丝, 基内菌丝多核而有分支, 吸收

营养, 进行营养生长。营养生长阶段后期, 基内菌丝不断降解, 代谢出不同色素, 形成不同颜色。培养基表面产生气生菌丝, 气生菌丝具有疏水性, 在气生菌丝上继而形成孢子丝, 孢子丝是由单核的孢子构成。孢子再萌发从而构成链霉菌的一个生长周期^[2]。在链霉菌分类系统中, 孢子链与孢子形态是重要的参考依据。链霉菌基因组染色体呈线状, 结构复杂, 是目前已知最大的原核生物基因组。

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链霉菌具有多种功能,有些能够产生抗生素与植物生长激素类物质,促进植物生长,提高植物对于生物与非生物逆境的抵御能力^[3]。目前已知的链霉菌产生的9 000多种具有生物活性的物质中,超过120多种物质得到了应用,占微生物来源的生物活性物质应用品种数量的75%^[4]。目前已知抗生素种类有16 500种,其中51%是由链霉菌产生。链霉菌分泌的农用抗生素作为低毒、低残留的生物农药逐步受到人们的关注。

微生物与植物之间通过互相作用各取所需。微生物通过在植物根部附近吸收植物分泌的营养物质,进行生长繁殖,而植物则摄取微生物的代谢物质促进自身生长。链霉菌作为一类具有多种功能的微生物,在农业生产活动中得到了广泛的应用。本文对国内外有关链霉菌在植物生长上的功能研究进行综述,并展望其应用前景和将来的研究方向,为进一步发挥其生物防治作用,开发出环境友好型的低毒、高效与高产的抗生素提高帮助,从而更好地服务于国家生态文明建设。

1 链霉菌

链霉菌是细菌界、放线菌目中的一类细菌。大部分链霉菌具有菌丝与孢子,少数链霉菌在多次继代培养过程中会丧失产生孢子能力。链霉菌定殖的植物种类广泛,如在棉花(*Gossypium* spp.)、黄瓜(*Cucumis sativus*)、毛白杨(*Populus tomentosa*)、黄花蒿(*Artemisia annua*)、水稻(*Oryza sativa*)、大麦(*Hordeum vulgare*)和花生(*Arachis hypogaea*)等30多种植物上都可以定殖,定殖部位多,从根、茎、叶片中都有链霉菌分离出来(表1)。有多种技术手段可以研究链霉菌在植物中的定殖情况。如携带绿色荧光蛋白基因的生防链霉菌株SSD49-pIJ8660Ep能够定殖到毛白杨组培苗的茎和叶片中,当接种SSD49-pIJ8660Ep后,在茎段切片中可以看到明显的绿色荧光,在叶片中也能看到散布的微弱绿色荧光,但根中并未观察到绿色荧光。表明链霉菌沿着伤口进入植物体内,在茎中分布较多,随后迁移至叶片中,但链霉菌难以进入根部^[5]。壮观链霉菌(*S. spectabilis*)在棉花根际土壤和根部长期待定殖,30 d的定殖密度分别为 1.38×10^5 和 2.95×10^3 CFU g⁻¹^[6]。譙天敏等^[7]利用实时荧光定量PCR技术监测铁核桃(*Juglans sigllata*)根中绛红褐链霉菌(*S. purpeofuscus*)特异性基

因表达量,结果表明其呈先增大后降低的趋势,40 d后稳定。

在室内培养时,不同的链霉菌在同种培养基上会有不同的形态特征,这也是早期链霉菌归类的主要依据。目前链霉菌分类主要依靠表观分类、数值分类、化学分类、分子分类与多相分类,从早期人为因素多、试验结果重复性差逐步向着更加客观与标准的方向发展。20世纪50~60年代,链霉菌分类主要依靠链霉菌孢子链的形态、孢子大小、孢子表面特征、气生菌丝、基内菌丝的颜色,是否产生可溶性色素、是否产生黑色素、对不同碳氮源的利用和对抗生素的敏感性等指标^[8]。20世纪70年代开始,Lechevalier^[9]将细胞壁化学组分分析应用于细菌分类,提出将形态学分类与化学分类相结合的方法来划分属,链霉菌属细胞壁类型为I型。20世纪80年代,分子生物学技术开始应用于放线菌的分类,Woese等^[10]利用16S rDNA序列相似性,采用DNA-rRNA和DNA-DNA杂交等技术建立了放线菌的系统进化树。目前,链霉菌分类通常采用多相分类的方法,将表观分类、化学分类和分子分类综合起来进行分析。依据链霉菌的生存环境不同,可以将链霉菌初步分为土壤链霉菌、海洋链霉菌与植物内生链霉菌。

大部分链霉菌对植物具有促进生长、增强营养吸收、提高抵御生物与非生物逆境等有益作用^[11-12],但也有研究表明某些链霉菌具有病原菌的特性,如由链霉菌引起的马铃薯(*Solanum tuberosum*)疮痂病^[13],马铃薯品种对于土壤中链霉菌的丰度具有显著影响,感病植株周围存在大量链霉菌,而抗病植株附近链霉菌较少存在。链霉菌还可以提高其他微生物在植物根部的定殖能力,Nadine等^[14]研究表明链霉菌AcH 505可以提高担子菌331在云杉(*Picea asperata*)根部的定殖率,链霉菌能诱导担子菌331体内水杨酸类似物的分泌。对链霉菌这些正面与负面影响的研究,为后续病原菌针对性防控奠定了一定的基础。

2 链霉菌促进植物生长,增强营养吸收

研究表明,链霉菌主要通过分泌植物生长调节剂如IAA、嗜铁素等发挥促进植物生长的作用^[15]。

利迪链霉菌(*S. lydicus*)能促进西红柿(*Lycopersicon esculentum*)生长,增加叶片数目,增强光合作用,

表 1 链霉菌在植物生长和生物防治中的功能

Table 1 Effects of *Streptomyces* on plant growth and biological control

植物 Species	菌株 Strain	功能 Function	途径 Pathway	文献 Reference
花生 <i>Arachis hypogaea</i>	<i>Streptomyces</i> sp. RP1A-12	促进生长, 抑制茎腐病 Growth promotion, inhibit stem rot	代谢粗提物或嗜铁素, 生长素, 脂酶 Crude extract or siderophore, auxin, lipase	17,26,34
	<i>S. nigrifaciens</i>	抑制根腐病 Inhibit root rot	粗提物 Crude extract	
鹰嘴豆 <i>Cicer arietinum</i>	<i>Streptomyces</i> CAI-21, CAI-26, MMA-32	促进生长, 提高产量 Growth promotion, increase yield	增强根际碳氮磷营养, 葡萄糖酶, 嗜铁素与生长素 Enhance rhizosphere C, N, P content, glucose enzyme, siderophore and auxin	27,35
	<i>S. rochei</i> SM3	抑制菌核病, 提高耐盐性 Inhibit stalk break, enhance salt tolerance	提高抗氧化酶系统活性和乙烯含量 Enhance antioxidant enzyme activity and ethylene content	
香蕉 <i>Musa nana</i>	<i>S. lunalinharesii</i>	抑制枯萎病 Inhibit wilt	上清液 Supernatant	36
玉米 <i>Zea mays</i>	<i>S. roche</i> D74, <i>S. pactum</i> Act12	促进生长, 提高产量 Growth promotion and increase yield	促进根茎生长, 提高光合速率和酶活 Root and stem growth promotion, increase photosynthetic rate and enzyme activity	37-41
	DAUFPE 11470, DAUFPE 14632	抑制穗腐病, 促进生长 Inhibit ear rot and growth promotion	代谢物 Metabolite	
	DAUFPE 11470, DAUFPE 14632	抑制镰刀菌病 Inhibit <i>Fusarium</i> disease	活性物质, 碳源竞争 Active substances, carbon source competition	
	<i>Streptomyces</i> spp.	抑制叶斑病 Inhibit leaf spot disease	代谢物 Metabolite	
	<i>S. rubrogriseus</i> HDZ-9-47	根结病 Root knot disease	—	
番茄 <i>Lycopersicon esculentum</i>	<i>S. griseocarneus</i> Benedict	立枯病, 根腐病 Damping-off and root rot	降解病原菌细胞壁 Pathogen cell walls degrade	42-46
	<i>S. globisporus</i> JK-1	灰霉病 Gray mold	抑制挥发性物质, 病原菌细胞壁增厚, 液泡增大 Inhibit volatile matter, cell wall thickening, vacuole enlargement	
	<i>S. avermitilis</i>	促进生长 Growth promotion	代谢物 Metabolite	
	<i>Streptomyces</i> sp. Di-944	立枯病 Damping off	代谢物 Metabolite	
	<i>S. lavendulae</i> Xjy	叶霉病 Leaf mould	—	
	<i>Streptomyces</i> sp. CC5	疮痂病 Scab	上清液 Supernatant	
马铃薯 <i>Solanum tuberosum</i>	<i>S. anulatusisolate</i> S07	谷囊线虫, 提高产量 Cereal cyst nematode, increase yield	过滤液 Filtrate	47
小麦 <i>Triticum aestivum</i>	<i>S. mutabilis</i> strain IA1	促进生长, 抑制镰刀菌病 Growth promotion and inhibit <i>Fusarium</i> disease	IAA, GA	48-52
	<i>S. atroolivaceus</i>	促进生长 Growth promotion	激活基因 Activate gene	
	<i>S. griseoviridis</i>	提高产量 Increase yield	代谢物 Metabolite	
	<i>Streptomyces</i> sp. MM10	促进生长, 提高产量, 增强耐盐 Growth promotion, increase yield and enhance salt tolerance	增加 N、P 和 Mg 吸收, 提高脯氨酸含量 Increase N, P and Mg absorption, increase proline content	
	<i>S. hydrogenans</i> DH16	黑叶斑与立枯病, 促进生长 Damping-off, black leaf spot, growth promotion	代谢物 Metabolite	
萝卜 <i>Raphanus sativus</i>	<i>Streptomyces</i> sp. MBRL 10	促进生长 Growth promotion	几丁质酶, 葡萄糖酶, 脂酶, 蛋白酶, 嗜铁素 Chitinase, glucosaminase, lipase, protease, siderophore	53-54
水稻 <i>Oryza sativa</i>	<i>Streptomyces</i> sp. A01059	稻瘟病 Rice blast	活性物质 Active compounds	23,55-56
	<i>S. sindeneusis</i> 263	稻瘟病 Rice blast	代谢物 Metabolite	
	<i>S. lavendulohygroscopicus</i>	白秆病 Picea meyeri disease	代谢物 Metabolite	
	<i>Streptomyces</i> BCA	黄萎病 <i>Verticillium</i> wilt	诱导系统抗性 Induce systemic resistance	
棉花 <i>Gossypium</i> spp.	<i>S. griseoflavus</i> P4	促进生长 Growth promotion	增强固氮作用 Enhance nitrogen fixation	57
大豆 <i>Glycine max</i>	<i>S. albospinus</i>	根腐病, 促进生长 Root rot, growth promotion	固体剂 Solid preparation	

续表(Continued)

植物 Species	菌株 Strain	功能 Function	途径 Pathway	文献 Reference
大豆 <i>Glycine max</i>	<i>S. sioyaensis</i>	白根病, 促生作用 White root disease, growth promotion	溶磷作用, 嗜铁素, 几丁质酶和生长素 Phosphorolysis, siderophore, chitinase, and auxin	18,59
草莓 <i>Fragaria</i>	<i>S. felleus</i> YJ1	菌核病 Stalk break	代谢物 Metabolite	
橡胶树 <i>Hevea brasiliensis</i>	<i>Streptomyces</i> Tra69	枯萎病 <i>Fusarium</i> wilt	代谢物 Metabolite	60
油菜 <i>Brassica campestris</i>	<i>S. philanthi</i> RL-1-178	茎腐病, 枯萎病 Stem rot, <i>Fusarium</i> wilt	代谢物 Metabolite	25
烟草 <i>Nicotiana tabacum</i>	<i>S. rochei</i>	根腐病 Root rot	分泌物 Secrete substance	61
	<i>S. chibaensis</i>	促进生长 Growth promotion	营养生长, 维生素, 矿物质和碳水化合物 Vegetative growth, vitamin, mineral substance and carbohydrates	62
辣椒 <i>Capsicum annuum</i>	<i>Streptomyces</i> sp. A6	枯萎病 <i>Fusarium</i> wilt	代谢物 Metabolite	63-64
	<i>Streptomyces</i> St7c5	根腐病 Root rot	代谢物 Metabolite	
蚕豆 <i>Vicia faba</i>	<i>S. isolates</i>	白粉病 Powdery mildew	—	33
木豆 <i>Cajanus cajan</i>	<i>S. cyanoviridis</i>	根腐病 Root rot	—	65
豌豆 <i>Pisum sativum</i>	<i>Streptomyces</i>	根腐病 Root rot	—	66
亚麻 <i>Linum usitatissimum</i>	<i>Streptomyces</i>	根食线虫 Root nematode	—	67
白羽扇豆 <i>Lupinus albus</i>	<i>Streptomyces</i> sp.	根腐病 Root rot	—	68
苜蓿 <i>Medicago Sativa</i>	<i>S. isolate</i>	根腐病 Root rot	—	52,69
	<i>Streptomyces</i> sp.	茎腐病 Stem rot	—	
叶菜 <i>Brassica chinensis</i>	<i>S. griseoviridis</i>	提高产量 Increase yield	—	70
花椰菜 <i>B. oleracea</i> var. <i>botrytis</i>	<i>S. olivaceus</i> .	叶斑病 Leaf spot disease	—	71
水仙 <i>Narcissus tazetta</i> var. <i>chinensis</i>	<i>Streptomyces</i> sp. (C-26)	黄萎病 <i>Verticillium</i> wilt	—	72
大麦 <i>Hordeum vulgare</i>	<i>S. albovinaceus</i>	榆病 Dutch elm disease	—	52,73
茄子 <i>Solanum melongena</i>				74
榆树 <i>Ulmus pumila</i>				75

西红柿体内脱落酸、茉莉酸与水杨酸等植物生长调节剂含量都有增加^[16]。链霉菌 RP1A-12 能够促进花生种子发芽, 提高茎与芽的长度^[17]。温室与大田试验表明, 链霉菌 C2012 与 C801 可以提高薄荷(*Mentha canadensis*)地上部分的鲜质量与干质量^[18]。分离自双孢蘑菇(*Agaricus bisporus*)培养基质的链霉菌 A06, 对双孢蘑菇产量提升 31.5%^[19]。

IAA 是一类含有 1 个不饱和芳香族环和 1 个乙酸侧链的内源生长调节剂, 对植物生长具有两重性作用。植物不同部位对其敏感度不同, 一般根的敏感性大于芽, 芽又大于茎。不同植物对 IAA 敏感度也不同。植物内生菌中产生大量生物活性物质, 其中就包含 IAA 等吲哚衍生物^[20]。最初报道链霉菌产生 IAA 的菌株是灰绿链霉菌(*S. griseoviridis*), 经过制作成孢子悬浮液、菌体冻干粉末和上清液粉末制剂, 施用后提高了黄瓜产量^[21]。近期研究也表明链霉菌 A1RT 能分泌 IAA 等植物生长调节剂, 促进了马铃薯块茎质量增加和茎部发育。IAA 在链霉菌体内主要通过吲哚-3-乙酰胺(Trp-IAM-IAA)途径合成^[22]。

土壤中存在氮、磷、钾等大量元素, 同时也存

在钙、铁、镁等微量元素。植物从土壤中吸收营养进行生长。固氮作用是指将大气中的氮转变为氨态氮或含氮化合物的过程, 主要分为生物固氮与非生物固氮。而生物固氮主要通过一些微生物的固氮作用, 将氮素提供给植物吸收。链霉菌能够协助一些微生物进行固氮作用, 如链霉菌 AUR4 单独处理鹰嘴豆(*Cicer arietinum*), 可以促进生长, 提高种子质量和数量的同时也提升豆荚的质量与数量。链霉菌 AUR4 与链霉菌 ARR2 同时接种, 对鹰嘴豆促生具有协同作用。链霉菌 AUR4 与链霉菌 ARR2 分别同固氮菌同时处理鹰嘴豆, 提高了鹰嘴豆根部固氮瘤的产生与根内固氮酶活性^[23]。灰黄链霉菌(*S. griseoflavus*) P4 能刺激大豆(*Glycine max*)根瘤的形成, 促进生长。大豆品种‘Yezin-9’与‘Shan Seine’接种灰黄链霉菌 P4 后, 根瘤形成分别提升 75%与 39%^[24]。

嗜铁素是一类微生物产生的水溶性小分子化合物, 能够特异性地结合铁离子^[25]。按照结合铁的官能基团不同, 嗜铁素可以分为 4 种类型: 异羟肟酸型、儿茶酚型、羟基羧酸型和混合型^[26]。微生物分泌嗜铁素, 结合环境中的铁离子, 一部分供给自

身营养生长,一部分作为物质交换,传递给植物。在灭菌的土壤中,植物生长出现缺绿现象,表明微生物在植物营养吸收中占有重要地位^[27]。分离的酸性疮痂链霉菌(*S. acidiscabies*)可以产生异羟肟酸型嗜铁素,能够促进镍离子胁迫下豇豆(*Vigna unguiculata*)的生长^[28]。接种分泌嗜铁素的链霉菌后,水稻种子的发芽率与生长势明显提高^[29],橡胶树(*Hevea brasiliensis*)与葡萄(*Vitis vinifera*)也同样表现出良好的生长趋势^[30]。盐屋链霉菌(*S. sioyaensis*)发酵上清液中富含嗜铁素,铬天青(CAS)平板法检测时,链霉菌菌落周围透明圈直径达到(11.75 ± 0.76) mm,上清液处理橡胶树幼苗后,促进生长并提高株高,并对橡胶树根腐病起到防控的作用^[25]。链霉菌 RP1A-12 分泌嗜铁素,抑制 *S. rolfii* 产生草酸,控制由 *S. rolfii* 引起的花生茎腐病的蔓延,促进生长^[31]。

链霉菌也可以提高植物对磷、钾等元素的吸收,促进生长。链霉菌能够提高鹰嘴豆植株体内生物碳

和磷含量^[32]。链霉菌提高植物体内矿质营养元素具有选择性,链霉菌可提高大麦体内氮、磷、钾含量,但钙含量并未见明显变化。千叶链霉菌(*S. chibaensis*)能提高蚕豆(*Vicia faba*)体内氮、磷、钾含量,并且促进营养蛋白的积累和提高矿质含量,提升产量^[33]。

3 提升植物逆境耐受力

植物在生长过程中,随着环境变化,会遭遇各种各样的逆境,大体上可以分为生物逆境与非生物逆境。生物逆境主要为病虫与病害,可以通过外界喷施含有抑制病原菌或病虫害生长的药物和提高植物系统抗性来减轻病虫害。非生物逆境主要为干旱、盐碱、水渍与重金属污染等外在条件引起的不适合植物生长的环境因素,主要的预防措施是提高植物体内脯氨酸、抗氧化酶活性及相关抗性蛋白基因的表达来抵御(图 1)。

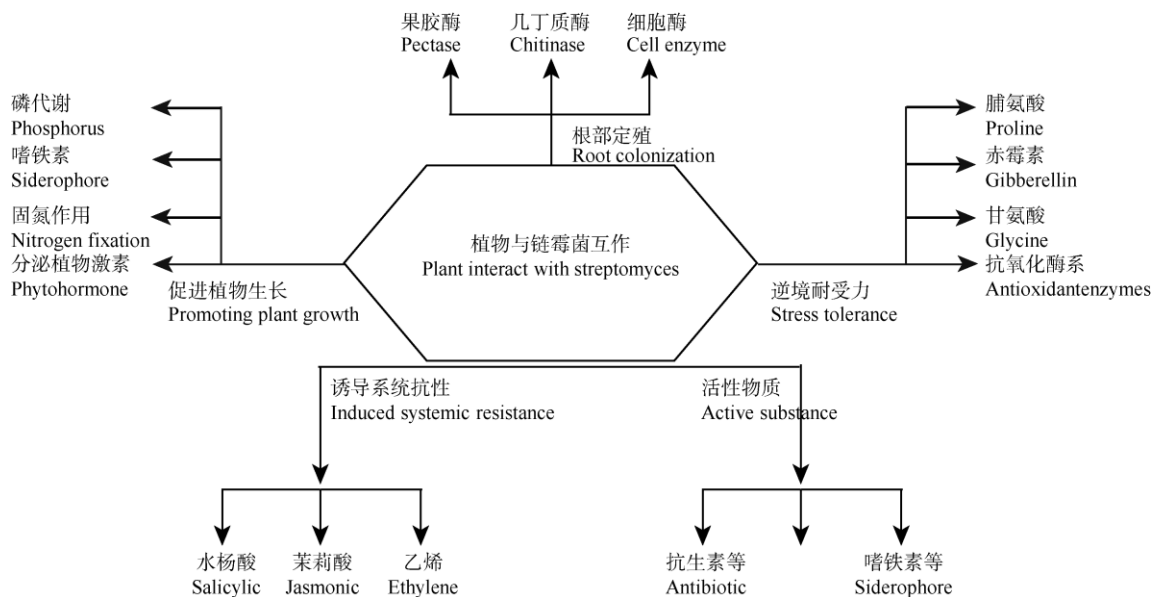


图 1 链霉菌与植物的互作(引自 Vardharajula 等^[76], 略加修改)

Fig. 1 Interaction between *Streptomyces* and plants (Revised from Vardharajula^[76])

微生物在与植物互相作用的过程中逐渐形成了互惠互利的关系。植物供给微生物合适的生长环境,微生物提供植物必需的矿质营养。微生物协助植物抵抗逆境的方式有直接分泌具有抑菌抗虫作用的代谢物(化合物、几丁质酶、葡萄糖酶等)抑制病原菌生长,或者间接促进植物生长、提高系统抗性(抗氧化酶系、抗性蛋白)来抵御病原菌的入侵。

链霉菌分泌的代谢物包含多种类型的抑菌化

合物,链霉菌的初期研究主要集中在医学抗生素的发掘上,近期链霉菌分泌的代谢物在农业上也得到了广泛的应用。链霉菌代谢物中具有生物活性的物质主要分为生物碱类化合物、聚酮类化合物、萜类化合物、多肽类化合物、糖苷类化合物与酮类化合物^[77],这些活性物质在农业生产与医学应用中发挥重要作用。白叶枯病菌造成水稻叶片枯萎,导致重大经济损失,其致病力与生物膜的形成能力有关,

抑制白叶枯病菌生物膜的形成,就能够减轻水稻白叶枯病害的发生和产量的降低。链霉菌菌株 0320 和 4359 可以抑制白叶枯病菌生物膜的形成,而不影响白叶枯病菌细胞的生长^[78]。进一步研究表明,是链霉菌分泌的化合物邻氨基苯甲酰氨在起作用,由于并未影响白叶枯病菌细胞的生长,所以未来出现对该化合物有耐受性的白叶枯病菌的几率较小^[78]。链霉菌代谢物不仅自身具有抑菌活性,也可以活化其他无抑菌活性的物质。最近的研究表明,链霉菌代谢物还能够合成纳米粒子,进而增强代谢物抑制病原菌生长的能力。Vijayabharathi 等^[79]的研究表明链霉菌 SAI-25 具有合成 AgNPs 的能力,通过在上清液中加入 AgNO₃,可以反应生成 AgNPs, AgNPs 可以有效抑制芽腐病菌(*Macrophomina phaseolina*)的生长,降低高粱(*Sorghum bicolor*)芽腐病的发生。

在链霉菌与病原真菌的寄生过程中,几丁质酶是一种关键因素。微生物通过分泌几丁质酶降解病原真菌细胞壁,从而进入病原真菌体内并获取营养。这也为植物病害防治提供了有效措施,盐屋链霉菌能够分泌几丁质酶抑制病菌生长,降低橡胶树(*Hevea brasiliensis*)白根病的发病率。Shivalee 等^[80]通过添加胶体几丁质和优化培养条件等措施,使得链霉菌 KLSL55 产生的几丁质酶含量提升 14.30 倍。Gao 等^[81]从链霉菌 ATCC 27414 中克隆到一种新的几丁质酶基因,转入大肠杆菌中得到表达,且几丁质酶活性具有 pH 与温度稳定性。

链霉菌作用于植物根部,可以激活叶片对于病原菌的抵御能力,诱导植物产生系统性抗性。植物系统性抗性主要通过水杨酸等信号途径进行传导,诱导抗氧化酶系统、脯氨酸和蛋白酶的改变,增强对病虫害的防御,促进植物生长。Sunpapao 等^[82]的研究表明,链霉菌 V76-12 对米弯孢菌(*Curvularia oryzae*)生长的抑制率达到 85.71%,椰子(*Cocos nucifera*)幼苗经链霉菌 V76-12 处理后,病情指数由 75.33% 降至 21%,提高了幼苗的抗氧化酶系统(PAL、PPO 和 POD)的活性。Shariffah-Muzaimah 等^[83]筛选的链霉菌 AGA347,使椰子幼苗茎腐病病情指数降低 73.1%。链霉菌 JD211 可以诱导水稻的系统抗性,几丁质酶与抗病相关蛋白 1 (PR1)的基因表达量提升,抗氧化酶(PAL 与葡聚糖酶)的活性得到增强,有效控制水稻稻瘟病的蔓延^[84]。*Streptomyces rochei* SM3 通过提升鹰嘴豆的抗氧化酶(POD、CAT 和 PPO 等)活性和酚类物质含量,增强抵御葡萄球菌的侵染

能力^[35]。

链霉菌不仅能够协助植物抵御病虫害的侵染,也能够帮助植物顺利渡过非生物逆境的不利影响,并改善生态环境。温室与大田试验表明,链霉菌 C2012 和 C801 可以提高薄荷地上部分鲜质量和干质量^[12],薄荷在水渍逆境中,鲜质量和干质量都降低,但接种链霉菌后有效缓解了水渍逆境带来的负面影响,有效提高鲜质量和干质量,提高了薄荷油与挥发油含量。链霉菌 MM10 也能够显著提高小麦对高盐土壤的耐受力,并且提高产量^[52]。二氯喹啉酸是一种广泛应用于水稻等作物中的除草剂,可有效控制杂草生长,由于其较难降解,长期大量使用后,在土壤中残留过多,对环境造成不良影响。Lang 等^[85]报道链霉菌 AB-H 对二氯喹啉酸具有降解作用,实验室研究表明,其降解率达到 97.2%,应用于土壤后,降解率为 87.5%。因此,链霉菌 AB-H 在生态环境的优化方面具有良好的市场前景。链霉菌 HBUM174787 具有产生生物絮凝剂的能力,絮凝剂具有羟基、羧基、甲氧基与氨基基团,能够降低 63.1% 的河流含氧量和 46.6% 的肉制品加工废水含氧量,使其混浊度分别降低 84.3% 和 75.6%,在河流污染治理方面具有广阔的应用前景^[86]。龟裂链霉菌能够从水溶液中吸收重金属(铅和镍),为治理重金属污染的土壤提供思路^[87]。

4 链霉菌在农业生产中的应用

目前,国内生物菌肥产业还处于初步发展阶段,微生物菌肥生产厂家大约在 1 000 家左右,微生物肥料年产量在 1.0×10^8 t 水平,推广应用面积 1.3×10^7 hm²^[88],产品数量、类型与企业分布在逐渐走向多元化的过程中。随着人们对于生态环境的关注,生物菌肥的需求将逐步递增。

微生物在农业生产上的应用形态主要有粉剂、颗粒剂和水剂。粉剂和颗粒剂便于运输,水剂的活性更好。具体应用何种形态的微生物制剂,需随菌种不同选择更加高效的成品制剂。微生物制剂的主要问题是活性问题,大部分微生物受环境影响较大,温度变化会对微生物制剂活性产生较大影响。关于微生物制剂的保存条件,湿度与温度都是需要考虑的因素。在应用上,主要处理方式有浸种、灌根与喷施叶片,浸种方法省时省力,是目前微生物处理的主要方式;灌根需要微生物菌量大,但效果

持久; 喷施叶片具有见效快的优点。近期有一种含金黄垂直链霉菌 HN6 的可湿性粉剂, 是将润湿剂、分散剂、稳定剂、填料投入到气流粉碎机中粉碎, 过 325 目筛, 降温后, 加入金黄垂直链霉菌 HN6 液体发酵物, 继续粉碎, 使其最终水分含量 $\leq 5\%$, 活性孢子数为 $(0.1\sim 10)\times 10^9\text{ g}^{-1}$, 该药剂属于微生物活体制剂, 对香蕉枯萎病有显著防治效果, 对其它病害也有较好的防治作用, 同时对生态环境无毒副作用, 保障了农产品的质量与安全^[89]。货架期短是生物菌肥应用过程中, 需要克服的一个技术难点, 开发出高效、贮存期长的生物菌肥是农业生产上所急需的。目前的研究大多数以实验室以及温室等控制条件为主, 在这种条件下, 链霉菌作为生防菌能取得良好的效果。但在大田等复杂环境中, 链霉菌应用的成功报道还相对较少, 今后需要进一步在大田等复杂环境中进行链霉菌生物防治的试验。

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