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香柱菌属内生真菌影响宿主禾草微生物群落结构与多样性的研究进展

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摘要: 香柱菌属内生真菌主要定殖于宿主禾草的地上组织, 并与宿主形成稳定的非致病性共生体系。该类真菌不仅增强宿主对生物和非生物胁迫的抗性, 还能通过调控宿主生理代谢与多样微生物群落的互作, 塑造根际、叶际及种带微生物群落的结构与功能。本研究综述了香柱菌属内生真菌影响禾草根际(与土壤)、叶际和种带微生物群落组成与多样性的研究进展。系统介绍了香柱菌属内生真菌通过改善宿主水分利用效率、调节根系分泌物、影响叶片次生代谢产物及改变土壤理化性质等, 选择性地促进或抑制宿主植物不同部位特定微生物类群的定殖, 并普遍降低病原菌丰度和菌根侵染率的相关研究成果。进一步阐释了此类调控作用在代际间垂直传播, 及其助力宿主植物适应胁迫环境的潜在机制。综上, 本研究介绍了香柱菌属内生真菌在禾草微生物群落调控及生态功能中的关键作用, 总结梳理了其在抗逆育种、微生物资源开发及可持续草地管理方面已经发挥或潜在的应用价值。

关键词: 禾草; 香柱菌属内生真菌; 根际; 叶际; 微生物

Research progress on the effects of *Epichloë* endophytes on the structure and diversity of microbial communities in host grasses

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Abstract: *Epichloë* endophytes primarily colonize the aboveground tissues of host grasses, forming a stable, non-pathogenic symbiotic system. These endophytes not only enhance the host's resistance to biotic and abiotic stresses but also shape the structure and function of rhizosphere, phyllosphere, and seed-associated microbial communities by regulating host physiological metabolism and interacting with diverse microbial populations. This review summarizes recent research on the effects of *Epichloë* endophytes on the composition and diversity of microbial communities in the rhizosphere (and soil), phyllosphere, and seeds of grasses. Present studies demonstrate that *Epichloë* endophytes can selectively promote or inhibit the colonization of specific microbial groups in different plant compartments by improving host water-use efficiency, modulating root exudates, altering foliar secondary metabolites, and modifying soil physicochemical properties, while generally reducing pathogen abundance and mycorrhizal infection rates. This review further elaborates on the vertical transmission of these regulatory effects

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across plant generations and their potential mechanisms in enhancing host adaptation to environmental stresses. In conclusion, this review highlights the pivotal roles of *Epichloë* endophytes in regulating grass-associated microbial communities and maintaining ecological functions, and summarizes their established and potential applications in stress-resilient breeding, microbial resource development, and sustainable grassland management.

Key words: grasses; *Epichloë* endophyte; rhizosphere; phyllosphere; microorganisms

在植物的组织表面及内部广泛栖息着多类微生物,包括细菌、真菌和古菌[1],共同构成了与植物不同部位密切相关的微生物生境[2]。这些微生物贯穿植物生长发育的各个阶段[3]。在长期进化过程中,植物与微生物相互选择、相互适应,逐渐建立起复杂而稳定的共生体系[4]。植物为微生物提供生境、营养基质及信号分子,而微生物则协助宿主获取营养、抑制病原侵染、缓解非生物胁迫[5],构成具有功能互补性的共生网络[6]。这一网络在调控植物生长、健康与适应性中发挥关键作用,并对植物的生长和进化过程产生深远影响。因此,植物微生物群落被视为植物的“第二基因组”或“泛基因组”[7]。

在植物微生物群落中,香柱菌属(*Epichloë*)内生真菌[子囊菌门(Ascomycota)、肉座菌目(Hypocreales)、麦角菌科(Clavicipitaceae),以下简称“内生真菌”]是一类长期定殖于植物组织、通常不引起病害的特殊成员[8]。作为丝状单系类群,其可与宿主建立永久性的共生关系,并在多项生态功能中发挥关键作用,是许多草原生态系统中的关键物种[9]。其菌丝主要沿细胞间隙生长,通过种子实现高效垂直传播;部分有性型还可通过子囊孢子进行水平传播[10-11]。这一兼具稳定性与扩散潜力的传播方式在国际学界受到广泛关注。我国相关研究于20世纪90年代逐步展开。李翠英[12]检测了高羊茅(*Festuca arundinacea*)和多年生黑麦草(*Lolium perenne*)中的内生真菌,但并未进一步开展系统研究;南志标[13-14]开展了国产及引进禾草品种的带菌状况与野外多样性调查,首次系统揭示了我国乡土禾草中内生真菌的广泛存在[15-16],为我国开展此类研究奠定了坚实的基础。迄今,全球已鉴定出51种香柱菌属内生真菌,其中我国分布有12种,主要宿主包括醉马草(*Achnatherum inebrians*)、中华羊茅(*Festuca sinensis*)和草地早熟禾(*Poa pratensis*)等植物[17-19]。其种类构成及宿主分布格局见图1。

大量研究表明,内生真菌在促进宿主植物生长、增强抗逆性及改善养分获取方面具有重要功能,但其共生关系也表现出一定的双重性[21-23]。一方面,内生真菌可合成多种生物碱,可能引发家畜中毒[24];另一方面,内生真菌侵染植株在生长和生态适应性方面表现出明显优势,包括生物量增加、种群竞争力提升,以及在多种环境胁迫下表现出更强的耐受能力[25]。内生真菌不仅能直接影响宿主的生理生化过程,还能够通过塑造宿主的微生物群落,间接调控其环境适应性。传统观点认为,植物是微生物群落的“筛选者”并主导微生物在其体表或体内的定殖[7],近年来研究显示,内生真菌能够影响宿主植物多个组织部位的微生物群落组成、多样性及营养元素的循环与转化等[26]。来自干旱、盐碱等逆境环境的研究进一步表明,该类内生真菌还可通过影响土壤养分和地下微生物网络,增强宿主对逆境的适应能力[27]。由此可见,内生真菌可作为关键调控者,塑造微生物群落的结构与功能[28]。此外,它在禾草组织中表现出明显的时空定殖优势,其独特的传播方式不仅影响宿主当代的微生物群落构建,还可能通过垂直传播作用于后代植物的微生物群落组成[29-30]。因此,深入探究内生真菌对根际(与土壤)、叶际和种带等不同生态位微生物群落的调控机制,对于理解植物-微生物互作过程、优化农业管理措施以及推进微生物辅助育种具有重要的科学与应用价值[31]。

已有研究虽为理解内生真菌的生态功能提供了部分重要线索,但其如何在根际(与土壤)、叶际与种带等多个生态位中调控宿主微生物群落结构与功能,仍缺乏总结,尤其是内生真菌如何在土壤-植物连续体尺度上塑造微生物群落结构及其功能,尚未得到全面讨论。为此,本综述以禾草-内生真菌共生体为研究对象,在整合既有研究成果的基础上,梳理内生真菌对宿主根际(与土壤)、叶际与种带微生物群落多样性及组成的影响,尝试解析其与微生物群落互作的潜在机制,以期为微生物调控宿主植物研究和草类植物甚至作物的改良策略提供参考。

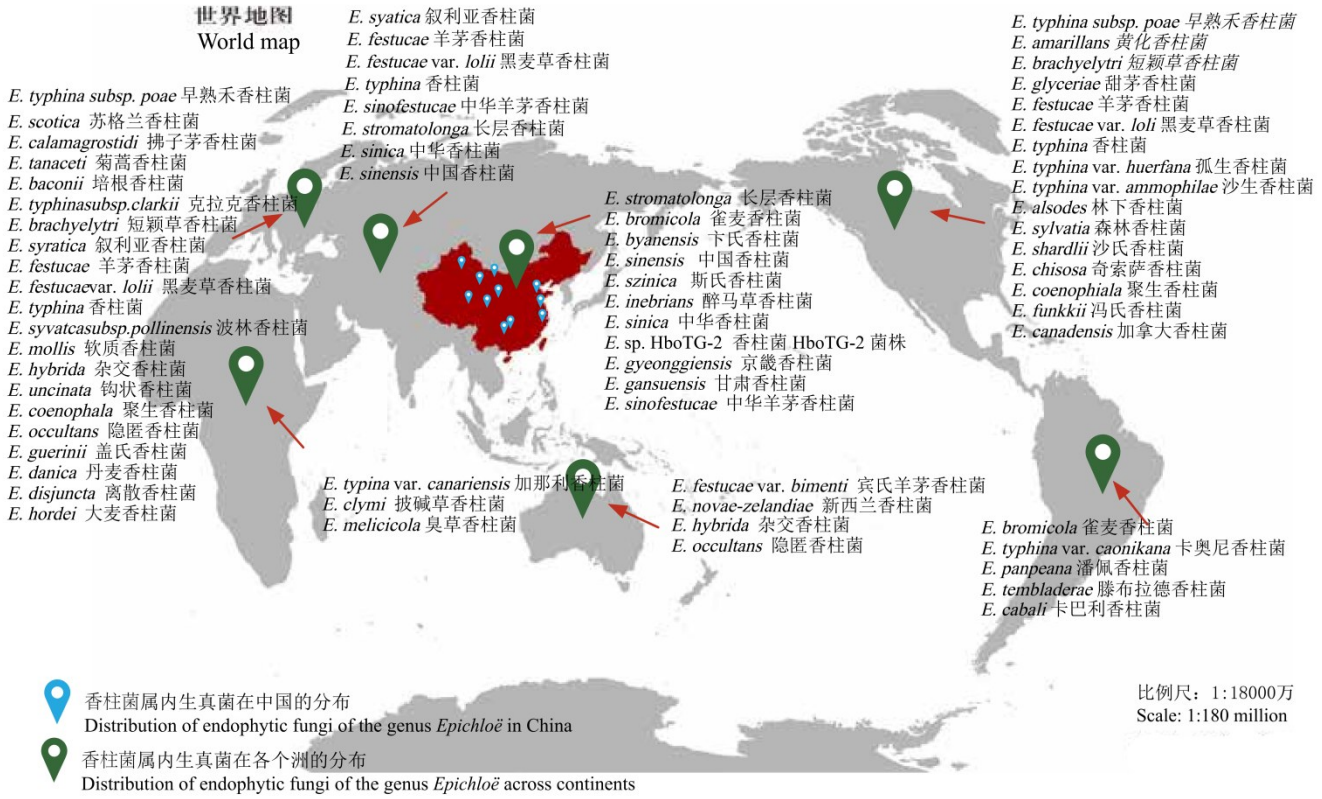


图 1　香柱菌属内生真菌在世界范围的分布(改编自杜明祥等[20])

Fig. 1　Worldwide distribution of *Epichloë* endophytes (Adapted from Du Mingxiang *et al* [20])

基于自然资源部标准地图服务网站 GS(2016)1613 号标准地图制作，底图边界无修改。Based on the standard map service website GS(2016)1613 of the Ministry Resources, the boundary of the base map is not modified.

1　内生真菌对根际(与土壤)微生物的影响

根系是植物吸收水分和养分的主要器官，其周围定殖的微生物统称为根际微生物群落，这些微生物在促进植物生长、改善养分和水分利用以及增强抗逆性方面发挥关键作用[32-33]。内生真菌主要定殖于冷季型禾草的叶片、茎和生殖器官的细胞间隙，尚未在根部直接发现。然而，它们仍可通过调节宿主地上组织的生理和代谢过程作用于根际微生物群落[34-35]，这种影响会因环境、禾草种类和内生真菌基因型的不同而表现出差异[36-37]。

近年来的研究表明，内生真菌能够显著影响宿主植物在不同水分条件下的根际细菌和真菌多样性。例如，在 *E. amarillans* 内生真菌存在时，美洲沙茅草(*Ammophila breviligulata*)根际细菌多样性随土壤含水量的增加而下降[38]；而在无内生真菌条件下则呈相反趋势。类似地，*E. gansuensis* 内生真菌亦可降低醉马草根际细菌和真菌的多样性[39]。这些结果表明，内生真菌可能抑制某些对植物产生不利影响的微生物类群，从而间接增强宿主植物的生长和抗逆能力，即产生整体的正效益[40]。然而，这种调控效应并非恒定。在某些生态背景中，内生真菌反而可能提高微生物多样性[41]。已有研究表明，这些富集类群多表现为富养型(copiotrophic)，对土壤水分变化较为敏感，因此，一些优势土壤细菌门的生长和摄食策略具有系统发育保守性，即在不同物种或系统中表现出相似的营养利用策略和对环境变化的响应模式，使得群落组成对土壤水分变化表现出一定的可预测性[42]。除此之外，内生真菌还可能通过直接调控植物根系特征，将影响细菌多样性的主要限制因子由碳源转变为水分条件，从而增强根际细菌群落对水分变化的响应[38]。

内生真菌亦可通过改变宿主凋落物的数量与化学组成，从而间接调控土壤微生物群落[43-48]。含有内生真菌的凋落物会显著降低土壤中浮霉菌门(Planctomycetes)和六球菌门(Rokubacteria)的相对丰度，并减少细菌群落

多样性[45]。这可能是因为内生真菌改变了宿主代谢及根际分泌物，进而影响了根际微生物组成[49]。在*E. guerinii*与德兰臭草(*Melica transsilvanica*)的研究中[50]，与无菌株对照相比，内生真菌侵染(endophyte-infected，EI)植株显著富集了根际促生细菌，如假单胞菌属(*Pseudomonas*)、布拉氏根瘤菌属(*Bradyrhizobium*)和硝化螺旋菌属(*Nitrospira*)，这些细菌的富集与EI植株根系分泌物的有机酸、氨基酸和糖醇含量升高显著相关[51]。同时，内生真菌合成的黑麦草碱(loline alkaloids)也可能参与根际微生物群落的重塑过程。已有研究证实，能够以黑麦草碱为营养源的细菌类群会在群落中占据竞争优势[52]。在水分胁迫条件下，黑麦草碱在植株地上部与根系中的积累量均会显著升高，这类代谢物可随根系分泌物进入土壤环境，进而改变根际化学微环境，并特异性吸引目标微生物类群定殖。因此，内生真菌通过选择性调控宿主代谢物的释放模式，例如以黑麦草碱为关键介导物质，为特定功能微生物的富集提供资源保障，进而影响根际微生物群落结构，并增强宿主在不同水分条件下的适应能力。

在自然界中，禾草通常能同时与内生真菌和丛枝菌根真菌(arbuscular mycorrhizal fungi，AMF)建立共生关系[53]。AMF是一种普遍存在于土壤中的共生微生物，通过与植物根系形成共生体，促进植物的养分吸收和抗逆性[54]。目前关于两者互作的研究多聚焦于内生真菌对AMF根系定殖的影响[55-57]。例如，当*E. coenophiala*内生真菌侵染高羊茅后，显著降低了AMF的总定殖率[56]。内生真菌对AMF也可能产生促进效应，一定浓度的内生真菌浸提液可以增加AMF的菌丝长度[58]，且在温室条件下能显著提高烟管雀麦(*Bromus auleticus*)菌根定殖率[59]。综上，内生真菌通过调控宿主水分利用、根系代谢物分泌及凋落物输入，间接或直接影响根际微生物群落的结构与功能。在不同水分条件和宿主－真菌组合下，其作用表现出差异性，并可通过与丛枝菌根真菌的竞争或协同作用，进一步影响植物生长、养分吸收和抗逆能力，凸显其在根际(和土壤)微生物组调控中的关键角色(表1)。

2 内生真菌对叶际微生物的影响

叶际微生物是植物地上部分形成的独特微生态系统，由叶片、茎等表面的附生微生物及定殖于组织内部的微生物组成，表现出高度的组成复杂性和动态变化特征[85]。与根际系统相比，叶际微生物与内生真菌的互作研究相对有限，现有研究主要集中于黑麦草属(*Lolium*)[86]、羊茅属(*Festuca*)[87]和醉马草体系[85]。

研究表明，内生真菌对叶际微生物的调控是多机制协同作用的结果，而非单一效应。一方面，内生真菌可抑制病原菌侵染，降低宿主草类植物的病害发生率[88]。例如，在高羊茅－*E. coenophiala*共生体系中，内生真菌显著降低了叶片中链格孢属(*Alternaria*)和布氏白粉菌属(*Blumeria*)的孢子数量，使病害的发生率和病害严重度明显低于未侵染植株[89]。内生真菌也可通过改善叶片生理状态，如提高叶绿素含量和光合作用效率，为叶片微生物群落提供更稳定的生境，从而进一步增强宿主的抗病能力[90]。另一方面，内生真菌可通过调控叶片次生代谢物，间接影响叶际微生物群落结构。这些代谢物既可能由内生真菌自身合成，也可能由内生真菌通过调控宿主代谢产生。在醉马草－*E. gansuensis*体系中，内生真菌侵染显著改变了叶片中嘌呤衍生物、吲哚衍生物、酚类及黄酮类化合物的种类和含量，这些代谢物具有抗菌、抗虫及调控微生物群落的功能，且叶际附生细菌种群数量与叶片总酚含量呈显著负相关，表明内生真菌可通过诱导宿主代谢物的分布和积累重塑叶际微生物群落结构[85]。此外，内生真菌对叶片微生物群落的调控还与宿主的繁殖策略密切相关[91]。受内生真菌侵染的植株会出现花粉产量下降而种子产量上升的表型(即生殖投资从雄性功能向雌性功能转移)，生殖分配的改变会通过影响植物体的生理和化学状态波及叶片微生境，从而间接改变叶际微生物群落。需要注意的是，叶际微生物因直接暴露于外界环境中，其群落组成易受湿度、温度、光照及叶片老化等外源因素的干扰，进而可能削弱内生真菌的调控信号。这一现象在多年生黑麦草－*E. festucae*共生体系中已得到证实：该内生真菌对叶际真菌群落的调控效应并不显著[86]，充分表明内生真菌对叶际微生物群落的调控作用具有明显的环境依赖性，其效应强弱易受外部环境条件的调控(表2)。综上，内生真菌作为叶际微生态系统的关键调控者(keystone species)，其作用受环境条件和宿主特性的共同影响，同时，植物相关微生物群落也可通过调控宿主代谢物和内源激素，对植物－微生物互作形成反馈调节[92-95]。

表 1　香柱菌属内生真菌对根际微生物的影响

Table 1　Effects of *Epichloë* endophytes on rhizosphere microorganisms

内生真菌 Endophytes	宿主 Host	作用 Function	参考文献 Reference
隐匿香柱菌 *E. occultans*	多花黑麦草 *Lolium multiflorum*	对根际土壤细菌的呼吸作用没有显著影响。Has no significant effect on the respiratory activity of rhizosphere soil bacteria.	[60]
		改变了宿主根际土壤细菌群落组成。Alters the composition of the host rhizosphere soil bacterial community.	[61]
		增加真菌活性,降低菌根真菌侵染率。Enhances fungal activity, and lower the mycorrhizal fungi infection rate.	[62]
黄化香柱菌 *E. amarillans*	美洲沙茅草 *A. breviligulata*	在水分胁迫条件下降低了植株根系相关细菌群落的多样性。Reduces the diversity of plant root-associated bacterial communities under water stress conditions.	[38]
		增加了根部内生真菌的丰富度并且在氮肥富集条件下改变了根部内生真菌群落的组成。Increases the abundance of root endophytic fungi and alters the composition of root endophytic fungal communities under nitrogen fertilizer enrichment conditions.	[63]
聚生香柱菌 *E. coenophiala*	高羊茅 *F. arundinacea*	增加了根际土壤细菌的多样性。Enhances the diversity of rhizosphere soil bacteria.	[41]
		降低了宿主在黏土生境下的革兰氏阳性细菌(G+)的多样性。Decreases the diversity of Gram' positive bacteria (G+) in the host under clay habitat conditions.	[64]
		对根部溶磷细菌多样性没有显著的相互作用。There is no significant interaction with the diversity of phosphate-solubilizing bacteria (PSB) in the roots.	[42]
		降低了古细菌的群落多样性,抑制了黏壤土中革兰氏阳性菌的生长。Reduces the community diversity of archaea and inhibits the growth of Gram-positive bacteria in clay loam.	[65]
	苇状羊茅 *Schedonorus arundinaceus*	降低菌根真菌的定殖。Reduces the colonization of mycorrhizal fungi.	[66]
		在不同的土壤含水量下,对丛枝菌根真菌的定殖率不同。The colonization rate of AMF varies under different soil moisture contents.	[67]
		减少了根部的菌根定殖。Decreases mycorrhizal colonization in roots.	[29]
黑麦草香柱菌 *E. festucae* var. *lolii*	多年生黑麦草 *L. perenne*	显著增加了 16S rRNA 基因的绝对丰度以及土壤细菌群落的多样性。Significantly increases the absolute abundance of the 16S rRNA gene and the diversity of soil bacterial communities.	[68]
		改变了根际土壤中与氮循环相关的细菌基因丰度,尽管对土壤真菌群落的绝对丰度和多样性没有显著影响。Alters the abundance of bacterial genes related to nitrogen cycling in rhizosphere soil, although it has no significant effect on the absolute abundance and diversity of soil fungal communities.	[69]
甘肃香柱菌 *E. gansuensis*	醉马草 *A. inebrians*	减少了根际土壤中可培养细菌的种类数目。Decreases the number of culturable bacterial species in the rhizosphere soil.	[70]
		降低了根相关细菌多样性,增加了根际土壤细菌群落的多样性。Reduces root-associated bacterial diversity while increasing the diversity of rhizosphere soil bacterial communities.	[39]
		在盐胁迫下,显著增加了宿主养分提取和土壤微生物丰度。Significantly enhances host nutrient uptake and soil microbial abundance under salt stress.	[43]
		宿主抵抗 $CdCl_2$过程中,内生真菌增强了根际细菌物种间的协作。During the host's resistance to $CdCl_2$, strengthen the cooperation between rhizosphere bacterial species.	[71]
		在 NH_4^+-N处理下增加了宿主根部细菌的 α-多样性。Increases the α-diversity of host root bacteria under NH_4^+-N treatment.	[72]
		降低了根系相关真菌群落的多样性,显著降低了根相关真菌多样性。Reduces the diversity of root-associated fungal communities, significantly reduces the diversity of root-associated fungi (RAF).	[54]
		减少了根际土壤中真菌的数目。Decreases the number of fungi in rhizosphere soil.	[73]
		降低盐胁迫对真菌群落多样性的影响。Mitigates the impact of salt stress on fungal community diversity.	[74]
雀麦香柱菌 *E. bromicola*	羊草 *Leymus chinensis*	提高丛枝菌根真菌的侵染率和孢子密度。Improves the infection rate and spore density of arbuscular mycorrhizal fungi (AMF).	[75]
		增加根际土壤中真菌的数目。Increases the number of fungi in rhizosphere soil.	[76]

续表 Continued Table

内生真菌 Endophytes	宿主 Host	作用 Function	参考文献 Reference
雀麦香柱菌 *E. bromicola*	羊草 *Leymus chinensis*	增加根系和根际土壤中的真菌群落多样性和丰富度。Enhances the diversity and richness of fungal communities in roots and rhizosphere soil.	[77]
		随植物生长时间的延长,内生真菌与生长时间互作对真菌和细菌丰度影响显著。With the extension of plant growth period, the interaction between endophytic fungi and growth time has a significant impact on the abundance of fungi and bacteria.	[36]
		对宿主根部丛枝菌根真菌总定殖率没有影响。Has no effect on the total colonization rate of arbuscular mycorrhizal fungi (AMF) in host roots.	[53]
	高羊茅 *F. arundinacea*	减少丛枝菌根真菌定殖率。Reduces the colonization rate of arbuscular mycorrhizal fungi (AMF).	[56]
		降低菌根真菌的定殖。Reduces the colonization of mycorrhizal fungi.	[40]
		在盐碱胁迫条件下,显著增加了宿主根部植物促生真菌的多样性并改变了其组成。Significantly increases the diversity of plant growth-promoting fungi (PSE) in host roots and alters their composition under saline-alkali stress conditions.	[42]
	短芒大麦草 *Hordeum brevisubulatum*	提高土壤中的氨氧化细菌丰度。Increases the abundance of ammonia-oxidizing bacteria in soil.	[78]
	布顿大麦草 *Hordeum bogdanii*	抑制了土壤真菌的丰富度,但提高了土壤真菌的多样性。Inhibits the abundance of soil fungi but improves the diversity of soil fungi.	[79]
		降低菌根真菌的定殖。Reduces the colonization of mycorrhizal fungi.	[80]
羊茅香柱菌 *E. festucae*	多年生黑麦草 *L. perenne*	显著增加了植物刈割返田后和植物自然生长土壤中真菌群落的多样性。Significantly increases the diversity of fungal communities in soil after plant mowing and returning to the field, as well as in soil with natural plant growth.	[81]
	紫羊茅 *Festuca rubra*	显著提高根际土壤真菌群落的代谢途径和次生代谢产物生物合成功能。Significantly improves the metabolic pathways and secondary metabolite biosynthesis functions of the rhizosphere soil fungal community.	[82]
潘佩香柱菌 *E. panpeana*	奥氏雀麦 *Bromus auleticus*	增加根际溶磷真菌多样性。Increases the diversity of phosphate-solubilizing fungi in the rhizosphere.	[59]
西伯利亚香柱菌 *E. sibirica*	西伯利亚羽茅 *Achnatherum sibiricum*	降低菌根真菌的定殖。Reduces the colonization of mycorrhizal fungi.	[83]
滕布拉德香柱菌 *E. tembladerae*	刚毛雀麦 *Bromus setifolius*	增加菌根真菌的定殖。Increases the colonization of mycorrhizal fungi.	[58]
香柱菌 *E. typhina*	多年生黑麦草 *L. perenne*	降低菌根真菌的定殖。Reduces the colonization of mycorrhizal fungi.	[57]
		抑制菌根侵染率。Inhibits the mycorrhizal infection rate.	[84]
披碱草香柱菌 *E. elymi*	刺毛披碱草 *Elymus hystrix*	增加菌根真菌摩西球囊霉(*Glomus mosseae*)的定殖,降低菌根真菌明球囊霉(*Glomus claroideum*)的定殖。Increases the colonization of the mycorrhizal fungus *G. mosseae* and decreases the colonization of the mycorrhizal fungus *G. claroideum*.	[40]

3 内生真菌对种带微生物的影响

种子微生物群落在组成和多样性上通常比土壤、幼苗或成株植物的群落更为简单[93],但其对植物苗期的环境适应和生存能力至关重要。母本叶片和穗部组织相关的微生物菌群是种子微生物的重要来源,因此,任何影响母本微生物群落的生态因子都可能改变种子微生物群落的组成与多样性[94]。研究表明,内生真菌能够显著影响宿主种子所携带的微生物群落,并通过代际传递促进后代植物的适应性提升。

在种子中,内生微生物群落以互利共生为主,而附生微生物群落则常富集潜在病原菌,因此区分内生与附生群落对于理解种子微生物组成结构至关重要[95]。在醉马草体系中,*E. gansuensis*的侵染可影响种子内生细菌多样性,同时降低附生细菌多样性[96]。这一差异可能源于内生真菌通过增加有益细菌的相对丰度并抑制附生病原

表 2　香柱菌属内生真菌对叶片微生物的影响

Table 2　Effects of *Epichloë* endophytes on leaf-associated microorganisms

内生真菌 Endophytes	宿主 Host	作用 Function	参考文献 Reference
香柱菌 *E. typhina*	博纳早熟禾 *Poa bonariensis*	对内生菌群落丰富度和多样性指数没有显著差异。Shows no significant difference in the richness and diversity index of endophytic microbial communities.	[91]
聚生香柱菌 *E. coenophiala*	高羊茅 *F. arundinacea*	对叶际内生细菌群落没有显著影响。Has no significant effect on the phyllosphere endophytic bacterial community.	[92]
羊茅香柱菌 *E. festucae*	多年生黑麦草 *L. perenne*	对叶片真菌群落没有显著影响。Has no significant effect on the leaf fungal community.	[86]
甘肃香柱菌 *E. gansuensis*	醉马草 *A. inebrians*	增加了细菌和真菌群落的Shannon多样性指数，但降低了Simpson多样性指数。Increases the Shannon diversity index of bacterial and fungal communities, but decreases the Simpson diversity index.	[85]
钩状香柱菌 *E. uncinata*	草地羊茅 *Festuca pratensis*	改变了叶片中的真菌微生物群落。Alters the fungal microbial community in leaves.	[87]

真菌在种皮和稃片中的生长[93]，从而降低病害风险[97−98]。内生真菌对种子微生物群落的调控还通过垂直传递实现[99−100]，这一传播过程使部分有益细菌在幼苗生长早期即成功定殖。例如，带有内生真菌的幼苗中泛菌属（*Pantoea*）和假单胞菌属（*Pseudomonas*）的丰度相较不带菌植株显著增加[93]。同时，也有研究观察到在种子阶段部分微生物丰度下降，但在幼苗生长后重新富集和表达[101−102]，说明种子微生物组成在代际传递中存在动态变化。此外，内生真菌还可通过调节宿主种子化学成分间接塑造微生物群落[103]，这些化学成分会影响微生物资源的可获得性及生长竞争关系。同时，内生真菌还可调控宿主免疫信号通路（水杨酸和茉莉酸通路），通过改变防御状态影响母体组织及种子表面微生物的选择性排斥。食草作用诱导的植物防御反应也会进一步改变叶面和穗部微生物定殖环境，从而间接影响最终进入种子的微生物组成[104]（表 3）。综上所述，内生真菌通过垂直传播进入种子，并通过调控种子化学环境、影响母本免疫状态及叶际微生物来源等多重途径协同作用，塑造种子微生物的结构。这些调控不仅增强种子阶段的病原抵抗能力，还对子代幼苗阶段的微生物群落结构、植物建植能力及整体适应性产生深远影响。

4　内生真菌影响微生物的机制

植物相关微生物群落的结构和功能受多种因素调控[107]，包括植物种类、土壤理化性质、栽培方式及环境条件

表 3　香柱菌属内生真菌对种带微生物的影响

Table 3　Effects of *Epichloë* endophytes on seed-associated microorganisms

内生真菌 Endophytes	宿主 Host	作用 Function	参考文献 Reference
甘肃香柱菌 *E. gansuensis*	醉马草 *A. inebrians*	显著降低了种带微生物群落的丰富度和多样性。Significantly reduces the richness and diversity of the seed-borne microbial community.	[95]
		显著降低了种子内生和附生细菌群落的多样性。Significantly decreases the diversity of endophytic and epiphytic bacterial communities in seeds.	[96]
		改变不同世代之间细菌和真菌的群落组成。Alters the community composition of bacteria and fungi across different generations.	[102]
隐匿香柱菌 *E. occultans*	多花黑麦草 *L. multiflorum*	增加了细菌多样性，并使细菌群落更加均衡。Increases bacterial diversity and makes the bacterial community more balanced.	[93]
香柱菌 *E. typhina*	散穗雀麦 *Puccinellia distans*	影响真菌群落的组成。Affects the composition of the fungal community.	[105]
中华香柱菌 *E. sinensis*	中华羊茅 *F. sinensis*	对种带真菌多样性无显著影响。 Has no significant effect on the diversity of seed-borne fungi.	[106]

等[73]。然而,作为宿主植物内部的重要共生因子,内生真菌在调节微生物群落组装方面具有不可忽视的作用,通过多种直接或间接机制深度参与植物微生物群落的构建,表现出显著的调控能力[102]。

内生真菌可合成多种具有生物活性的次生代谢物,尤其是黑麦草碱、麦角缬氨酸(ergovaline)和波胺(peramine)等生物碱类物质,这些化合物在植物组织中积累,并可释放至根际、叶面或种子表面[108-110],直接作用于植物相关微生物群体[111]。部分代谢产物表现出广谱抑菌活性,能够抑制潜在病原微生物的生长;另一些则可被特定微生物作为碳源利用,从而在竞争中获得优势地位[111]。此外,内生真菌还可调控宿主植物的根系分泌模式,诱导植物分泌有机酸、磷脂类物质和酮酸等信号或营养化合物。这些物质不仅为微生物群落提供可利用的碳源和能量,也通过调节微生物的趋化、黏附和代谢活性,间接影响其群落结构[112-113],然而,叶际微生物直接暴露于开放环境,其群落结构易受气候波动、人为干预等外源因素干扰,可能削弱内生真菌的调控效应[85]。

内生真菌还可通过调控宿主植物的代谢和生理状态间接影响微生物群落,激活宿主植物的防御激素信号通路,诱导茉莉酸、水杨酸等信号分子大量积累[93]。这些激素除增强植物本身的抗性外,还会影响细胞壁结构、渗透调节与抗氧化代谢水平,间接改变植物不同部位微环境的选择性,进而驱动特定微生物类群的优势化[114]。同时,可通过影响植物凋落物的质量与分解速率,调节根际土壤中铵态氮、有效磷、速效钾等关键养分的可获得性,进而重塑土壤微生物群落的营养基础,推动其多样性与功能稳定性的形成[37]。此外,内生真菌能够通过垂直传播机制影响植物后代的微生物组装过程[115]。在宿主繁殖阶段,内生真菌可将菌丝延伸至受精子房,并进一步进入胚及其他种子结构,将内生真菌菌丝表面或内部共栖微生物一并传递给种子,并随种子进行繁殖,从而实现自身与部分共生微生物的稳定代际传递[116]。在此过程中,真菌改变种子中糖类(如甘露醇、海藻糖)、抗氧化剂(如谷胱甘肽和生育酚类)以及生物碱的含量,间接塑造种子微生物的存活环境与营养基础,影响其组成与结构特征[117]。这种通过影响种子代谢与微生物来源实现的微生物组装干预,有助于提升宿主植物对环境胁迫的适应能力,并促进微生物群落在世代间的稳定延续。

内生真菌具备垂直传播特性,客观上促使其深度参与了根际(与土壤)、叶际和种带等微生物群落的组装过程。这些机制不仅影响微生物的定殖与选择,还在一定程度上介入了植物与微生物的代际互作。此外,植物所处的微生境以及外界环境条件同样对微生物群落的结构产生重要影响。它们可能与内生真菌的作用相互叠加或抵消,塑造植物微生物组成的多样性与稳定性[118]。综上,内生真菌通过多途径调控微生物群落,并与环境因素共同作用,构建起复杂的互作网络(图2)。这为理解其生态功能与应用潜力提供了重要基础。

5 结论与展望

内生真菌种类丰富,其与宿主植物形成的共生体系在生态系统中具有重要功能。本研究系统综述了香柱菌属内生真菌对禾草根际(与土壤)、叶际及种带微生物群落组成与多样性的调控作用。随着分子生物学和高通量测序技术的快速发展,关于内生真菌介导微生物群落结构与功能变化的研究取得了显著进展。作为冷季型禾草的重要共生体,其发挥的作用已超越对宿主植物的生长促进或抗逆作用,表现出在宿主-微生物-环境互作网络中的核心调控作用。

内生真菌可通过调控宿主生理结构与代谢过程,影响微生物群落的组装与传播,从而形成复杂的生态互作网络。这种网络不仅对宿主当代的生长发育、环境适应及抗逆性具有重要影响,还可通过种子垂直传播调节后代植物的微生物定殖与生态适应性。潜在机制包括改善宿主水分利用效率、调控根系分泌物、影响叶片次生代谢产物及改变土壤理化性质,从而选择性地促进或抑制特定微生物类群,同时普遍降低病原菌丰度和菌根侵染率。然而,内生真菌在不同发育阶段的菌丝动态、代谢产物变化及其对宿主微生物群落组成、功能潜力和代谢网络的具体影响,仍缺乏系统性和定量研究。未来应在多时空尺度上,结合多组学手段与生态网络分析,进一步阐明内生真菌在微生物群落组装及宿主生态适应中的作用机制。

在应用前景方面,我国已有人工接种该类真菌获得禾草新种质的初步进展,例如将来自野生大麦(*H. brevisubulatum*)的内生真菌(*E. bromicola*)引入栽培大麦获得抗性新种质[119]。并持续采集、鉴定和发掘具有潜在应用价值的优良内生真菌菌株,如从德兰臭草中分离获得了对多种病原真菌有抑制作用的*E. guerinii* SC012。

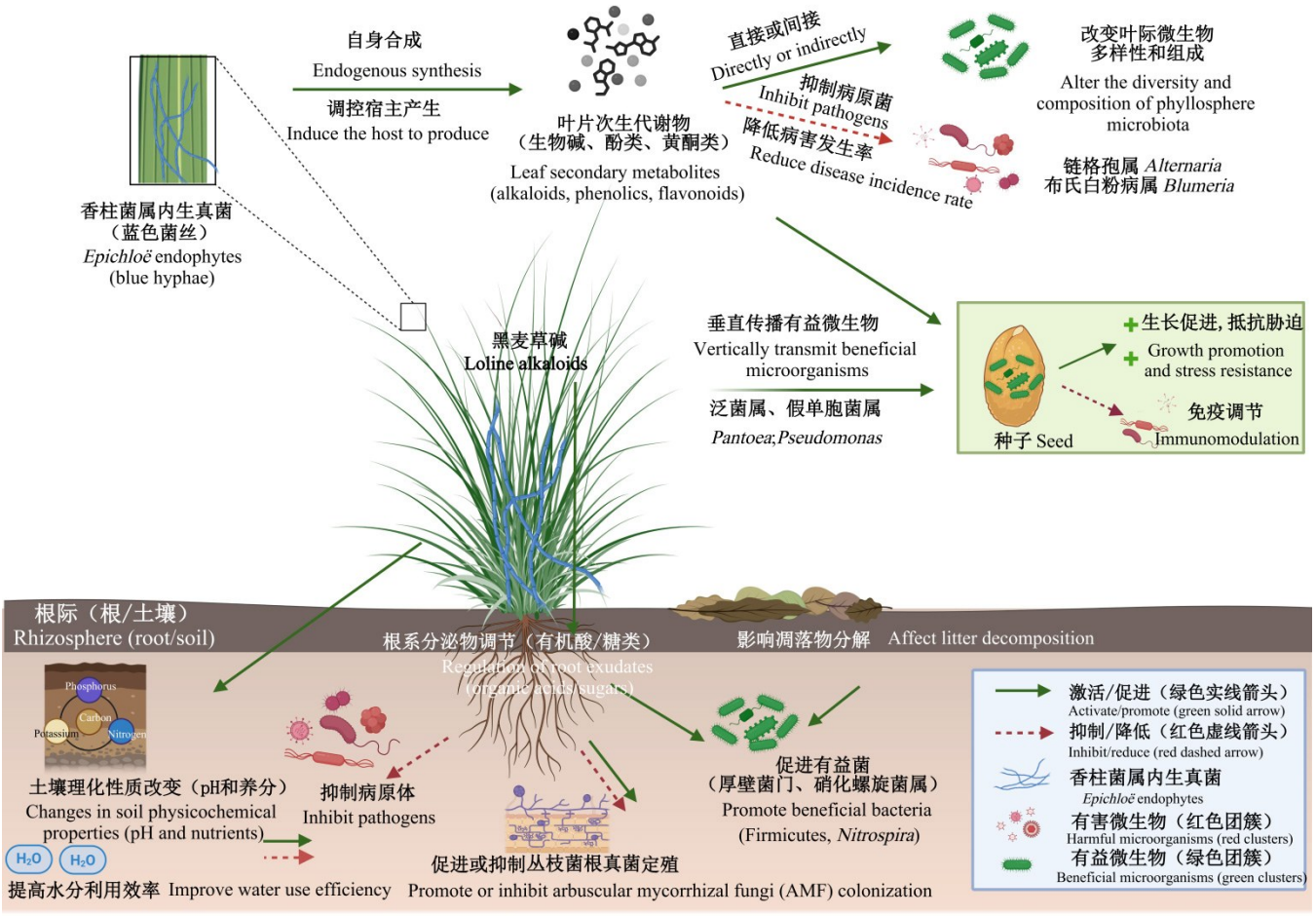


图 2　香柱菌属内生真菌与宿主相关微生物的互作机制

Fig. 2　Interaction mechanisms between *Epichloë* endophytes and host-associated microorganisms

然而，人工接种的成功率和稳定性仍受宿主特性与环境条件限制，菌丝长期定殖及垂直传播规律尚不明确，这在一定程度上限制了其大规模推广应用。此外，单一内生真菌在宿主抗性或适应性方面的作用存在一定的局限性。自然环境中，植物根际和地上组织通常存在复杂的微生物群落，多种微生物通过互作共同影响着宿主生长和抗逆性。因此，未来在抗逆育种及应用推广中，应关注多种有益微生物的组合应用，探索内生真菌与其他功能性微生物（如丛枝菌根真菌、促生细菌等）的协同效应，以提高宿主－微生物体系在田间环境下的稳定性和生态功能，推动可持续的微生物辅助育种策略的实现。

总体而言，内生真菌在禾草微生物群落调控及生态功能中发挥着核心作用。未来研究应在多组学与生态模型框架下，系统解析其对宿主微生物组动态、植物表型及环境适应性的定量调控机制。这不仅有助于深入理解共生体系的生态功能，也为培育高抗逆性、高产量及优良品质的禾草品种提供科学依据。

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