李子正,张蕾蕾,褚鹏飞,等. 球孢白僵菌植物内生性及其应用特性研究进展[J]. 江苏农业科学,2022,50(10):1-8.
doi:10.15889/j.issn.1002-1302.2022.10.001

球孢白僵菌植物内生性及其应用特性研究进展

李子正,张蕾蕾,褚鹏飞,杨　婧,华学文,郭尚敬,刘婷婷,姜会岭
(聊城大学农学院,山东聊城 252000)

摘要:球孢白僵菌(*Beauveria bassiana*)是一种广泛应用于农林业害虫防治的昆虫病原真菌,亦有研究证实其对某些植物病原菌存在拮抗作用,是一种双重生防真菌。最新研究表明,球孢白僵菌还可以在自然条件下或通过人工接种定殖于植物体内,其显著的病虫害防治效果和较长的内生持续期为高效生物防治研究提供了新思路。此外,诸多研究表明内生球孢白僵菌可通过以提高植物对营养物质的吸收或引起相关激素的变化促进植物生长、增强植物在生物和非生物胁迫下的抗逆性,还可以与其他有益微生物协作对植物生长与抵御病虫害过程产生积极影响。基于国际最新研究成果,在综述球孢白僵菌内生性生物学机制基础上,总结其作为双重生防真菌在病虫害防治以及促进植物生长中的作用机制,探讨内生球孢白僵菌-其他内生菌-植物之间的互作效应,以期为利用昆虫病原真菌内生特性所展开的深入研究和应用提供理论参考。

关键词:球孢白僵菌;内生性;双重生防真菌;促生性;抗逆性
中图分类号:S476.12　　**文献标志码:** A　　**文章编号:**1002-1302(2022)10-0001-08

目前已探明的能够感染昆虫且致死的虫生真菌种类高达 750 多种[1]。在害虫综合治理(IPM)中利用昆虫病原真菌,不仅能够减轻害虫的危害程度,还可以极大地降低害虫耐药性的风险,保持田间生态系统长久的稳定性,使害虫数量维持在环境可持续发展的阈值下。越来越多的昆虫病原真菌,如球孢白僵菌(*Beauveria bassiana*)[2-6]、金龟子绿僵菌(*Metarhizium anisopliae*)[7-10]、淡紫拟青霉(*Paecilomyces lilacinus*)[5,11]等广泛应用于农田、温室等害虫防治中。研究表明,昆虫病原真菌在寄生虫体的同时可以通过人工接种或在自然条件下作为内生菌在植物体内生长[12-15],进一步提高植食性害虫的死亡率[12],并对植物生长具有积极作用[5,16-17],相关研究拓宽了内生昆虫病原真菌与植物间互作的视野。

球孢白僵菌是一种广泛应用于农林业害虫生物防治的丝孢类昆虫病原真菌,可寄生包括棉铃虫、小菜蛾、马尾松毛虫等咀嚼式口器害虫,以及白粉虱、蚜虫等刺吸式口器害虫在内的 700 多种昆虫[18],寄主范围广泛。同时,球孢白僵菌还具有易于培养、利于规模化生产和杀虫效果显著等优势,因此相关制剂广泛应用于商业化生产,被公认为是最有应用前景的化学杀虫剂替代品之一[19],但其施用效果尚受紫外线、雨水、温度等非生物因素的制约[20],亟需进一步研究完善施用方法,降低环境的影响。近年来有研究表明,可将球孢白僵菌人工接种至寄主植物中,且接种成功一次即能够使植物长期带菌,在整个生活史中发挥防治虫害的作用,为提升害虫综合治理效果提供了新思路[21-23]。

诸多研究表明,球孢白僵菌作为一种双重生防真菌,其在植物体内的定殖不仅能够有效防治害虫,还能提高植物的抗病性[15],此外,它还具有促进植物生长[24-27]、提高植物对非生物胁迫的耐受性[28-29]的作用。本文基于前人关于球孢白僵菌在植物中内生化的最新研究成果,总结其内生特性在生物防治及植物生长过程中的积极作用,探讨内生球孢白僵菌-其他有益微生物-植物之间的互作效应,以期为利用昆虫病原真菌内生特性所展开的深入研究和应用提供理论参考。

收稿日期:2021-11-02
基金项目:山东省农业科技园区产业提升工程项目(编号:2019YQ037);山东省自然科学基金(编号:ZR2018LC016);国家重点研发计划(编号:2017YFD0301003);国家自然科学基金(编号:32001929)。
作者简介:李子正(1998—),男,山东潍坊人,硕士研究生,主要从事作物栽培与耕作学研究。E-mail:247532857@qq.com。
通信作者:褚鹏飞,博士,副教授,主要从事作物高产生理生态研究。E-mail:chupengfei@lcu.edu.cn。

1　球孢白僵菌的植物内生性

球孢白僵菌内生性的研究始于 1992 年 Bing 等首次通过叶面喷施和茎部注射 2 种方式将球孢白僵菌孢悬浮液接种至 V7 期玉米植株内，并成功观测到选择性培养基上成熟期玉米各组织内白僵菌的生长[2]。Wagner 等利用光学和电子显微镜首次观察到球孢白僵菌分生孢子萌发的菌丝透过玉米叶表面进入植株内部及其在植物中的传播过程[30]。Chambers 等利用扫描电镜和分子生物学技术确认了球孢白僵菌在番茄植株中的定殖，为进一步确定其内生性提供了便捷方法[31]。Landa 等利用两步巢式 PCR(two - step nested specific - PCR)和 RT - qPCR 等分子生物学新技术检测到罂粟植株内球孢白僵菌的存在，并对其在各组织内的定殖进行了定量研究[32]。Landa 等分别利用共聚焦显微镜(CLSM)明确了已转入绿色荧光蛋白(GFP)的球孢白僵菌在罂粟、菜豆等植物组织内的分布特征[32-33]，为进一步探索内生菌在植物不同组织的定殖特点提供了技术支持。

研究表明，利用叶面喷施[27,32-35]、灌根[7,24-25]、浸种[24-25,36]、茎部注射[2,37-38]、根茎浸泡[3,39-41]等多种人工接种方式都可成功地将球孢白僵菌定殖于罂粟[32]、可可[42]、咖啡[21]、小麦、芸豆、南瓜[27]、葡萄[33]、大豆、烟草[43]、枣椰树[39]、黄瓜[36]、木薯[44]、花椰菜[45]、白黄麻[3]、山核桃树[4]等多种植物体内。Jaber 等利用球孢白僵菌孢子悬浮液对蚕豆进行浸种处理后发现，在接种 14、28 d 后不同器官内均有球孢白僵菌的存在[17]。Sánchez - Rodríguez 等在小麦上的研究亦得出相似结果，证明球孢白僵菌作为植物内生菌可以从接种部位扩散至植株各组织并长期存活[24]。更多研究显示，球孢白僵菌成功定殖后的内共生过程可在黄麻中持续 3 个月[22]，在咖啡中持续 8 个月[21]，在辐射松中持续 9 个月[23]。

2　植物内生球孢白僵菌在害虫管理上的作用

球孢白僵菌最早作为高效的生防杀虫菌剂被广泛应用，其定殖对植食性害虫的影响已成为植物内生菌研究的热点之一[46]。与传统化学杀虫剂相比，球孢白僵菌在杀死植食性害虫时，对常见传粉性昆虫以及天敌昆虫等非靶标昆虫危害微小[47-51]，更利于保护农田生态环境、维持农田生态系统稳定发展。内生球孢白僵菌通过产生细胞毒素、白僵菌素等次生代谢物直接或间接对害虫产生负面影响，常导致害虫发育迟缓[27,52-53]、抑制昆虫食物消耗率[12,54]、降低幼虫存活率[10,55]和成虫的产卵率[10,27,56]等。

Bing 等通过叶面喷施和茎部注射的方式向玉米植株接种球孢白僵菌孢悬浮液，显著降低了欧洲玉米螟的危害，首次证明内生球孢白僵菌的杀虫作用[2]。其后，Lopez 等研究发现，浸种处理后的棉花植株能够有效降低棉蚜危害，并能显著抑制棉蚜的繁殖[5]。Biswas 等的研究表明，茎象甲虫对接种球孢白僵菌 ITCC5408 和 ITCC6063 菌株的黄麻植株的危害株数从未接种组的 35.44% 分别大幅降至 10.44%、14.06%[3]。Toffa 等使用 B15 菌株进行种子包衣处理后显著抑制了棉铃虫对番茄叶片的危害，且显著降低了棉铃虫的平均存活时间[6]。Mwamburi 采用灌根的方式将球孢白僵菌 BbC1 菌株定殖于番茄植株体内，显著降低了草地贪夜蛾幼虫的体质量，有效减小了其对叶片的危害[7]。Ramakuwela 等的研究表明，山核桃害虫取食接种球孢白僵菌的叶片后死亡率显著升高[4]。此外，内生球孢白僵菌还显著提高了番茄上番茄潜叶蝇的死亡率[57]，增强了烟草对桃蚜的耐受性[58]，降低了大豆荚虫在大豆上的繁殖力[59]，减小了葡萄叶蝉对葡萄叶片的危害[60]，抑制了蝗虫对玉米植株的取食[61]等。

为提高害虫综合治理的高效性，研究人员在保护生态环境的前提下对植物内生球孢白僵菌与其他生物防治方法的结合展开了一系列探索，如与捕食性昆虫或寄生性昆虫相结合双重防治害虫[49-51]。Jaber 等通过研究内生昆虫病原真菌 - 害虫 - 天敌昆虫三者间的关系发现，内生性球孢白僵菌显著减小了桃蚜对甜椒损害的同时不会对天敌昆虫科列马·阿布拉小蜂(*Aphidius colemani*)造成负面影响[49]。González - Mas 等利用孢悬液喷施处理甜瓜植株后针对叶片上的蚜虫进行天敌昆虫选择性取食性测试，结果表明草蛉更趋于捕食经球孢白僵菌处理后的甜瓜上的蚜虫，且茧蜂在蚜虫上的寄生产卵行为未受显著影响[50]。表明内生球孢白僵菌防治害虫对天敌昆虫不仅未造成负面影响，还可能与其存在协作效应，进而提高防治效果，对农田生态系统的稳定具有积极意义。

3　植物内生球孢白僵菌对植物病害的生防潜力

利用有益微生物降低病原体在组织内的扩繁率[15,62]是目前植物病害生物防治的有效途径之一。有研究发现，内生昆虫病原真菌在防治害虫的同时，还可以通过寄生、竞争、拮抗、诱导植物系统性抗性等方式直接或间接地抵御、减轻病原体对植物造成的危害[5]，其功能类似于木霉菌、枯草芽孢杆菌等“植物疫苗”。内生球孢白僵菌可以通过竞争感染部位的碳、氮等多种养分抑制植物病原体的扩繁，这种竞争常发生在根际、叶片或细胞间[5]，但会受温湿度[63]等多种因素的影响。

Ownley 等利用孢子悬浮液进行种子包衣处理使球孢白僵菌 11 – 98 菌株在番茄和棉花植株组织内定殖，显著增强了寄主植物对立枯丝核菌（*Rhizoctonia solani*）、群结腐霉菌（*Pythium myriotylum*）和细菌性叶枯病病菌（*Xanthomonas axonopodis*）的抵御能力，提高了幼苗的存活率，促进了含病菌土壤中棉花幼苗株高的增加[64–65]。Jaber 等研究发现，叶面喷施白僵菌孢悬液后显著降低了西葫芦黄花叶病毒（zucchini yellow mosaic virus，ZYMV）对南瓜叶片的危害[66]；次年用相同方式对葡萄植株进行处理的结果表明，内生球孢白僵菌也可以显著降低霜霉病病菌（*Plasmopara viticola*）引起的葡萄霜霉病在葡萄藤上的发病率及危害程度[34]。Dara 等的研究表明，接种球孢白僵菌显著提高了棉花在含枯萎病病菌（*Fusarium oxysporum* f. sp. *vasinfectum*）土壤上的存活率，并显著促进了植株的生长[67]。Dara 等分别利用球孢白僵菌和绿僵菌处理草莓，均显著降低了炭腐病病菌（*Macrophomina phaseolina*）的危害，改善了植株的生长状况[68]。Barra – Bucarei 等对辣椒、番茄进行浸根处理后发现，球孢白僵菌 RGM547 和 RGM644 菌株成功定殖于植株组织内并对灰霉病病菌（*Botrytis cinerea*）产生显著拮抗作用[69]。Jaber 研究发现，球孢白僵菌处理种子后显著提高了小麦根长、鲜质量等生长参数，并有效抑制了小麦冠腐根腐病（CRR）的发病率[37]。

诸多针对不同植物的研究均已证明，球孢白僵菌作为内生真菌能够降低病原体对寄主植物的危害，但其内在机制仍未详解，综合分析前人的研究结果，后续研究可从以下 3 个方面进行深入探索：其一，内生球孢白僵菌通过竞争、产生抗生素等次生代谢物直接抑制病原体发展[15,62,70]；其二，通过激活茉莉酸（JA）、乙烯（ET）途径从而使植物产生植物诱导性系统抗性（ISR）以及触发水杨酸（SA）途径来激活系统获得抗性（SAR），致使植物自身产生次生代谢产物和免疫化合物以及诱导相关氧化酶的产生，从而间接帮助植物抵御病原体侵害[62,70–71]；其三，促进植物生长，提高植物自身免疫力[39,62,66,72]。

4　植物内生球孢白僵菌对寄主植物的促生作用

存在于土壤中的球孢白僵菌等昆虫病原真菌可以促进土壤微生物群中的有益微生物竞争性地取代有害微生物，改善土壤结构，优化土层中的养分物质以利于植物吸收利用[71]。球孢白僵菌通过土壤施用等多种接种方式定殖于植物体不同组织时，会以一种或多种方式使植物受益。Gurulingappa 等利用孢悬液叶面喷施处理后的小麦植株地上、地下部分干质量均显著高于未处理组，有利于小麦的干物质积累[27]。Afandhi 等研究发现，叶面喷施和灌根处理后的菜豆植株在接种 20 d 后根长显著增加，促进了根系的延伸，有利于植株对土壤水分和养分的吸收[25]。Lopez 等研究发现，经球孢白僵菌孢悬液浸种处理的陆地棉，其生物量、株高、营养生长阶段开花数量均显著增加[26]。Dash 等通过球孢白僵菌 B13 菌株对绿豆进行种子处理，植株株高、地上和地下部鲜质量显著高于对照组[73]。Raya – Díaz 等通过土壤处理的方式，发现内生球孢白僵菌和绿僵菌能够在钙质基质条件下显著促进高粱对铁（Fe）的吸收，进而提高叶片光合能力、促进根系生长，最终提高产量[74]。Sánchez – Rodríguez 等利用球孢白僵菌孢子悬浮液接种硬粒小麦，与对照相比，灌根处理植株的磷（P）、铁（Fe）、镁（Mg）、钾（K）含量分别提高了 17.86%、19.44%、22.22%、21.43%，而叶面喷施处理分别提高了 14.29%、14.29%、22.22%、42.86%；拌种处理后的面包小麦的籽粒产量和根长分别均约提高了 40%[24]。Moloinyane 等对盆栽葡萄植株进行球孢白僵菌孢悬液处理后，叶片中的钙（Ca）、Mg 含量显著增加[75]。Macuphe 等的研究表明，内生球孢白僵菌定殖显著增加了生菜锰（Mn）、Fe、铜（Cu）和硼（B）等微量元素的含量，促进地上部分生长，提高了产量[76]。Dara 等在模拟干旱条件下卷心菜的生长情况时发现，经球孢白僵菌处理后卷心菜的存活率、株高、根

冠比和生物量均显著增加，对氮（N）、P、K 养分的吸收亦相应提高[77]。

内生球孢白僵菌对寄主植物的促生作用已在多种植物中得到验证，但其促生机制仍存在争议。有研究表明，内生球孢白僵菌通过增加寄主植物对 N、P、K 等营养元素的吸收参与植物的能量代谢、提高光合产物的积累与转运、促进根系对水分的获取并维持高水分利用效率，从而促进植物地上、地下部分的生长[39,75-77]；亦有学者认为，它与其他具有促生作用的真菌相似，通过产生次生代谢物（如黄酮类、类固醇、吲哚-3-乙酸等）刺激植物生长[78-80]；还有研究示出，它可以增加如吲哚乙酸（IAA）、赤霉素（GAs）等植物体内促生激素的含量，减少乙烯的含量以促进植物生长[81-82]。

虽然内生球孢白僵菌能够在很大程度上促进植物生长，但仍不能忽略环境因子对这一过程的影响。Tall 等研究发现，高营养条件下玉米植株内球孢白僵菌的定殖率升高，同时植株生长也得到提高，表明土壤肥力对微生物发展和植物生长发育均具有重要的调控作用[83]。此外，Heinz 等利用多种昆虫病原真菌菌株进行种子处理，发现仅球孢白僵菌能够显著缩短种子的发芽时间、提高发芽率，表明昆虫病原真菌作为内生菌对植物生长过程的调控可能受特定真菌与植物的特异性结合影响[84]。因此，球孢白僵菌对植物的促生效果，应从菌株特性、施用条件、土壤特性等多方面进行更加深入的探讨。

5　植物内生球孢白僵菌对植物非生物胁迫抗性的诱导作用

球孢白僵菌等内生真菌不仅能够提高植物对害虫和病原体的抵御能力，同时还可以增强植物对高温、干旱、盐碱等非生物胁迫的耐受性[85]。Kuzhuppillymya-Prabhakarankutty 等利用不同球孢白僵菌菌株的孢子悬浮液对玉米种子进行处理，发现在断水模拟干旱处理 10 d 后，处理组玉米幼苗活力的恢复率显著增加，证明内生球孢白僵菌可诱导植物提高抗旱能力[28]。Ferus 等研究发现，在干旱胁迫下，接种球孢白僵菌的红橡树苗叶片相对含水量和气孔导度降低速率减缓，并且利用回归分析得出严重干旱胁迫下接种球孢白僵菌的红橡树苗较对照组显著促进了根系生长、提高了水分利用效率[29]。Dara 等研究指出，内生性球孢白僵菌可以通过影响根冠比来维持植物在缺水条件下的稳定生长[77]。内生球孢白僵菌对植物在非生物胁迫的影响多集中于抗旱生理研究领域，与其他内生真菌相比研究范围较窄。目前，关于非生物胁迫条件下植物内生球孢白僵菌是否像淡紫拟青霉[86]、长枝木霉菌（*Trichoderma longibrachiatum*）[87]等其他内生真菌一样增强寄主植物在冷害、盐碱等不同非生物胁迫下的耐受性还有待进一步研究。

6　植物内生球孢白僵菌与其他内生菌的协作

有研究表明，内生菌之间存在协作效应，可增加作用方式的多样性并提高对病虫害的防治效果，同时还能够促进植物生长[88-93]。Karthiba 等将荧光假单胞菌（*Pseudomonas fluorescens*）Pf1 和 AH1 菌株与球孢白僵菌 B2 菌株混合使用，通过灌根和叶面喷施 2 种接种方式分别在播种后 25、30 d 处理水稻幼苗，均显著降低了水稻纹枯病的发病率，减轻了稻纵卷叶螟幼虫的危害，且处理后的植株几丁质酶、脂氧合酶、过氧化物酶、多酚氧化酶等防御酶活性显著增强[88]。Senthilraja 等研究发现，采用荧光假单胞菌 TDK1、Pf1 菌株与球孢白僵菌 B2 菌株结合防治花生潜夜蛾和腐烂病具有显著效果[89]。Shrivastava 等将丛枝菌根真菌与球孢白僵菌混合定殖于番茄植株，显著增加了植株内萜类化合物的含量，降低了甜菜夜蛾对叶片的危害[90]。Batool 等采用种子包衣和土壤浸湿 2 种方式，使用不同混合比例的球孢白僵菌与棘孢木霉（*Trichoderma asperellum*）处理玉米植株，通过扫描电镜在玉米组织内观察到了 2 种真菌的定殖，并明确了 2 种内生菌协同作用增加了植株蛋白酶，如超氧化物歧化酶、过氧化物酶、多酚氧化酶活性和脯氨酸含量以介导植物防御系统，显著减少了亚洲玉米螟的危害，增加了幼虫的死亡率[91]。Farias 等使用球孢白僵菌与其他 4 种生防真菌的混合孢子悬浮液对甘蔗、玉米和大豆分别进行浸种与叶片喷施处理，显著增加了玉米、大豆根系鲜质量和大豆根系干质量，但甘蔗的各生长指标与对照无显著差异[92]。Prabhukarthikeyan 等利用球孢白僵菌菌株 B2 和枯草芽孢杆菌（*Bacillus subtilis*）菌株 EPC8 混合后对番茄植株进行处理，不仅显著提高了株高、叶片数、结实数、产量等生长相关指标，而且还显著降低了棉铃虫的危害和枯萎病的发病率[93]。

7 展望

近年来,植物内生球孢白僵菌应用潜力研究已逐渐成为植物 - 微生物互作研究领域的新热点,人工接种定殖的内生球孢白僵菌不仅对植物害虫和病原体具有良好的持续抑制效果,其对寄主植物的促生作用和抗逆诱导作用的发现为丰富高产、优质、高效、可持续发展的农作物栽培措施和生物防治方案提供了新的思路。目前,采用人工接种定殖的方式利用内生球孢白僵菌综合防治病虫害在实际生产中的推广应用仍受诸多因素制约。首先,不同接种方式对球孢白僵菌在植物体内的定殖效果和作用发挥存在显著影响[46,53],应进一步明确其内在机制并探索出更加简便、高效的接种方法;其次,目前可推广应用的菌株较少,应有针对性地选育活性高、对害虫毒力高、定殖成功率高、综合防治持续期长的优良内生球孢白僵菌菌株;此外,还需要进一步探明胁迫条件下内生真菌基因型与植物基因型间相互作用的内在机制,为利用共生微生物提升植物防御系统的新路径提供理论依据。

虽然前人已从不同角度对内生球孢白僵菌促进植物生长的生物学基础进行了较多研究[24-27,73-77],并对其在生物和非生物胁迫下诱导植株抗性的生理机制以及与其他有益微生物的互作效应进行了初步探索[28-29,39,52-56,70-72,77,88-93],但其实际应用仍需开展诸多深入探索。未来,应利用分子生物学、微生物组学、蛋白质组学、生理学以及生态学等多学科工具对内生真菌 - 植物 - 病虫害三者相互关系的内在机制进行更加系统深入的研究,进一步阐明内生昆虫病原真菌的作用机制,提升病虫害综合治理水平,推动农业可持续发展。

参考文献:

[1] Barelli L, Moonjely S, Behie S W, et al. Fungi with multifunctional lifestyles: endophytic insect pathogenic fungi[J]. Plant Molecular Biology, 2016, 90(6): 657 - 664.

[2] Bing L A, Lewis L C. Temporal relationships between *Zea mays*, *Ostrinia nubilalis* (Lep.: Pyralidae) and endophytic *Beauveria bassiana*[J]. Entomophaga, 1992, 37(4): 525 - 536.

[3] Biswas C, Dey P, Satpathy S, et al. Endophytic colonization of white jute (*Corchorus capsularis*) plants by different *Beauveria bassiana* strains for managing stem weevil (*Apion corchori*) [J]. Phytoparasitica, 2013, 41(1): 17 - 21.

[4] Ramakuwela T, Hatting J, Bock C, et al. Establishment of *Beauveria bassiana* as a fungal endophyte in pecan (*Carya illinoinensis*) seedlings and its virulence against pecan insect pests[J]. Biological Control, 2020, 140: 104102.

[5] Lopez D C, Zhu - Salzman K, Ek - Ramos M J, et al. The entomopathogenic fungal endophytes *Purpureocillium lilacinum* (formerly *Paecilomyces lilacinus*) and *Beauveria bassiana* negatively affect cotton aphid reproduction under both greenhouse and field conditions[J]. PLoS One, 2014, 9(8): e103891.

[6] Toffa J, Loko Y L E, Kpindou O K D, et al. Endophytic colonization of tomato plants by *Beauveria bassiana* Vuillemin (Ascomycota: Hypocreales) and leaf damage in *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) larvae[J]. Egyptian Journal of Biological Pest Control, 2021, 31: 82.

[7] Mwamburi L A. Endophytic fungi, *Beauveria bassiana* and *Metarhizium anisopliae*, confer control of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), in two tomato varieties[J]. Egyptian Journal of Biological Pest Control, 2021, 31: 7.

[8] Mantzoukas S, Lagogiannis I. Endophytic colonization of pepper (*Capsicum annum*) controls aphids (*Myzus persicae* Sulzer)[J]. Applied Sciences, 2019, 9(11): 2239.

[9] Russo M L, Jaber L R, Scorsetti A C, et al. Effect of entomopathogenic fungi introduced as corn endophytes on the development, reproduction, and food preference of the invasive fall armyworm *Spodoptera frugiperda*[J]. Journal of Pest Science, 2021, 94(3): 859 - 870.

[10] Akello J, Sikora R. Systemic acropedal influence of endophyte seed treatment on *Acyrthosiphon pisum* and *Aphis fabae* offspring development and reproductive fitness[J]. Biological Control, 2012, 61(3): 215 - 221.

[11] Kepenekci I, Oksal E, Saglam H D, et al. Identification of Turkish isolate of the entomopathogenic fungi, *Purpureocillium lilacinum* (syn: *Paecilomyces lilacinus*) and its effect on potato pests, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) and *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae)[J]. Egyptian Journal of Biological Pest Control, 2015, 25(1): 121 - 127.

[12] Vega F E. Insect pathology and fungal endophytes[J]. Journal of Invertebrate Pathology, 2008, 98(3): 277 - 279.

[13] Vidal S, Jaber L R. Entomopathogenic fungi as endophytes: plant - endophyte - herbivore interactions and prospects for use in biological control[J]. Current Science, 2015, 109: 46 - 54.

[14] Card S, Johnson L, Teasdale S, et al. Deciphering endophyte behaviour: the link between endophyte biology and efficacious biological control agents[J]. FEMS Microbiology Ecology, 2016, 92(8): fiw114.

[15] Ownley B H, Gwinn K D, Vega F E. Endophytic fungal entomopathogens with activity against plant pathogens: ecology and evolution[J]. BioControl, 2010, 55(1): 113 - 128.

[16] Liao X G, O'Brien T R, Fang W G, et al. The plant beneficial effects of *Metarhizium* species correlate with their association with roots [J]. Applied Microbiology and Biotechnology, 2014, 98(16):

7089 – 7096.

[17] Jaber L R, Enkerli J. Effect of seed treatment duration on growth and colonization of *Vicia faba* by endophytic *Beauveria bassiana* and *Metarhizium brunneum*[J]. Biological Control, 2016, 103: 187 – 195.

[18] Inglis G D, Goettel M S, Butt T M, et al. Use of hyphomycetous fungi for managing insect pests[M]//Butt T M, Jackson C W, Magan N. Fungi as biocontrol agents: progress, problems and potential. Wallingford, UK: CABI Publishing, 2001: 23 – 55.

[19] de Faria M R, Wraight S P. Mycoinsecticides and mycoacaricides: a comprehensive list with worldwide coverage and international classification of formulation types[J]. Biological Control, 2007, 43(3): 237 – 256.

[20] Zhang Y J, Zhao J H, Fang W G, et al. Mitogen – activated protein kinase hog1 in the entomopathogenic fungus *Beauveria bassiana* regulates environmental stress responses and virulence to insects[J]. Applied and Environmental Microbiology, 2009, 75(11): 3787 – 3795.

[21] Posada F, Vega F E. Inoculation and colonization of coffee seedlings (*Coffea arabica* L.) with the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales)[J]. Mycoscience, 2006, 47(5): 284 – 289.

[22] Biswas C, Dey P, Satpathy S, et al. Establishment of the fungal entomopathogen *Beauveria bassiana* as a season long endophyte in jute (*Corchorus olitorius*) and its rapid detection using SCAR marker[J]. BioControl, 2012, 57(4): 565 – 571.

[23] Brownbridge M, Reay S D, Nelson T L, et al. Persistence of *Beauveria bassiana* (Ascomycota: Hypocreales) as an endophyte following inoculation of radiata pine seed and seedlings[J]. Biological Control, 2012, 61(3): 194 – 200.

[24] Sánchez – Rodríguez A R, Raya – Díaz S, Zamarreño Á M, et al. An endophytic *Beauveria bassiana* strain increases spike production in bread and durum wheat plants and effectively controls cotton leafworm (*Spodoptera littoralis*) larvae[J]. Biological Control, 2018, 116: 90 – 102.

[25] Afandhi A, Widjayanti T, Emi A A L, et al. Endophytic fungi *Beauveria bassiana* Balsamo accelerates growth of common bean (*Phaeseolus vulgaris* L.)[J]. Chemical and Biological Technologies in Agriculture, 2019, 6(1): 11.

[26] Lopez D C, Sword G A. The endophytic fungal entomopathogens *Beauveria bassiana* and *Purpureocillium lilacinum* enhance the growth of cultivated cotton (*Gossypium hirsutum*) and negatively affect survival of the cotton bollworm (*Helicoverpa zea*)[J]. Biological Control, 2015, 89: 53 – 60.

[27] Gurulingappa P, Sword G A, Murdoch G, et al. Colonization of crop plants by fungal entomopathogens and their effects on two insect pests when *in planta*[J]. Biological Control, 2010, 55(1): 34 – 41.

[28] Kuzhuppillymyal – Prabhakarankutty L, Tamez – Guerra P, Gomez – Flores R, et al. Endophytic *Beauveria bassiana* promotes drought tolerance and early flowering in corn[J]. World Journal of Microbiology & Biotechnology, 2020, 36(3): 47.

[29] Ferus P, Barta M, Konôpková J. Endophytic fungus *Beauveria bassiana* can enhance drought tolerance in red oak seedlings[J]. Trees, 2019, 33(4): 1179 – 1186.

[30] Wagner B L, Lewis L C. Colonization of corn, *Zea mays*, by the entomopathogenic fungus *Beauveria bassiana*[J]. Applied and Environmental Microbiology, 2000, 66(8): 3468 – 3473.

[31] Chambers A, Geary B, Black S, et al. Confirmation of artificial endophyte inoculation in maize (*Zea mays*) and tomato (*Lycopersicon esculentum*) by scanning electron microscopy and PCR amplification of ITS sequences[J]. Phytopathology, 2007, 97(7): S19.

[32] Landa B B, López – Díaz C, Jiménez – Fernández D, et al. *In – planta* detection and monitorization of endophytic colonization by a *Beauveria bassiana* strain using a new – developed nested and quantitative PCR – based assay and confocal laser scanning microscopy[J]. Journal of Invertebrate Pathology, 2013, 114(2): 128 – 138.

[33] Behie S W, Jones S J, Bidochka M J. Plant tissue localization of the endophytic insect pathogenic fungi *Metarhizium* and *Beauveria*[J]. Fungal Ecology, 2015, 13: 112 – 119.

[34] Jaber L R. Grapevine leaf tissue colonization by the fungal entomopathogen *Beauveria bassiana* s. l. and its effect against downy mildew[J]. BioControl, 2015, 60(1): 103 – 112.

[35] Reddy N P, Ali Khan A P, Devi U K, et al. Treatment of millet crop plant (*Sorghum bicolor*) with the entomopathogenic fungus (*Beauveria bassiana*) to combat infestation by the stem borer, *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae)[J]. Journal of Asia – Pacific Entomology, 2009, 12(4): 221 – 226.

[36] Rajab L, Ahmad M, Gazal I. Endophytic establishment of the fungal entomopathogen, *Beauveria bassiana* (Bals.) Vuil., in cucumber plants[J]. Egyptian Journal of Biological Pest Control, 2020, 30(1): 143.

[37] Jaber L R. Seed inoculation with endophytic fungal entomopathogens promotes plant growth and reduces crown and root rot (CRR) caused by *Fusarium culmorum* in wheat[J]. Planta, 2018, 248(6): 1525 – 1535.

[38] Quesada – Moraga E, Landa B B, Muñoz – Ledesma J, et al. Endophytic colonisation of opium poppy, *Papaver somniferum*, by an entomopathogenic *Beauveria bassiana* strain[J]. Mycopathologia, 2006, 161(5): 323 – 329.

[39] Gómez – Vidal S, Salinas J, Tena M, et al. Proteomic analysis of date palm (*Phoenix dactylifera* L.) responses to endophytic colonization by entomopathogenic fungi[J]. Electrophoresis, 2009, 30(17): 2996 – 3005.

[40] Akello J, Dubois T, Coyne D, et al. The effects of *Beauveria bassiana* dose and exposure duration on colonization and growth of tissue cultured banana (*Musa* sp.) plants[J]. Biological Control, 2009, 49(1): 6 – 10.

[41] Muvea A M, Meyhöfer R, Subramanian S, et al. Colonization of onions by endophytic fungi and their impacts on the biology of *Thrips*

tabaci[J]. PLoS One,2014,9(9):e108242.

[42] Posada F,Vega F E. Establishment of the fungal entomopathogen *Beauveria bassiana* (Ascomycota:Hypocreales) as an endophyte in cocoa seedlings (*Theobroma cacao*)[J]. Mycologia,2005,97(6):1195 – 1200.

[43] Russo M L,Pelizza S A,Cabello M N,et al. Endophytic colonisation of tobacco,corn,wheat and soybeans by the fungal entomopathogen *Beauveria bassiana* (Ascomycota, Hypocreales)[J]. Biocontrol Science and Technology,2015,25(4):475 – 480.

[44] Greenfield M,Gómez – Jiménez M I,Ortiz V,et al. *Beauveria bassiana* and *Metarhizium anisopliae* endophytically colonize cassava roots following soil drench inoculation[J]. Biological Control,2016,95:40 – 48.

[45] Gautam S,Mohankumar S,Kennedy J S. Induced host plant resistance in cauliflower by *Beauveria bassiana*[J]. Journal of Entomology and Zoology Studies,2016,4(2):476 – 482.

[46] Mantzoukas S,Eliopoulos P A. Endophytic entomopathogenic fungi:a valuable biological control tool against plant pests[J]. Applied Sciences,2020,10(1):360.

[47] Akmal M,Freed S,Malik M N,et al. Efficacy of *Beauveria bassiana* (Deuteromycotina:Hypomycetes) against different aphid species under laboratory conditions[J]. Pakistan Journal of Zoology,2013,45(1):71 – 78.

[48] Bajya D R,Ranjith M,Raza S. Evaluation of *Beauveria bassiana* against chickpea pod borer,*Helicoverpa armigera* and its safety to natural enemies[J]. Indian Journal of Agricultural Sciences,2015,85(3):86 – 89.

[49] Jaber L R,Araj S E. Interactions among endophytic fungal entomopathogens (Ascomycota:Hypocreales),the green peach aphid *Myzus persicae* Sulzer (Homoptera:Aphididae),and the aphid endoparasitoid *Aphidius colemani* Viereck (Hymenoptera:Braconidae)[J]. Biological Control,2018,116:53 – 61.

[50] Gonzúlez – Mas N,Cuenca – Medina M,Gutiérrez – Súnchez F,et al. Bottom – up effects of endophytic *Beauveria bassiana* on multitrophic interactions between the cotton aphid,*Aphis gossypii*,and its natural enemies in melon[J]. Journal of Pest Science,2019,92(3):1271 – 1281.

[51] Canassa F,Tall S,Moral R A,et al. Effects of bean seed treatment by the entomopathogenic fungi *Metarhizium robertsii* and *Beauveria bassiana* on plant growth,spider mite populations and behavior of predatory mites[J]. Biological Control,2019,132:199 – 208.

[52] Dannon H F,Dannon A E,Douro – Kpindou O K,et al. Toward the efficient use of *Beauveria bassiana* in integrated cotton insect pest management[J]. Journal of Cotton Research,2020,3:24.

[53] McKinnon A C,Saari S,Moran – Diez M E,et al. *Beauveria bassiana* as an endophyte:a critical review on associated methodology and biocontrol potential[J]. BioControl,2017,62(1):1 – 17.

[54] Cherry A J,Banito A,Djegui D,et al. Suppression of the stem – borer *Sesamia calamistis* (Lepidoptera;Noctuidae) in maize following seed dressing,topical application and stem injection with African isolates of *Beauveria bassiana*[J]. International Journal of Pest Management,2004,50(1):67 – 73.

[55] Akutse K S,Maniania N K,Fiaboe K K M,et al. Endophytic colonization of *Vicia faba* and *Phaseolus vulgaris* (Fabaceae) by fungal pathogens and their effects on the life – history parameters of *Liriomyza huidobrensis* (Diptera:Agromyzidae)[J]. Fungal Ecology,2013,6(4):293 – 301.

[56] Bamisile B S,Dash C K,Akutse K S,et al. Endophytic *Beauveria bassiana* in foliar – treated *Citrus limon* plants acting as a growth suppressor to three successive generations of *Diaphorina citri* Kuwayama (Hemiptera:Liviidae)[J]. Insects,2019,10(6):176.

[57] Klieber J,Reineke A. The entomopathogen *Beauveria bassiana* has epiphytic and endophytic activity against the tomato leaf miner *Tuta absoluta*[J]. Journal of Applied Entomology,2016,140(8):580 – 589.

[58] Qin X,Zhao X,Huang S S,et al. Pest management via endophytic colonization of tobacco seedlings by the insect fungal pathogen *Beauveria bassiana*[J]. Pest Management Science,2021,77(4):2007 – 2018.

[59] Russo M L,Scorsetti A C,Vianna M F,et al. Effects of endophytic *Beauveria bassiana* (Ascomycota:Hypocreales) on biological,reproductive parameters and food preference of the soybean pest *Helicoverpa gelotopoeon*[J]. Journal of King Saud University – Science,2019,31(4):1077 – 1082.

[60] Rondot Y,Reineke A. Endophytic *Beauveria bassiana* in grapevine *Vitis vinifera* (L.) reduces infestation with piercing – sucking insects[J]. Biological Control,2018,116:82 – 89.

[61] Pelizza S A,Mariottini Y,Russo L M,et al. *Beauveria bassiana* (Ascomycota:Hypocreales) introduced as an endophyte in corn plants and its effects on consumption,reproductive capacity,and food preference of *Dichroplus maculipennis* (Orthoptera:Acrididae:Melanoplinae)[J]. Journal of Insect Science,2017,17(2):53.

[62] Jaber L R,Ownley B H. Can we use entomopathogenic fungi as endophytes for dual biological control of insect pests and plant pathogens? [J]. Biological Control,2018,116:36 – 45.

[63] Busby P E,Ridout M,Newcombe G. Fungal endophytes:modifiers of plant disease[J]. Plant Molecular Biology,2016,90(6):645 – 655.

[64] Ownley B H,Griffin M R,Klingeman W E,et al. *Beauveria bassiana*:endophytic colonization and plant disease control[J]. Journal of Invertebrate Pathology,2008,98(3):267 – 270.

[65] Ownley B H,Pereira R M,Klingeman W E,et al. *Beauveria bassiana*,a dual purpose biocontrol organism,with activity against insect pests and plant pathogens[M]//Lartey R T,Caesar A J. Emeging concepts in plant health management:research signpost. Kerala,India,2004:255 – 269.

[66] Jaber L R,Salem N M. Endophytic colonisation of squash by the fungal entomopathogen *Beauveria bassiana* (Ascomycota:Hypocreales) for managing *Zucchini yellow mosaic virus* in cucurbits [J]. Biocontrol Science and Technology,2014,24(10):1096 – 1109.

[67] Dara S K, Dara S S, Dara S S R, et al. First report of three entomopathogenic fungi offering protection against the plant pathogen, *Fusarium oxysporum* f. sp. *vasinfectum* [J]. E – Journal of Entomology and Biologicals, 2016.

[68] Dara S S R, Dara S S, Dara S K. Preliminary report on the potential of *Beauveria bassiana* and *Metarhizium anisopliae* s. l. in antagonizing the charcoal rot causing fungus *Macrophomina phaseolina* in strawberry [J]. E – Journal of Entomology and Biologicals, 2018, 5(6): 7.

[69] Barra – Bucarei L, France Iglesias A, Gerding González M, et al. Antifungal activity of *Beauveria bassiana* endophyte against *Botrytis cinerea* in two *Solanaceae* crops [J]. Microorganisms, 2019, 8(1): 65.

[70] Yan L, Zhu J, Zhao X X, et al. Beneficial effects of endophytic fungi colonization on plants [J]. Applied Microbiology and Biotechnology, 2019, 103(8): 3327 – 3340.

[71] Dara S K. Non – entomopathogenic roles of entomopathogenic fungi in promoting plant health and growth [J]. Insects, 2019, 10(9): 277.

[72] Kuldau G, Bacon C. Clavicipitaceous endophytes: their ability to enhance resistance of grasses to multiple stresses [J]. Biological Control, 2008, 46(1): 57 – 71.

[73] Dash C K, Bamisile B S, Keppanan R, et al. Endophytic entomopathogenic fungi enhance the growth of *Phaseolus vulgaris* L. (Fabaceae) and negatively affect the development and reproduction of *Tetranychus urticae* Koch (Acari: Tetranychidae) [J]. Microbial Pathogenesis, 2018, 125: 385 – 392.

[74] Raya – Díaz S, Sánchez – Rodríguez A R, Segura – Fernández J M, et al. Entomopathogenic fungi – based mechanisms for improved Fe nutrition in *Sorghum* plants grown on calcareous substrates [J]. PLoS One, 2017, 12(10): e0185903.

[75] Moloinyane S, Nchu F. The effects of endophytic *Beauveria bassiana* inoculation on infestation level of *Planococcus ficus*, growth and volatile constituents of potted greenhouse grapevine (*Vitis vinifera* L.) [J]. Toxins, 2019, 11(2): 72.

[76] Macuphe N, Oguntibeju O O, Nchu F. Evaluating the endophytic activities of *Beauveria bassiana* on the physiology, growth, and antioxidant activities of extracts of lettuce (*Lactuca sativa* L.) [J]. Plants, 2021, 10(6): 1178.

[77] Dara S K, Dara S S R, Dara S S. Impact of entomopathogenic fungi on the growth, development, and health of cabbage growing under water stress [J]. American Journal of Plant Sciences, 2017, 8(6): 1224 – 1233.

[78] Schulz B, Boyle C, Draeger S, et al. Endophytic fungi: a source of novel biologically active secondary metabolites [J]. Mycological Research, 2002, 106(9): 996 – 1004.

[79] Lu H, Zou W X, Meng J C, et al. New bioactive metabolites produced by *Colletotrichum* sp., an endophytic fungus in *Artemisia annua* [J]. Plant Science, 2000, 151(1): 67 – 73.

[80] Khare E, Mishra J, Arora N K. Multifaceted interactions between endophytes and plant: developments and prospects [J]. Frontiers in Microbiology, 2018, 9: 2732.

[81] 车永梅,赵方贵,陈同金,等. AM 真菌、木霉和 PGPR 组合的促生效应研究[J]. 青岛农业大学学报(自然科学版),2019,36(2):95 – 102.

[82] Zhang F L, Liu Z H, Gulijimila M, et al. Functional analysis of the 1 – aminocyclopropane – 1 – carboxylate deaminase gene of the biocontrol fungus *Trichoderma asperellum* ACCC30536 [J]. Canadian Journal of Plant Science, 2016, 96(2): 265 – 275.

[83] Tall S, Meyling N V. Probiotics for plants? Growth promotion by the entomopathogenic fungus *Beauveria bassiana* depends on nutrient availability [J]. Microbial Ecology, 2018, 76(4): 1002 – 1008.

[84] Heinz K M, Harding P A, Ek – Ramos M J, et al. Fungal endophytes in knock out® rose and performance effects of entomopathogens on marigold and zinnia [J]. HortScience, 2018, 53(12): 1791 – 1798.

[85] Fontana D C, de Paula S, Torres A G, et al. Endophytic fungi: biological control and induced resistance to phytopathogens and abiotic stresses [J]. Pathogens, 2021, 10(5): 570.

[86] Bilal S, Shahzad R, Imran M, et al. Synergistic association of endophytic fungi enhances *Glycine max* L. resilience to combined abiotic stresses: heavy metals, high temperature and drought stress [J]. Industrial Crops and Products, 2020, 143: 111931.

[87] Zhang S W, Gan Y T, Xu B L. Application of plant – growth – promoting fungi *Trichoderma longibrachiatum* T6 enhances tolerance of wheat to salt stress through improvement of antioxidative defense system and gene expression [J]. Frontiers in Plant Science, 2016, 7: 1405.

[88] Karthiba L, Saveetha K, Suresh S, et al. PGPR and entomopathogenic fungus bioformulation for the synchronous management of leaffolder pest and sheath blight disease of rice [J]. Pest Management Science, 2010, 66(5): 555 – 564.

[89] Senthilraja G, Anand T, Durairaj C, et al. Chitin – based bioformulation of *Beauveria bassiana* and *Pseudomonas fluorescens* for improved control of leafminer and collar rot in groundnut [J]. Crop Protection, 2010, 29(9): 1003 – 1010.

[90] Shrivastava G, Ownley B H, Augé R M, et al. Colonization by arbuscular mycorrhizal and endophytic fungi enhanced terpene production in tomato plants and their defense against a herbivorous insect [J]. Symbiosis, 2015, 65(2): 65 – 74.

[91] Batool R, Umer M J, Wang Y Z, et al. Synergistic effect of *Beauveria bassiana* and *Trichoderma asperellum* to induce maize (*Zea mays* L.) defense against the Asian corn borer, *Ostrinia furnacalis* (Lepidoptera, Crambidae) and larval immune response [J]. International Journal of Molecular Sciences, 2020, 21(21): 8215.

[92] Farias C P, De Carvalho R C, Resende F M L, et al. Consortium of five fungal isolates conditioning root growth and arbuscular mycorrhiza in soybean, corn, and sugarcane [J]. Anais da Academia Brasileira de Ciências, 2018, 90(4): 3649 – 3660.

[93] Prabhukarthikeyan R, Saravanakumar D, Raguchander T. Combination of endophytic *Bacillus* and *Beauveria* for the management of *Fusarium* wilt and fruit borer in tomato [J]. Pest Management Science, 2014, 70(11): 1742 – 1750.