

邹曼, 陈雨诗, 许春艳, 等. 生防芽孢杆菌对果蔬采后病害防治的研究进展 [J]. 食品工业科技, 2023, 44(4): 488–495. doi: 10.13386/j.issn1002-0306.2022040319

ZOU Man, CHEN Yushi, XU Chunyan, et al. Research Progress of Biocontrol *Bacillus* on Postharvest Diseases of Fruits and Vegetables[J]. Science and Technology of Food Industry, 2023, 44(4): 488–495. (in Chinese with English abstract). doi: 10.13386/j.issn1002-0306.2022040319

· 专题综述 ·

生防芽孢杆菌对果蔬采后病害防治的研究进展

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摘要: 果蔬在采后贮藏运输过程中易受到病原菌的侵染而腐烂变质, 采后病害的控制主要依赖化学合成杀菌剂, 但长期使用会导致环境污染和食品安全等问题。生物防治具有绿色环保的特点, 正在逐渐被应用。芽孢杆菌作为重要的生防菌, 在果蔬采后病害防治中发挥了重要作用, 目前国内外已有大量生防杆菌在果蔬采后病害防治中的研究。本文对生防芽孢杆菌防治采后病害的种类、作用机制和在采后病害的应用现状进行了综述, 以为生防芽孢杆菌在果蔬采后病害的发展和创新提供借鉴思路。

关键词: 芽孢杆菌, 果蔬, 病原菌, 抑制作用, 防治效果

中图分类号: TS205.9

文献标识码: A

文章编号: 1002-0306(2023)04-0488-08

DOI: 10.13386/j.issn1002-0306.2022040319

本文网刊:



Research Progress of Biocontrol *Bacillus* on Postharvest Diseases of Fruits and Vegetables

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Abstract: During postharvest storage and transportation, fruits and vegetables are prone to decay and deterioration due to the infection of pathogenic bacteria. The control of postharvest diseases mainly relies on chemical synthetic fungicides, but

收稿日期: 2022-04-28

基金项目: 山东省自然科学基金 (ZR2021MC183); 山东省果品产业技术体系 (SDAID-06-13); 山东省重点研发计划 (2021CXGC010809); 山东省农业科学院农业科技创新工程 (CXGC2022C06)。

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long-term use will lead to environmental pollution and food safety problems. Biological control has the characteristic of green environmental protection and is gradually being applied. *Bacillus*, as an important biocontrol bacterium, plays an important role in the prevention and control of postharvest diseases of fruits and vegetables. At present, there are a lot of studies on the prevention and control of postharvest diseases of fruits and vegetables by biocontrol *Bacillus*. In this paper, the species, action mechanism and application status of biocontrol *Bacillus* in postharvest diseases are reviewed in order to provide reference for the application and development of biocontrol *bacillus* in postharvest diseases of fruits and vegetables.

Key words: *Bacillus*; fruits and vegetables; pathogenic bacteria; inhibitory effect; control effect

果蔬营养丰富,富含维生素、膳食纤维、矿物质、有机酸和果胶等,在居民膳食构成中占有重要地位。我国果蔬资源丰富,果蔬产业是仅次于粮食作物的第二大农业产业,其中水

果年产量近 2.8 亿吨,蔬菜年产量达 7.4 亿吨,均居世界第一位^[1]。由于采后保鲜、预冷、分级、包装与处理不当,冷链设施不足,水果和蔬菜的损耗率分别高达 30% 和 40%,而发达国家仅为 7%^[2],我国每年因采后腐烂导致的经济损失约 750 亿元,占果蔬产业总值的 30% 以上^[3]。果蔬在采后贮运过程中发生病害和腐烂的原因包括果蔬自身组织的衰老,病原菌的侵染和运输过程中引起的机械损伤等,其中病原菌侵染是主要原因。果蔬采后病害的控制主要依赖化学合成杀菌剂,但长期使用会导致环境污染、病原菌耐药性增强等问题。生物防治具有绿色环保的特点,是近年来发展起来的新的研究领域。生防菌是一类抑制病原菌活性、控制病害发生和发展的有益微生物。

芽孢杆菌(*Bacillus*)是应用最为广泛的生防菌,其种类多分布广,易分离纯化^[4],所产芽孢可制成粉剂、可湿性粉剂等多种剂型,且与化学农药混用后不失活,是理想的生防菌^[5]。目前国内外研究报道的生防芽孢杆菌主要有枯草芽孢杆菌(*Bacillus subtilis*)、解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*)、多粘芽孢杆菌(*Bacillus polymyxa*)、蜡状芽孢杆菌(*Bacillus cereus*)、地衣芽孢杆菌(*Bacillus licheniformis*)、巨大芽孢杆菌(*Bacillus megaterium*)和短小芽孢杆菌(*Bacillus pumilis*)等^[6]。

真菌侵染造成的果蔬腐烂是当前需迫切解决的问题,拮抗微生物作为生物防治的一种,其无毒、绿色、安全和无抗药性等特点使其具有更为广阔的发展前景。本文对生防芽孢杆菌防治采后病害的种类、作用机制和在采后病害的应用现状进行综述,以期为其应用提供理论基础。

1 生防芽孢杆菌防治采后病害的种类

1.1 对软腐病害的防治

软腐病是由欧氏杆菌属(*Erwinia*)细菌和根霉属(*Rhizopus* spp.)真菌引起的植物病害,病菌均为弱寄生菌,其主要侵染植物多汁肥厚的器官,如块根、块茎、果实、茎基等,主要侵染的果蔬种类包括草莓、樱桃、马铃薯等。病菌从植物表面的伤口侵入,在扩展过程中分泌原果胶酶,分解寄主细胞间中

胶层的果胶质,使细胞解离崩溃、水分外渗,致病组织呈软腐状。研究发现,枯草芽孢杆菌可抑制桃软腐病原菌匍枝根霉(*Rhizopus stolonifer*)^[7]、猕猴桃软腐病的主要致病菌葡萄座腔菌(*Botryosphaeria dothidea*)和拟茎点霉菌(*Diaporthe nobilis*)^[8]。枯草芽孢杆菌 Y-6 抗菌肽对桃软腐菌孢子壁具有溶解作用,抑制桃软腐菌呼吸代谢、琥珀酸脱氢酶(succinate dehydrogenase, SDH)和苹果酸脱氢酶(malate dehydrogenases, MDH)的活性^[9]。解淀粉芽孢杆菌对由胡萝卜软腐果胶杆菌(*Pectobacterium carotovorum*)引起的马铃薯软腐病具有抑制作用^[10]。浓度为 1×10^9 CFU/mL 的贝莱斯芽孢杆菌对甜樱桃软腐病的防治效果达到 79.42%,能够有效抑制匍枝根霉的生长^[11]。埃吉类芽孢杆菌(*Paenibacillus elgii*)对白菜软腐病的预防和治疗作用分别为 79.7% 和 64.4%,且能促进白菜种子萌发和生长^[12]。

1.2 对炭疽病害的防治

炭疽菌是一类重要的致病真菌,主要包括胶孢炭疽菌(*Colletotrichum gloeosporioides*)、尖孢炭疽菌(*Colletotrichum acutatum*)、博宁炭疽菌(*Colletotrichum boninense*)等,主要侵染果实、叶片和茎秆,在果蔬全生育期均可发病,易侵染草莓、苹果、香蕉、黄瓜、辣椒等果蔬。果实染病时先出现湿润状、褐色椭圆形或不规则形的病斑,稍凹陷,斑面出现明显环纹状的橙红色小粒点,后转变为黑色小点^[13]。据报道,巨大芽孢杆菌的优势种群 BM-3103 对芒果炭疽病菌(*Colletotrichum gloeosporioides*)具有拮抗活性^[14],该菌的乙酸乙酯粗提物对采后芒果炭疽病的体内防治效果与化学杀菌剂施保克相似,7 d 后生防效果高达 $89.55\% \pm 1.12\%$ ^[15]。另外,短小芽孢杆菌和苏云金芽孢杆菌(*Bacillus thuringiensis*)对芒果炭疽病的抑制率分别高达 94.28% 和 87.06%^[16]。多粘类芽孢杆菌和枯草芽孢杆菌的悬液处理收获的苹果,可减轻由两种真菌病原体(胶孢炭疽菌和尖孢炭疽)引起的炭疽病^[17]。枯草芽孢杆菌^[18]和短短芽孢杆菌(*Brevibacillus brevis*)对柑橘采后炭疽病(*Colletotrichum gloeosporioides*)具有较好的防治效果^[19]。贝莱斯芽孢杆菌对胶孢炭疽菌引起的草莓炭疽病具有良好的防治效果^[20]。萎缩芽孢杆菌(*Bacillus atrophaeus*)对牛油果炭疽病(*C. gloeosporioides*)具有拮抗作用^[21]。

1.3 对褐腐病害的防治

褐腐病又名菌核病、果腐病、实腐病等,是由于

囊链核盘菌(*Monilinia* spp.)引起的侵染性病害,致病菌分为以下4种:果生链核盘菌 [*Monilinia fructigena* (Aderh. et Ruhl.) Honey]、核果链核盘菌 [*Monilinia laxa* (Aderh. et Ruhl.) Honey]、美澳型核果褐腐病菌 [*Monilinia fructicola* (Winter) Honey] 和串珠霉 (*Monilia polystroma*)^[22]。采前褐腐病通常在盛花期和采收前发生,在环境条件适宜时,采后褐腐病在运输、贮藏、过程中发生比采前更为严重。褐腐病菌易侵染桃、杏、樱桃、梨、白菜、西葫芦等,最初在果面产生褐色圆形病斑,数日扩散全果,果肉也随之变褐软腐。褐腐病菌繁殖的最适温度是 25℃,在 0℃ 的低温下也可生存。研究表明,枯草芽孢杆菌对桃褐腐菌具有抑制作用^[23],且对果生链核盘菌引起的采后梨褐腐病具有抑制效果^[24]。苏云金芽孢杆菌不仅可以防治油桃采后褐腐病,还可用于油桃的采后保鲜^[25]。地衣芽孢杆菌也可抑制油桃褐腐病^[26-27]。解淀粉芽孢杆菌抑菌谱广,对桃褐腐病菌的拮抗作用最强,以细菌悬浮液处理桃果实,对桃褐腐病防病效果可达 70% 左右^[28]。特基拉芽孢杆菌(*Bacillus tequilensis*)对甜樱桃褐腐病的病原菌美澳型核果褐腐病菌具有较好的抑制效果^[29]。

1.4 对青霉病害的防治

扩展青霉(*Penicillium expansum*)是一种多细胞的丝状真菌,是导致果实采后青霉病的主要致病菌,不仅会引起水果由外到内的腐烂,在侵染的过程中还会分泌真菌毒素-展青霉素^[30]。扩展青霉孢子普遍存在于果实采后环境中并能长时间存活,在感染早期只潜伏于果实表面,当水果抗性下降时,孢子就通过伤口进入果实并快速蔓延,导致水果腐败。果实被侵染后症状为腐烂后充水略变色的斑点中心出现白霉,或受害果实变软,果肉褐色,病果表面生有灰绿色霉层,易受侵染的果蔬包括苹果、梨、猕猴桃、黄瓜等。芽孢杆菌属中的枯草芽孢杆菌、短小芽孢杆菌和巨大芽孢杆菌均对柠檬果实上的青霉病具有显著的抗性,主要作用方式为抑制桔青霉的菌丝生长和孢子萌发,同样的抑制作用在柑橘果实上也被发现^[31]。枯草芽孢杆菌对苹果^[32]和柑桔^[33]青霉同样具有抑制作用,解淀粉芽孢杆菌对苹果^[34]、梨^[35]和柑桔的采后青霉病^[36]均具有抑制效果。

1.5 对灰霉病害的防治

灰霉病(*Gray Mold*)是一类由灰霉菌(*Botrytis cinerea*)侵染而引起的导致果蔬腐烂的真菌性病害。葡萄孢属真菌(*Botrytis* spp.)包含 30 多个种,俗称灰霉病菌,其中灰葡萄孢是分布及寄主范围最广的一种。灰葡萄孢是一种死体营养型病原真菌,无性态属于半知菌亚门葡萄孢属,有性态属于富氏葡萄孢盘菌属。灰霉菌既可寄生也可腐生,其分生孢子可通过气流、水滴等途径传播,因而不仅危害果蔬的花、萼、茎、叶、果实的正常生长,也严重危害果蔬采后贮藏。灰霉菌侵染果实后病斑处凹陷,引起褐变,覆

盖灰霉状物,最后整个果实软化腐烂,主要易发病果蔬包括桃、杏、樱桃、葡萄、番茄和辣椒等。研究发现,芽孢杆菌对梨^[37]和蓝莓^[38]的灰霉病具有抑制作用,可显著降低梨贮藏过程中灰霉病菌的发病率。枯草芽孢杆菌可抑制番茄灰霉病^[39]。贝莱斯芽孢杆菌能引起灰霉菌菌丝膨大、畸形^[40],对梨灰霉菌的活体抑制率为 92.88%,其无细胞上清液对番茄和苹果的灰霉菌感染率分别控制了 67.3% 和 60.5%^[41]。短短芽孢杆菌和多粘类芽孢杆菌可抑制草莓的灰霉病^[42]。接种耐盐芽孢杆菌的草莓,培养 4 d 后灰霉病率明显低于对照,且具有显著的诱导酶活性和抗病性相关化合物^[43]。

1.6 对链格孢属引起的采后黑斑病的防治

链格孢属(*Alternaria*)真菌是极为常见的一类真菌,在自然界中分布十分广泛,对生态环境和基质的适应性较强,95% 以上的种均能兼性寄生于植物上,是引起果蔬发病的主要病原菌,其病斑多为圆形或近圆形,常有轮纹,深色,具暗色霉层,一般被称为黑斑病^[44]。众多链格孢属中茄链格孢(*A. solani*)和芸薹链格孢(*A. brassicae*)是世界广泛分布的种,芸薹链格孢常导致十字花科蔬菜发生黑斑病。果蔬被侵染后局部产生淡褐色或棕色腐败病斑,组织裂缝中长出绒毛状灰色真菌菌丝,梨、马铃薯、辣椒和番茄等极易被侵染。郑香香等^[45]研究发现三种芽孢杆菌 HB-2、B1 和 X 发酵液均能显著抑制链格孢菌菌落的生长,同时有效降低极早熟桃采后腐烂率,较好地维持果实品质。银杏内生芽孢杆菌 Q7 代谢产物能够破坏苹果链格孢霉的细胞膜,增加细胞膜的通透性,加剧膜脂质过氧化,对机体代谢酶的酶活力也有明显的抑制作用^[46]。枯草芽孢杆菌对冬枣^[47]和梨黑斑病^[48]有抑制作用,多黏类芽孢杆菌 HT16 对梨黑斑病菌的体外抑制率为 53.2%^[49],甲基营养型芽孢杆菌对白菜黑斑病菌具有强烈拮抗作用并具有较广抗菌谱,防效达到 79.08%^[50]。

2 生防芽孢杆菌的作用机制

2.1 营养和空间位点的竞争

营养和空间位点的竞争是指存在于同一微小生物环境中的两个或两个以上微生物争夺这一环境内的空间、营养和氧气等的现象^[51]。生防菌可迅速地抢占果蔬伤口的营养空间生长存活并大量繁殖,尽可能快地消耗掉伤口营养,使得病原菌得不到合适的营养与空间条件而不能繁殖从而抑制病害的发生^[52]。铁元素的竞争也会影响拮抗菌-病原体的相互作用。解淀粉芽孢杆菌可产生嗜铁素吸附土壤中的 Fe^{3+} ,通过螯合作用运至植物体内,通过与植物病原微生物竞争生物体直接可利用的 Fe^{3+} ,抑制病原菌的生长^[53-54]。同样的,解淀粉芽孢杆菌通过在采后枇杷果实上的定殖和占位抑制真菌病原菌生长^[55]。内生枯草芽孢解淀粉芽孢杆菌 B47 菌株通过在番茄维管束中定殖而抑制内生病菌的生长^[56]。

2.2 抗菌作用

抗菌作用是具有拮抗能力的微生物通过产生抗菌代谢物如毒素、抗生素和酶等来抑制病原菌的作用。芽孢杆菌最主要的特性就是能产生具有广谱抗菌活性的多种次级代谢物^[57]。芽孢杆菌全基因组中有 5% 至 8% 的基因专门用于次级代谢产物的合成,其中包含肽、脂肽、细菌素和其他生物活性物质^[58]。对采后致病真菌最常见的有效抗生素化合物包括: 芽孢杆菌属产生的伊枯草菌素 Iturin^[59]; 假单胞菌属产生的吡咯菌素 Pyrrolnitrin^[60] 和丁香假单胞杆菌产生的丁香霉素 Syringomycin^[61]。由芽孢杆菌合成的其它代谢物, 如 bacillomycin、surfactin 和 fengycin 等也表现出抗菌和抗真菌活性^[62]。环脂肽(lipopeptide, LPs)家族包括 iturin, surfactin 和 fengycin 等, 由于其表面活性可提高防效的特性, 是公认的具有潜在应用价值的化合物; 此外, 不同组的 LPs 对芽孢杆菌菌株具有不同优势, 刺激果实的抗性反应^[63]。贝莱斯芽孢杆菌 Y6 产生的脂肽类物质能够抑制大约 60% 的真菌孢子萌发, 其中伊枯草菌素对真菌孢子萌发表现出较强的抑制作用, 泛革素表现出较弱的抗真菌活性, 表面活性素则没有明显的抑制真菌活性^[64]。

贝莱斯芽孢杆菌 ZSY-1 脂肽物质在 200~400 $\mu\text{g/mL}$ 时可有效降低番茄采后早疫病发病率、延缓果实软化以及推迟番茄采后乙烯释放高峰^[65]。Calvo 等^[66] 研究表明解淀粉芽孢杆菌代谢产生的伊枯草素 iturin A 对灰葡萄孢菌、桃褐腐病菌、扩展青霉、指状青霉和意大利青霉等引起果蔬腐烂的病原真菌具有抑制作用; 付瑞敏等^[67] 利用从解淀粉芽孢杆菌 BA-16-8 菌株发酵液中分离到的脂肽类抗生素芬枯草菌素对病原菌扩展青霉 *P. expansum* 进行处理, 透射电镜观察发现, 病原菌细胞膜变形退化, 细胞核和线粒体被部分或完全破坏, 其余各细胞器均发生明显变化。解淀粉芽孢杆菌产生的挥发性有机物可抑制多种病原真菌生长, 其中对香蕉枯萎病菌抑制效果最强, 挥发性有机物中的 2-Pentadecanone、6,10,14-trimethyl-等酮类物质以及 Caryophyllene、Squalene 等烯烃类物质可能是主要抑菌组分^[68]。

2.3 诱导抗性

芽孢杆菌防治果蔬采后病害, 不仅直接合成真菌活性代谢产物, 也间接启动多个防御反应机制。植物受到病原微生物侵染时, 植物体内的防御保护酶活性会被诱导, 从而提高植株体本身的抗病能力^[69]。Jayapala 等^[70] 研究表明芽孢杆菌 BSp.3/aM 通过增强防御相关酶的活性和增加酚类化合物的积累, 来诱导果实对入侵病原体的抗性; 蜡样芽孢杆菌 AR156 处理可显著诱导几丁质酶和 β -1,3-葡聚糖酶的活性, 促进 H_2O_2 的积累, 提高总酚含量和 DPPH 自由基清除能力, 有效抑制匍枝根霉引起的腐烂^[71]。研究表明, 生防菌产生的抗真菌化合物也有助于诱导寄主对病原微生物的防御机制, 防治果蔬采后病害。枯草芽

孢杆菌产生的 Iturin 和 Fungicin, 可以诱导植物类苯丙烷代谢基因的表达, 触发 ISR 机制^[72]。枯草芽孢杆菌产生的 Bacillomycin D, 可以显著提高植物防御相关酶的活性, 直接抑制真菌和激活樱桃番茄防御相关基因、酶, 控制匍枝根霉的生长^[73]。枯草芽孢杆菌 ABS-S14 及其粗提物 Iturin A, Fengycin 和 Surfactin, 能控制青霉引起的柑橘病害, 提高过氧化物酶 (peroxidase Stain, POX) 和苯丙氨酸解氨酶 (phenylalanineammonialyase, PAL) 活性水平^[74]。拮抗菌代谢产物如抗菌蛋白、抗菌脂肽均可诱导植物产生抗性。

3 生防芽孢杆菌在采后病害的应用现状

3.1 生防芽孢杆菌制剂的开发

美国 Agrquest 公司研制的枯草芽孢杆菌菌株的活菌杀菌剂 Serenade TM 和 Souata AS, 用于防治疫病、白粉病、灰霉病、霜霉病等病害。Taensa 公司将解淀粉芽孢杆菌变种制成的商品 Taegro TM, 可用于防治根腐病和枯萎病^[75], 同时, Taensa 公司研发的生防芽孢杆菌菌剂 MBI600、QST713、GB03、FZB42 和 AS43.3 等可抑制白粉病、疫病和灰霉病等多种植物病害的致病真菌生长^[76]。

国内现已开发出一批生防效果优良的枯草芽孢杆菌菌株, 如 Bs-916、B908、B3、B903、BII、PRs5、ZH-2、BL03、XM16^[77]。孙力等^[78] 成功研制贝莱斯芽孢杆菌 Can L-30 可湿性粉剂, 其对油菜菌核病和黑胫病都有一定的防效, 并可提高油菜籽产量。张桂娟等^[79] 研制了多粘类芽孢杆菌 246-1 可湿性粉剂制剂, 其与小白链霉菌的复配菌剂处理的黄瓜植株长势茂盛, 在株高、单果重及小区产量等方面都显著高于其他处理, 并能够使黄瓜植株病害明显降低。王小兵等^[80] 研制出的复合芽孢杆菌水分散粒剂能够有效防治辣椒青枯病, 并提高辣椒的产量和品质。由膨润土、羧甲基纤维素钠、净洗剂等组成的解淀粉芽孢杆菌 Y-3 生物可湿性粉保鲜剂对番茄采后早疫病和灰霉病病原具有良好防治效果, 可有效减少红熟番茄货架期的腐烂率和病果率^[81]。

3.2 提高芽孢杆菌制剂生防效果技术的研究

一般情况下, 单一使用拮抗菌效果弱于化学杀菌剂, 且高浓度的拮抗菌生产成本高, 不利于商业应用推广, 将拮抗菌与其他物质结合使用是提高拮抗效果的有效途径。Alvindia^[82] 研究报道解淀粉芽孢杆菌 DGA14 与碳酸氢钠结合, 可以有效增强抑制效果, 降低冠腐病发病率, 处理效果与合成杀真菌剂效果相当, 对果实品质没有负面影响。史凤玉等^[83] 研究发现, $10^8 \sim 10^9$ CFU/mL 枯草芽孢杆菌与 2% CaCl_2 结合使用, 对苹果采后青霉病的抑制效果优于两者单独使用。巨大芽孢杆菌 A6 与两种基因存在差异的枯草芽孢杆菌分离株 (BY-2、Tu-100) 结合使用, 不仅能够控制 *Sclerotinia sclerotiorum* 引起的油菜病害, 还可促进油菜生长^[84]。枯草芽孢杆菌分别与其他生

防因子 CaCl_2 、水杨酸、壳聚糖复配后,可降低拮抗菌的使用浓度,显著提高生物拮抗菌的拮抗效果,其中与 2% CaCl_2 和 1% 壳聚糖复配后的拮抗菌悬液其防效分别为 72.81% 和 77.07%^[48]。由此可见,拮抗菌与外源物质结合能够显著提高生防效果,有效控制采后病害。

4 展望

利用芽孢杆菌防治植物病害是目前农业生产上最常用的生物防治技术之一,已经成为国内外研究热点。芽孢杆菌种类和数量众多,抗逆性强,繁殖速度快,发酵工艺成熟,便于生产应用,对许多病原菌都有良好的抑制作用,也可诱导植物自身产生抗性,在果蔬保鲜等领域具有良好的应用前景。但目前生防芽孢杆菌的研究与应用方面还有一些不足,例如,微生物菌体或其代谢产物易受环境的影响导致防腐效果不稳定,商业化应用的生防菌剂较少等。因此,将来还需基于现代多组学等技术进一步明确生防菌的作用机理,通过基因组学、代谢组学等技术选育具有广谱抗菌活性且耐不良环境的生防菌株,探究芽孢杆菌联合其他抑菌物质结合使用效果等,实现生防芽孢杆菌菌株的大规模商品化生产和应用。

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