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中国昆虫病原线虫研究和产业化进展*

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摘 要 昆虫病原线虫（Entomopathogenic nematodes）作为国际上已经商业化应用、对土栖性和钻蛀性害虫特效的昆虫寄生性天敌，自 20 世纪 60 年代被陆续引入我国后，在农林和卫生等重要害虫绿色治理中发挥了重要作用。全球分离和鉴定了 150 多种昆虫病原线虫，我国发现的斯氏线虫 *Steinernema* 有 27 种，异小杆线虫 *Heterorhabditis* 6 种，其中有 19 个斯氏线虫新种和 2 个异小杆线虫新种。对昆虫病原线虫共生细菌的研究，明确了共生细菌与昆虫病原线虫的共生专化性，并从共生细菌中鉴定了多种毒素和次生代谢物，具有杀虫、抗菌、杀线虫等生物活性，应用前景广阔。昆虫病原线虫田间应用的效果受环境因素的影响，通过对昆虫病原线虫环境耐性及机理的研究，筛选了适应环境压力的昆虫病原线虫品种和品系，应用于不同地区防控特定害虫。在昆虫病原线虫培养、剂型、保存和施用技术等方面开展的研发及技术创新工作，使昆虫病原线虫在我国实现了产业化。目前昆虫病原线虫已在我国推广应用，在防控桃小食心虫 *Carposina nipponensis*、蛴螬、韭菜迟眼蕈蚊 *Bradysia odoriphaga* 幼虫等害虫上取得了良好的效果。本文从昆虫病原线虫鉴定和分类、昆虫病原线虫产业化、昆虫病原线虫共生细菌、昆虫病原线虫与共生细菌专化性、昆虫病原线虫应用、昆虫病原线虫环境耐受性、昆虫病原线虫与外界因子（包含生物与非生物因子）等领域全面综述我国昆虫病原线虫的研发进展。

关键词 昆虫病原线虫；共生细菌；鉴定分类；产业化培养；剂型；田间应用

Research and commercialization progress on entomopathogenic nematodes in China

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Abstract Entomopathogenic nematodes (EPNs), as parasitic natural enemies of insects that have been commercially applied internationally and are highly effective against soil-borne and both-boring pests, have played a significant role in the green management of important pests in agriculture, forestry, and health since their introduction to China since the 1960s. Globally, over 150 species of EPNs have been isolated and identified. In China, 27 species of *Steinernema* and 6 species of *Heterorhabditis* have been discovered, including 19 new species of *Steinernema* and 2 new species of *Heterorhabditis*. Research on the symbiotic bacteria of EPNs has clarified the symbiotic specificity between these bacteria and the nematodes. Numerous toxins and secondary metabolites with insecticidal, antibacterial, and nematicidal activities have been identified from these symbiotic bacteria, demonstrating broad application prospects. The effectiveness of EPNs in field applications is influenced by environmental factors. Studies on the environmental tolerance and underlying mechanisms of EPNs have led to the selection of strains adapted to environmental pressures, which are being used to control specific pests in different regions. Research and technological innovations in the cultivation, formulation, preservation, and application techniques of EPNs have enabled their industrial production in China. Currently, EPNs have been widely adopted in China for pest control, achieving remarkable results in managing pests such as the peach fruit moth (*Carposina nipponensis*), grubs, and chive maggots (*Bradysia odoriphaga*) in Chinese chives. This paper comprehensively reviews the research and development progress of these nematodes in China on their identification and classification, industrialization and formulation, symbiotic bacteria, association with the symbiotic bacteria, applications, environmental tolerance, and the relationship with abiotic environmental factors.

Key words entomopathogenic nematodes; symbiotic bacteria; identification and classification; commercial production; formulation; field application

斯氏线虫科 Steinernematidae 和异小杆线虫科 Heterorhabditidae 昆虫病原线虫是目前国际上对土栖性和钻蛀性害虫特效的天敌类群。这类线虫以 3 龄感染期幼虫（Infective juveniles，IJ）主动寻找昆虫寄主，对非靶标生物和生态环境安全，可离体产业化生产，已广泛用于防治多种害虫（Ehlers，2001；Gaugler *et al.*，2002；吴文丹等，2014；Labaude and Griffin，2018；王杰等，2021），德国 E-nema、荷兰 Koppert、英国 Becker Underwood、日本 SDS 以及我国潍坊宏润农业科技有限公司、河南济源生物科技有限公司等多家公司企业均商业化生产这类生物农药（Han *et al.*，2000；Kaya *et al.*，2006；Peters，2013；Shapiro-Ilan *et al.*，2017；王杰等，2021）。

利用线虫防治有害昆虫的研究是 20 世纪 30 年代才开始的。我国从 20 世纪 60 年代开始昆虫病原线虫研究和应用，最早由中国科学院动物研究所沙搓云先生从捷克引入昆虫病原线虫。自 1978 年广东省科学院动物研究所（时称广东省昆虫研究所）所长李丽英研究员先后从澳大利亚、美国和加拿大引进了多种昆虫病原线虫，率先在我国开展昆虫病原线虫的大量繁殖与田间应用研究。从 1986 年起，广东省科学院动物研究所和中国农业科学院植物保护研究所（当时为中国农业科学院生物防治研究所）与澳大利亚 CSIRO 组织的昆虫学研究所共同实施长达 12 年的中澳国际合作项目，广东省科学院动物研究所与德国基尔大学、爱尔兰国立大学以及印度尼西亚 The University of Jember 共同承担欧盟第五框架国际合作项目。在国内外项目的资助下，我国昆虫病原线虫研究和产业化走进了新时代，昆虫病原线虫在农林和卫生等害虫的可持续治理中发挥了巨大的作用。

本文从昆虫病原线虫的鉴定和分类、产业化、共生细菌、环境耐受性和应用，昆虫病原线虫与非生物环境因子等领域全面综述我国对这一天敌种类的研发进展。

1　昆虫病原线虫的鉴定和分类

目前已从全球分离和鉴定了 120 种斯氏属 *Steinernema* 线虫和 30 种异小杆属 *Heterorhabditis* 线虫（Kozodoi，1984；Gardner *et al.*，1994；刘杰，1994；Stock，1996；Stock *et al.*，1996，2009；Ganguly and Singh，2000；Cutler and Stock，2003；Plichta *et al.*，2009；Clausi *et al.*，2011；Gorgadze *et al.*，2015；Shahina *et al.*，2017；Bhat *et al.*，2020，2023a，2023b；Didiza *et al.*，2021；Lis *et al.*，2021；Machado *et al.*，2022，2025；Tian *et al.*，2022；Patil *et al.*，2023；Soni *et al.*，2023；Baniya *et al.*，2024；Anes *et al.*，2025；Zhan *et al.*，2025；NCBI 数据库 https://www.ncbi. nlm.nih.gov/taxonomy/?term=Steinernema 和 https://www.ncbi.nlm.nih.gov/taxonomy/?term=heterorhabditis）。

我国气候、植被和生态系统的多样性使得昆虫病原线虫资源丰富。李小峰和王国汉（1989）调查结果表明，福建、广东、海南等地均有斯氏线虫和异小杆线虫的分布；陈书龙等（2006）调查河北省线虫资源，分离出斯氏线虫 17 个种群，异小杆线虫 49 个种群；Ma 等（2010）调查了中国北方线虫资源，共获得斯氏线虫 7 个种，103 个品系，异小杆线虫 3 个种，102 个品系；钱秀娟等（2014）获得 29 个线虫品系，其中 *S. affine*、*S. karil* 和 *S. kraussei* 为国内新记录种；Wang 等（2014）对辽宁省昆虫病原线虫资源进行调查，发现新记录种 *S. bicornutum*；张红玉（2016）调查山东地区线虫资源，获得 6 个品系；王思雨（2022）对华北北部地区进行调查，获得 53 个品系；刘佳等（2025）补充调查了甘肃昆虫病原线虫的资源情况，共获得 20 个品系。

目前，我国发现斯氏线虫共 27 种，其中新种 19 种，分别是 *Steinernema caudatum*（Xu *et al.*，1991）、*Steinernema longicaudum*（Shen and Wang，1992）、*Steinernema ceratophorum*（Jian *et al.*，1997）、*Steinernema guangdongense*（Qiu *et al.*，2004）、*Steinernema aciari*（Qiu *et al.*，2005c）、*Steinernema akhursti*（Qiu *et al.*，2005a）、*Steinernema beddingi*（Qiu *et al.*，2005b）、*Steinernema sichuanense*（Mráček *et al.*，2006）、*Steinernema hebeiense*（Chen *et al.*，2006a）、*Steinernema leizhouense*（Nguyen *et al.*，2006）、*Steinernema cholashanense*（Nguyen *et al.*，2008a）、*Steinernema xueshanense*（Mráček *et al.*，2009）、*Steinernema pui*（Qiu *et al.*，2011）、*Steinernema changbaiense*（Ma *et al.*，2012a）、*Steinernema xinbinense*（Ma *et al.*，2012b）、*Steinernema tielingense*（Ma *et al.*，2012c）、*Steinernema taiwanensis*（Tseng *et al.*，2018）、*Steinernema populi*（Tian *et al.*，2022）和 *Steinernema tarimense*（Zhan *et al.*，2025）。

我国报道的异小杆线虫种类较少，共 6 种，包含 2 个新种（其中 1 种为同种异名）。Hsieh 等（2009）在中国台湾地区发现 *Heterorhabditis brevicaudis*，并补充分子描述，Hunt and Subbotin（2016）认为 *H. brevicaudis* 和 *H. indica* 是同种异名。Li 等（2012）在北京樱桃树下发现昆虫病原线虫新种 *Heterorhabditis beicherriana*。异小杆线虫 *Heterorhabditis marelatus*、*H. bacteriophora*、*H. indica* 和 *H. megidis* 在我国均有分布，其中 *H. megidis* 分布范围最广，是主要的优势种群。Nguyen 等（2008b）基于系统进化分析，将异小杆属划分为 3 个分支：“*Indica*”、“*Bacteriophora*”和“*Megdis*”。我国发现的异小杆线虫属于“*Indica*”分支的为 *H. indica*；2 种属于 *Bacteriophora* 分支：*H. beicherriana* 和 *H. bacteriophora*；2 种属于 *Megdis* 分支：*H. marelatus* 和 *H. megidis*。

2　昆虫病原线虫的产业化

我国科研人员在昆虫病原线虫的培养、剂型配制及保存等方面开展了大量的研发，提高了昆虫病原线虫生产效率，延长货架时间，提高田间防效，降低使用成本。

2.1　昆虫病原线虫产业化培养

昆虫病原线虫的产业化培养方法包括昆虫活体培养及离体培养，离体培养则包括固体培养

和液体培养两种方法。在不同培养方法的工艺优化上开展的技术改进，为实现昆虫病原线虫的产业化培养和应用提供了有力的支撑（颜珣和韩日畴，2016）。

常用于昆虫病原线虫活体培养的昆虫包括大蜡螟 *Galleria mellonella*、黄粉虫 *Tenebrio molitor*、家蚕 *Bombyx mori*、适宜特定昆虫病原线虫品种的金龟子或其他直翅目昆虫等（Peters *et al.*，2017；Han *et al.*，2024；田成丽，2024）。徐洁莲和谢汝创（1992）比较了 *S. carpocapsae* 和 *S. anomali* 两种线虫在大蜡螟和鸡杂海绵培养基下连续传代培养后的差异。李春杰等（2008）使用繁殖袋，筛选蛭石作为培养介质，以末龄黄粉虫幼虫为活体寄主进行 *H. bacteriophora* Hb 的大量繁殖。阎爱华等（2015）研发了实验室内活体大量繁殖昆虫病原线虫的装置。姚红燕等（2018）以较易获得的甜菜夜蛾 *Laphygma exigua* 高龄幼虫为寄主，有效降低昆虫病原线虫活体繁殖的成本。李小龙等（2019）研发了智能一体化昆虫病原线虫活体培养装置，减少人力，提高了培养效率。*H. megidis* 0627M 和 *S. feltiae* 0619HT 两种品系可以通过寄主韭蛆复壮，使其生殖力、致病力和侵入率都明显升高（狄斌等，2021）。

共生细菌对昆虫病原线虫单菌培养发挥重要作用。足量的共生细菌才能提高昆虫病原线虫的产量（徐洁莲，1989；杨秀芬和杨怀文，1997）。固体培养系统中，初生型菌比次生型菌培养线虫的产量提高 3-10 倍（韩日畴等，1990a）。次生型共生细菌未被 *H. bacteriophora* 线虫携带，也不能支撑线虫生长（Han and Ehlers，2001）。*P. lumninescens* 初生型菌产生的细胞间晶体蛋白 CipA 和 CipB 可以诱导 *Steinernema* 线虫恢复、发育和繁殖（You *et al.*，2006）。韩日畴等（1990b）报道了通过消毒昆虫病原线虫卵获得无菌幼虫的方法。无菌 *H. bacteriophora* IJ 可在被感染的无菌大蜡螟幼虫血淋巴中恢复发育到 1 龄幼虫，但未能杀死大蜡螟幼虫，而无菌 *S. carpocapsae* 能够致死无菌大蜡螟幼虫并产生后代，但 IJ 产量低于有共生细菌存在时的产量（Han and Ehlers，2000）。丘雪红等（2004）发现共生细菌除了显著影响 IJ 的致病力，也影响线虫干重、蛋白质、氨基酸、糖原和脂肪酸等生化物质含量。

在建立昆虫病原线虫体外单菌培养技术的基础上，通过优化培养基组分、培养设备、培养流程等，提高体外培养的效率。最早使用的线虫固体培养基是从澳大利亚引进的鸡杂海绵培养基（Bedding，1981），早期的固体培养基主要包含猪杂/鸡杂、水、猪油/牛油等简单的成分，混合海绵配制而成（赵忠懿等，1991）。李素春等（1987）最早研究了培养基成分、培养基含水量、线虫接种量、共生细菌接入量及培养温度等因素对引进的 *Neoaplectana feltiae* 线虫在鸡杂海绵培养基中产量的影响。杨怀文等（1991）以容易获得的鸭肠、油脂和柞蚕 *Antheraea pernyi* 蛹配成培养基培养 *S. feltiae* 线虫，产量与鸡内脏配方相当。Han 等（1992）报道，添加玉米粉、鱼粉等含脂量高的成分可以提升 *Steinernema* sp. CB2B 和 *H. bacteriophora* H06 固体培养产量。Han 等（1993）以线虫接种量、温度和培养时间为参数，利用正交旋转组合设计方法优化了 *S. carpocapsae* 线虫的固体培养系统。潘洪玉等（1995）筛选利用植物蛋白质替代鸡肠的配方，以低成本获得稳定的线虫产量。韩日畴等（1995）优化了固体干粉培养基组分，获得 *S. carpocapsae* A24 和 *H. bacteriophora* H06 线虫最高产量达 5.8×10^5 和 4.8×10^5 IJ/g，并在此基础上制定线虫工厂化固体培养标准化流程和质量控制程序（韩日畴等，1997）。于固体培养基中加入大蜡螟幼虫组织匀浆，可使出现衰退的 *S. carpocapsae* Beijing 线虫恢复繁殖力（常韶华和杨怀文，1998）。王忠文等（1999）用鸡蛋替代鸡杂，固体培养可收获 6.07×10^5 IJ/g，发育历期最短，3-4 d 便可增殖一代。郝杰等（2017）对 *S. carpocapsae* HB310 线虫的固体培养基及培养条件进行优化，筛选到更为经济、高效的线虫固体培养基配方。Zhen 等（2018）比较了固体培养基中添加大蜡螟、黄粉虫和丝光绿蝇 *Lucillia sericata* 昆虫干粉对 *S. feltiae* SN 线虫产量的影响，发现添加 5% 黄粉虫干粉的产量最高，生产的 IJ 对斜纹夜蛾

Spodoptera litura 的致死速度也最高。Wang 等（2022）研究发现，线虫信息素蛔苷（Ascarosides）可显著提高昆虫病原线虫的产量。赵国玉和郭文秀（2023）在 *S. glaseri* 的固体培养基中添加黄粉虫干粉、蝇蛆干粉等成分并优化培养条件，可使线虫最高产量提高 47.5%，培养周期缩短 46.4%，解决了这一线虫培养周期长、产量低、培养成本高的问题。

液体大量培养技术是昆虫病原线虫的商品化发展方向。首先在摇床中建立了 *S. carpocapsae* A24 和 *H. bacteriophora* H06 线虫的液体培养，线虫接种量和培养时间显著影响线虫产量（Han，1996）。朱明军等（1998）在摇瓶培养的基础上，在国内率先开始了应用发酵罐进行昆虫病原斯氏线虫 A24 品系的液体培养，发现气升内环流反应器最适合昆虫病原线虫的培养，优化了液体培养条件，为反应器大规模培养线虫提供了依据（朱明军等，1999）。站丽莉等（2008）优化了 *S. carpocapsae* 线虫 2 种液体培养基的产量和效率。王丽芳等（2010）比较了 *H. bacteriophora* Hb-1 的液体和固体繁殖技术，优选了线虫培养基。李春杰等（2007）比较了固体、液体等 4 种不同方法培养 *H. bacteriophora* Hb-1 和 *S. carpocapsae* Sc-2 的效果。

在专利申报中，韩日畴和李丽英（2003）在昆虫病原线虫液体单菌培养系统中，于线虫发育的关键龄期加入 0.01-1 μg/mL 的链霉素，以改变菌体密度和诱导共生菌产生变异型，进而控制 IJ 的形成，提高 IJ 的产量。杨怀文等（2007）利用淀粉酶、糖化酶、蛋白酶和脂肪酶等酶制剂对线虫培养基进行酶解处理后培养昆虫病原线虫，线虫产量比未酶解培养基提高 40%，收获期提前 4-6 d。简恒等（2011）将昆虫酶解物作为组份加入到培养基中，可以提高线虫产量、缩短培养周期、降低生产成本。刘勇（2020）选用 20%（m/v）面包虫和 4%（m/v）玉米粉作为基本培养基，线虫繁殖量达 2.6×10^{7} IJ/瓶；添加 2%（m/v）活性炭和 3%（m/v）Fe_3O_4 能有效提高繁殖率。Kong 等（2022）和谷星慧等（2023）发现在培养基中添加二甲基亚砜（Dimethyl sulfoxide，DMSO）及蛔苷可显著提高 *S. carpocapsae* All 和 *H. bacteriophora* H06 的 IJ 产量。DMSO 主要通过抑制 *Hint module*、*PAN domain protein*、*Dpy-13* 3 个基因来调控线虫的怀卵量，从而提高 IJ 产量（Liu *et al.*，2024）。

广东省科学院动物研究所（原广东省昆虫研究所）改进的昆虫病原线虫固体培养技术已在多家公司转化，实现 *S. carpocapsae*、*S. feltiae*、*S. longicaudum*、*H. bacteriophora*、*H. indica* 等线虫的规模化生产及商品化，并通过技术转移及培训，在印度尼西亚、巴基斯坦、卢旺达、朝鲜、韩国等国家成功应用，改变了这些国家的害虫防治模式，在降低化学农药依赖、促进环境可持续发展方面成效显著（王杰等，2021；Yan *et al.*，2025）。此外，*S. feltiae* A24，*S. bibionis* T319 和 *S. glaseri* NC34（杨平和徐洁莲，1989）、*S. feltiae* OTIO（王慧等，1998）、异小杆线虫 NLK-1（布卡·欧尔娜等，2015）、*S. ceratohporum*（Yan *et al.*，2021）、*S. glaseri*（赵国玉和郭文秀，2023）等昆虫病原线虫品种和品系也已实现大量培养，用于田间害虫防控。

培养设备改进对昆虫病原线虫体外培养流程的优化同样具有重要意义。孙瑞红和李爱华（2011）设计了带有清洗筛的线虫清洗器。田会鹏等（2013）设计了 *S. carpocapsae* A24 的不锈钢培养盒。许艳丽等（2018）发明了一种可以同时进行灭菌和搅拌的装置，搅拌桨以电机驱动，相比人工操作简单，该装置用于昆虫病原线虫固体繁殖。郭文秀等（2019d，2019e）改进了昆虫病原线虫的培养盒，以简单的结构和低加工成本实现透气保湿环境及昆虫病原线虫的自动化洗出分离。陈瑞等（2020）采用耐高温塑料材质设计了新型培养瓶。李小龙等（2021）设计使用培养袋培养昆虫病原线虫。廖慧君等（2023a）发明了通过固定组件和隔断组件的配合，将长条状海绵经隔断组件和固定组件后被粉碎成海绵块的装置，用于昆虫病原线虫培养基混合粉碎，操作简单，自动化高，实用性强。廖慧军等（2023b）还发明了一种发酵菌种液体培养系统，解决了外部空气与发酵罐内部温差过大的问题。阮维斌

（2023）研发了利用挤压板运动挤压海绵分离线虫的装置。

2.2　昆虫病原线虫剂型、保存及施用技术

徐洁莲和刘秀玲（1997）研究昆虫病原线虫常温保存技术。韩日畴等（2000）筛选出国产硅藻土可以用于 *S. carpocapsae* 线虫的贮存，添加食品抗霉剂能维持 2 周的防霉效果。Feng 等（2006）筛选了甘油和加强型人工海水配制的渗透压溶液，能够诱导 *S. carpocapsae* All 线虫进入脱水休眠状态，进而提高线虫耐热性，延长保存时间。Yan 等（2010）在此基础上研究了该渗透压溶液对 15 个不同品种和品系线虫的作用效果，渗透压处理后线虫耐热性显著提高，为应用渗透压溶液诱导昆虫病原线虫进入脱水休眠状态进而长期保存线虫提供了基础。李春杰等（2014）研究了 *H. bacteriophora* HBN 在 4 种介质（蛭石、海绵、沙土和珍珠岩）中冷冻储存的最优条件；进一步研究发现逐渐降温预处理可以显著提高 *H. bacteriophora* HBN 和 *H. bacteriophora* NJ 两种线虫的冷冻存活率（李春杰等，2015）。马小雅（2016）发明了贮存线虫的多种保存剂。肖宇辉（2018）报道了海绵保存 *S. costaricense* 线虫的保水剂、防腐剂和洗出剂。郭文秀等（2020）发明了利用腐殖土保存多种昆虫病原线虫的方法。

剂型研发方面，也通过改进制剂配方，配制剂型延长昆虫病原线虫货架时间，同时针对不同的目标害虫研发适合田间应用的剂型。徐洁莲和杨平（2000）研究发现国产水溶性粘合剂 POA 对 *S. carpocapsae* A24 有增效的效果。陈松笔等（2001c）筛选了含有 10% CYL、1%羧甲基纤维素钠和 0.01% 4203 的蒸发抑制剂、保湿剂和乳化剂组合，作为 *S. carpocapsae* CB-16 线虫叶面用抗干燥剂。张安邦（2015）提供了 *S. glaseri* Sgib 的粉剂配方（含 30%白炭黑、69.4%水、0.5%羧甲基纤维素钠和 0.1%甲醛），该粉剂在 10 ℃储存 30 d 后线虫的存活率为 100%，储存 60 d 线虫存活率为 92.38%。Guo 等（2017b）筛选出 1：0.8-1：1.2（w/w）的蛭石和腐殖土适合作为载体保存线虫，添加 0.1%-0.2%的杀菌剂 Proxel GXL 可以延长线虫保存时间，保存过程中 IJ 的感染力不受影响。方分分等（2019）以蔗糖、葡萄糖、海藻糖、山梨醇等作为稳定剂（0.2%-1.0%质量比），以甘油、黄原胶、羧甲基纤维素等为保水剂（0.2%-1.0%质量比），以山梨酸钾、丙酸钠、富马酸二钾酯、甲醛等为防霉剂（0.1%-0.5%质量比），以硅藻土、白炭黑、可溶性淀粉、天然沸石粉等作为载体（40%-50%质量比），配制的昆虫病原线虫粉剂，在 10 ℃条件下贮存 3 个月后线虫存活率 80%以上。李星月等（2020）将 *H. beicherriana* 与硫脲复配成的制剂，含有有机硅、矿源黄腐酸钾、海藻糖及共生细菌培养基等成分，防治花生蛴螬及其他地下害虫防效达 60%以上。南宫自艳等（2022）以白炭黑和/或粘土为基质，以羟丙基甲基纤维素和/或羧甲基纤维素钠为保水剂，以海藻酸钠和/或黄原胶为紫外保护剂，以山梨酸钾和/或甲醛为防腐剂，加入甘油和水配制的线虫粉剂，能显著提高线虫长时间贮存后的存活率。李晶晶等（2023）混合黄粉虫、木屑、水并接种线虫，培养获得黄粉虫虫尸，可直接作为昆虫病原线虫制剂应用田间。刘琴等（2023）以草地贪夜蛾 *Spodoptera frugiperda* 的蛹生产 *S. carpocapsae*，形成蛹蜕自然包裹线虫的蛹胶囊，再以 10%聚乙烯醇溶液（w/w）喷淋蛹体，在蛹表面形成水溶性半透膜，获得斯氏线虫蛹胶囊制剂，在 20-25 ℃保存，线虫存活率仍高达 78%以上。郭文秀等（2024）研发了一种保湿缓释胶囊，可以保护昆虫病原线虫不受土壤干燥的影响。李星月等（2025）研发了包括昆虫病原线虫 *S. carpocapsae* 黄粉虫虫尸剂、甘薯小象甲 *Cylas formicarius* 人工饲料、多酚氧化酶抑制剂和海藻糖干粉的虫尸复配剂。

采用喷雾、滴注、挂物和涂布等不同方法施用格氏线虫 85011 品系防控直锥大象虫 *Cyrtorachelus longimanus* 时，发现在淀粉糊中加线虫做成糊剂涂布竹笋虫蛀口的方法防效最高（刘南欣等，1990）。以高压机动喷雾机施用昆虫病原线虫防控桃小食心虫 *Carposina nipponensis*，压力在 10-20 kg/cm^2 时，对线虫的

存活、寄主的侵染力和寄生强度均无明显影响（黎彦等，1991）。陈镜华和韩日畴（2014）发明了昆虫病原线虫喷施设备。郭文秀等（2019f）、廖慧军等（2023c）发明的储存装置，可以使水体中的昆虫病原线虫保持悬浮状态，解决昆虫病原线虫施用过程中水中存活时间较短的问题。郭文秀等（2019a，2019b）发明了昆虫病原线虫田间随水施加装置和可切换施用不同昆虫病原线虫的田间施用装置。郭文秀等（2019c）还研发了用于防治天牛的昆虫病原线虫注射装置，能够在田间防治天牛时实现连续定量注射。这些设备的研发，提升了田间作业效率，使昆虫病原线虫施放均匀，节省了时间，降低了人工成本和劳动强度，还相应提升了昆虫病原线虫的防治效果。

3 昆虫病原线虫-细菌共生体

昆虫病原线虫 IJ 体内携带有互利共生的共生细菌。昆虫病原线虫通过寄主的口、肛门、气孔等自然开口、伤口或体壁节间膜进入昆虫体腔内，释放共生细菌到寄主血淋巴中，共生细菌在昆虫病原线虫生活史中发挥重要作用：共生细菌在寄主体内繁殖，分泌多种毒素，使害虫患败血症死亡；同时产生多种胞外酶，将昆虫物质转化为能被线虫所吸收利用的营养物质，支持线虫生长；共生细菌还分泌抗菌物质抑制非共生细菌的生长，为线虫生长发育提供稳定环境（吴文丹等，2014；王杰等，2021）。昆虫体内营养耗尽后，昆虫病原线虫-细菌共生体重新形成，离开虫体，寻找新的寄主。

3.1 共生细菌的种类

隶属于变形菌门 Proteobacteria 的 γ-亚纲肠杆菌科 Enterobacteriaceae 的致病杆菌属 *Xenorhabdus* 和发光杆菌属 *Photorhabdus* 细菌，革兰氏阴性，不产孢，兼性厌氧，具有支持线虫的共生性与致死昆虫的病原性特点（Eckstein *et al.*，2019；Stock，2019）。*Xenorhabdus* 和 *Photorhabdus* 属共生细菌分别与斯氏线虫属和异小杆线虫属线虫共生。

目前已确定的 *Xenorhabdus* 属细菌有 27 种，*Photorhabdus* 属细菌有 19 种（Machado *et al.*，2021）。2003 年，第一版 *P. luminescens* 基因组公布（Duchaud *et al.*，2003），随后有多个共生细菌的基因组公布（Ghazal *et al.*，2017；Duong *et al.*，2019；Somvanshi *et al.*，2019），包括我国学者测序的多个共生细菌基因组（Qiu *et al.*，2014；Li *et al.*，2021a）。

3.2 共生细菌的特征

Xenorhabdus 和 *Photorhabdus* 属共生细菌在体外培养时出现“初生型”和“次生型”的菌落和菌体（Akhurst，1980）。能被 IJ 携带的仅为初生型细菌。初生型细菌更好地支持昆虫病原线虫生长和发育，次生型细菌会影响昆虫病原线虫产量（Akhurst and Boemare，1990；Han and Ehlers，2001）。初生型 *P. luminescens* 细菌产生两种胞内晶体蛋白 CipA 和 CipB，而次生型缺少晶体蛋白；胞内晶体蛋白被证明为线虫繁殖的营养因子（You *et al.*，2006）。

3.3 共生细菌的作用

我国学者发现，共生细菌培养液对昆虫、植物病原或植物线虫具有控制作用。*P. luminescens*、*X. nematophila* A24-1 和 *X. nematophila* HB310 菌液分别对甜菜夜蛾（王欢等，2007）、东亚飞蝗 *Locusta migratoria manilensis*（张园等，2013）、小菜蛾 *Plutella xylostella*（Wu *et al.*，2020）具有致死作用。共生细菌菌液对大蜡螟幼虫（付俊瑞等，2018a，2018b）、小菜蛾幼虫（张红玉等，2016）和南方根结线虫 *Meloidogyne incognita* 卵的孵化和幼虫具有抑制作用（王鑫鹏，2018；吴黎黎等，2024）。*Xenorhabdus* 和 *Photorhabdus* 菌株分别抑制番茄灰霉菌 *Botrytis cirerea*（刘霞等，2006）、苹果灰霉菌 *B. cinerea*（文旭等，2012）、葡萄灰霉病（曹林青等，2021）、辣椒疫霉菌 *Phytophthora capsici*（王永宏和张兴，2007）。共生细菌可控制玉米小斑病菌 *Bipolaris maydis*（王欢等，2009）、串珠镰刀菌 *Fusarium moniliforme*（崔安妮等，2015）、黑曲霉 *Aspergillus niger*（高宇洁等，

2022）、草莓炭疽菌 *Colletotrichum fragariae*、稻瘟病菌 *Magnaporthe oryza*、大豆疫霉菌 *Phytophthora sojae*、尖孢镰刀菌 *Fusarium oxysporum* 和辣椒立枯丝核菌 *Rhizoctonia solani*（张金花等，2024）等病菌引起的植物病害。

共生细菌产生的多种代谢产物应用潜力巨大（Tobias *et al.*，2017；Dreyer *et al.*，2018；Shi *et al.*，2019；Neubacher *et al.*，2020；Meesil *et al.*，2025）。不同种类或菌株产生功能和作用效果不同的多种代谢物活性成分（方香玲等，2008；Liu *et al.*，2019；Mollah *et al.*，2020；Wang *et al.*，2022）。*Xenorhabdus* 和 *Photorhabdus* 共生细菌分泌的各种抗菌物质已用于研发新型抗菌素（Shi and Bode，2018；Muangpat *et al.*，2020）。我国学者在这一领域做出了重要贡献，比如从共生细菌中分离了多种抗菌活性物质，包括 Xenocoumacin 1 和 Xenocoumacin 2（Guo *et al.*，2017a；Zhang *et al.*，2024）、Xenematide G（Xi *et al.*，2019）、PAX1 肽与异香豆素（Dreyer *et al.*，2019）、Nematophin（Zhang *et al.*，2019a）、Darobactin（Imai *et al.*，2019）、环肽 Photoditritide（Zhao *et al.*，2019）、非核糖体肽（Du *et al.*，2022）以及多种挥发性化合物（Baiome *et al.*，2022）。pH 调节（Guo *et al.*，2017a）、原位产品移除法（Dong *et al.*，2020）和发酵过程优化可提高 Xenocoumacin 1 的产率（Han *et al.*，2024）。由共生细菌从吩嗪 Phenazine 转化的抗菌素，有利于维持线虫-细菌复合体的特殊环境生态位（Shi *et al.*，2019）。此外，*X. bovienii* 通过合成放线菌素 D（Actinomycin D）诱导大蜡螟幼虫细胞凋亡和败血症（Zhang *et al.*，2023）。蒽醌可通过大肠杆菌 *Escherichia coli* 表达 *P. luminescens* 的 *antABCDEFGHI* 基因簇获得（Zhou *et al.*，2019）。大肠杆菌通过整合 *Photorhabdus* 属细菌 type II polyketide synthase 基因可大量生产胭脂红酸（Yang *et al.*，2021）。目前被认为极具商业价值的抗癌药物 Glidobactin A 和 Cepafungin I 便来源于共生细菌（Zhao *et al.*，2020）。于 *P. laumondii* 发现可用于抑制肿瘤的 Glidobactin 样蛋白酶体抑制剂（Zhao *et al.*，2021）。*X. stockiae* HN_xs01 菌株被证明具有抗肿瘤作用（Zhang *et al.*，2022）。共生细菌分泌抗菌物质的调控机制研究方面，*cpxR* 基因被认为影响 *X. nematophila* 抗菌物质合成（Guo *et al.*，2019；Zhang *et al.*，2019b）。*OmpR* 被证明间接调控 *X. nematophila* 菌株中 Xenocoumacin 1 的合成（Han *et al.*，2025）。产生 Odilorhabdins 抗菌素的共生细菌具有自我保护机制，编码 N-乙酰转移酶的基因 *oatA* 负责 Odilorhabdins 抗性（Lanois-Nouri *et al.*，2022）。

共生细菌产生的各类毒性蛋白可有效作用于不同种类昆虫、植物线虫和原生动物（Bowen *et al.*，2000；Pan *et al.*，2002；Tobias *et al.*，2018；Muangpat *et al.*，2020）。除了 *Photorhabdus* insect related protein（Pir）（Waterfield *et al.*，2005），Makes Caterpillars Floppy（Mcf）（Daborn *et al.*，2002），Photox（Visschedyk *et al.*，2012），几丁质酶（Liu *et al.*，2019；Mahmood *et al.*，2020）和 Galtox（Ahuja *et al.*，2021），我国学者还发现了可作为强效的蛋白传递系统（Jiang *et al.*，2022）的 *Photorhabdus* virulence cassettes（PVC）（Yang *et al.*，2006；Wang *et al.*，2022，2024）、*Photorhabdus* insecticidal toxin（Pit）（Li *et al.*，2009）和 PaxAB（Zhang *et al.*，2014）。证明 *X. nematophila* HB310 菌株的几丁质酶 *chi60* 和 *chi70* 基因对 Tc 毒性是必须的（Liu *et al.*，2022），N-聚糖和硫酸化糖胺聚糖介导 Tc 对哺乳动物细胞的毒性（Song *et al.*，2021）。这类细菌产生的胞内和胞外蛋白可抑制棉铃虫 *Helicoverpa armigera* 初孵幼虫（杨保军等，2007）。共生细菌中分离获得的非核糖体肽 Rhabdopeptides，可用于拮抗携带热带疾病病原体的原生动物（Wesche *et al.*，2018），致死南方根结线虫 *M. incognita*（Bi *et al.*，2018）。我国学者从 *X. innexi* DSM 16336 中获得了 7 个 Rhabdopeptide/xenortide 肽，经测定，这些多肽对布氏罗得西亚锥虫 *Trypanosoma brucei* 和恶性疟原虫 *Plasmodium falciparum* 产生抑制作用（Zhao *et al.*，2018），为新药物研发开辟途径。发光杆菌产生的 *TcaB*、*Txp40*、*PaTox*、*PirAB*、*PTC* 等毒素对昆虫具有口服或注射活性（Wu and Yi.，2016；Bogdanovic *et al.*，2019； Mathur *et al.*，2019；Nangong *et al.*，2020；Shankhu *et al.*，2020；Wang *et al.*，2023）。致病杆菌产生的 *Xax*、*srfABC*、*PirAB*、*Tp40*、*hipBA* 等毒素也具有强烈的杀虫活性（杨君等，2008；郭笑笑等，2019；Yang *et al.*，2019；Yadav and Rathore，2020）。*X. stockiae* 菌株产生的 *SrfABC* 毒素对棉铃虫幼虫呈现杀虫活性，推测在宿主定殖中起重要作用（Yang *et al.*，2019），并表现细胞毒性和导致细胞凋亡（Sun *et al.*，2019）。目前已从大蜡螟幼虫中获得与 *X. nematophila* PirAB 有交互作用的 Arylphorin 蛋白（Nangong *et al.*，2020）。转 *TcdA* 基因的拟南芥 *Arabidopsis thalian* 对烟草天蛾 *Manduca sexta* 和黄瓜点叶甲 *Diabrotica undecimpunctata* 幼虫具有毒杀作用（Liu *et al.*，2003）。转 *P. luminescens* 杀虫基因 *TcdA1* 和 *TcdB1* 的阴沟肠杆菌 *Enterobacter cloacae* 对台湾乳白蚁 *Coptotermes formosanus*（Zhao *et al.*，2008）和斜纹夜蛾、甜菜夜蛾、黄曲条跳甲 *Phyllotreta striolata* 均具有杀虫活性（张鹏波等，2010）。*P. temperata* Meg1 基因簇 *ptt*ABC 在大肠杆菌中表达可获得一种新的环脂肽 Phototemtide A，对恶性疟原虫具有选择性抗原生动物活性（Zhao *et al.*，2019，2020）。

前期研究发现，热灭活的 *P. luminescens* TT01 菌体（Wu *et al.*，2014）或脂多糖（Wu *et al.*，2015a）诱导大蜡螟幼虫免疫致敏，但 PirA2B2 蛋白免疫致敏的大蜡螟幼虫对 *P. luminescens* TT01 的感染没有明显的抵抗（Wu *et al.*，2015a）。胰岛素促进共生细菌的生长发育（杨亚贤等，2023；李茜童等，2024；钱秀娟等，2024）。T3SS 和鞭毛都促进了共生细菌在宿主细胞内的侵袭和定植，对次生代谢产物的形成和分泌影响较小（Huang *et al.*，2024）。

基于来自 *P. luminescens* 的寄主特异性噬菌体蛋白（Yin *et al.*，2015）和位点特异性重组酶系统 Cre/loxP 直接克隆基因簇（Hu *et al.*，2016）的重组技术已用于 *Photorhabdus* 和 *Xenorhabdus* 共生细菌。此外，重组酶介导的基因组工程（Chassis-independent recombinase- assisted genome engineering，CRAGE）已应用于将共生细菌复杂生物合成基因簇高效整合到细菌的染色体中，获得高效表达目的蛋白的宿主菌（Liu *et al.*，2020）。

4　昆虫病原线虫与共生细菌的专化性

我国在昆虫病原线虫与共生细菌的专化性领域的研究主要集中于如下方面：共生细菌的信息专化性，共生细菌的营养专化性，共生细菌的定殖专化性和共生细菌的杀线虫专化性。

国外学者业已发现，昆虫血淋巴和共生细菌培养物中含有信号物质（Food signal）诱导 IJ 恢复至取食态（Strauch and Ehlers，1998；Ciche and Ensign，2003；Hirao and Ehlers，2009）。*Xenorhabdus* 属细菌产生的信号物质不能诱导异小杆线虫发育，而 *Photorhabdus* 属中的一些共生菌菌株可诱导 *S. carpocapsae* 线虫发育（Ehlers and Han，1998）。不同种共生细菌产生不同的食物信号，目前未发现一种共生菌可诱导所有非特异共生的 IJ 恢复（Han and Ehlers，1999）。

斯氏属线虫可在高营养的人工培养基中（Ehlers *et al.*，1990；Friedman，1990；Lunau *et al.*，1993）和无菌活体昆虫中（Han and Ehlers，1999）无菌繁殖；但是，异小杆属线虫对共生细菌具有严格的特异性，必须在 *Photorhabdus* 属共生细菌或存在其代谢产物的培养基中才能繁殖（Akhurst and Boemare，1990；Ehlers *et al.*，1990；Han *et al.*，1990；Aguillera and Smart，1993；Han *et al.*，2000）。采用 Tn5 转座方法构建了共生细菌 *P. luminescens* LN2 突变体库，筛选出一个对其共生线虫 *H. indica* LN2 的生长繁殖有显著促进作用的突变菌株，为构建支持线虫高产的菌株提供了关键技术（胡素丽等，2014）。

共生细菌特异性定殖于 IJ 肠道。昆虫病原

线虫都携带特定的共生菌菌株。利用非特异共生细菌可获得肠道未携带细菌的无菌感染期线虫（Ehlers and Han，1998；Sicard *et al*.，2004）。

当两种线虫同时感染一头昆虫寄主时，两种线虫能否共存或对抗是有趣的问题。当昆虫病原线虫与非特异性共生的共生细菌共同培养时，一些共生细菌菌株能够产生对非特异性线虫有致死作用的毒素，比如 *H. indica* LN2 线虫的共生细菌会产生毒素致死 *H. bacteriophora* H06 线虫（Han and Ehlers，1999；Qiu *et al*.，2009）。研究发现，*H. indica* LN2 线虫共生细菌的 *namA* 基因参与了杀线虫毒素的合成（Qiu *et al*.，2009）。*P. luminescens* LN2 的 *rpoS* 基因也参与致死 *H. bacteriophora* H06 线虫，以及 *H. indica* LN2 线虫正常的感染期恢复和发育，但是，*rpoS* 基因未影响共生细菌在 LN2 和 H06 感染期线虫的定植，显然 *rpoS* 基因在昆虫病原线虫与共生细菌的互惠关系中发挥了关键作用（Qiu *et al*.，2016）。

5 昆虫病原线虫的环境抗性与机制

温湿度、土壤渗透压、紫外线辐射等多种环境因素影响线虫的生存、繁殖及对目标昆虫的感染力（武海斌等，2015c；王杰等，2021）。我国科研人员在昆虫病原线虫环境耐受品系筛选、昆虫病原线虫响应环境压力的行为和生理生化机制及分子机理方面开展了一系列的研究。

5.1 高温耐受力

杨平和李素春（1988）最早研究了温度对 *S. feltiae* 线虫发育、繁殖和感染力的影响，发现在 10 ℃以下 30 ℃以上不能发育至成虫，最适生长温度为 25 ℃。刘奇志等（2009）研究了 *S. longicaudum* BPS 的生物学特性和耐热性。Ma 等（2013）比较了 31 个品系的环境耐性，发现 *S. carpocapsae*、*S. ceratophorum*、*S. longicaudum*、*H. indica* 和 *H. bacteriophora* 比 *S. feltiae*、*S. hebeiense*、*S. monticolum* 和 *H. megidis* 等品系更耐热。张红玉（2016）发现，*H. bacteriophora* JNR 线虫有较好的耐热性，38 ℃条件下能存活近 32 h 且仍具有侵染活力。Yan 等（2018）比较了对黄曲条跳甲幼虫高毒力的 4 种昆虫病原线虫的环境耐受力，发现采自海南的 *S. pakistanense* 94-1 的耐热能力最强。马娟等（2022）发现 *S. tielingense* LFS65、*S. ceratophorum* HQA87 和 *S. carpocapsae* All 线虫对 40 ℃的耐性较强。陈澄等（2023）报道 *S. carpocapsae* X-94，40 ℃下处理 5 h 后存活率为 33%。总体而言，采自热带地区的昆虫病原线虫品系具有较高的耐热性。在耐热机理方面，郭笑笑（2020）研究发现 *S. ceratophorum* HQA-87 的抗逆性基因 *HSP20* 和 *CL9144* 均与线虫耐高温抗性有关，但基因沉默结果显示这两个抗逆性基因与线虫致病力不相关。Xie 等（2020）研究了经热驯化的 *S. carpocapsae* All 线虫在 38 ℃高温胁迫 5 h 后的转录组，发现了多个差异表达基因。

5.2 耐低温及抗冻能力

李春杰等（2011）在黑龙江省分离到 *H. bacteriophora* HBN 和 *H. bacteriophora* ZT 两个耐寒昆虫病原线虫品系，发现介质的含水量对 *H. bacteriophora* HBN 冷冻存活率产生显著影响（李春杰等，2014），而适当的预处理可提高 *H. bacteriophora* HBN 和 *H. bacteriophora* NJ 线虫的冷冻存活率（李春杰等，2015）。Ma 等（2013a）比较发现 *H. megidis*、*H. bacteriophora* 和 *S. carpocapsae* 比测定的其他昆虫病原线虫表现出更好的耐寒性。张红玉（2016）研究发现，*H. bacteriophora* JNR 在低温下的侵染力随温度升高而增加。陈桂梅（2021）发现，不同昆虫病原线虫耐寒能力强弱依次为 *S. monticolum* Sm、*S. feltiae* SN、*S. carpocapsae* All、*H. bacteriophora* Hb、*S. glaseri* KG。马娟等（2022）发现，在 - 5 ℃处理后，*Steinernema* sp. ZLS3 和 *S. carpocapsae* 线虫的死亡率低于 *S. feltiae* LFS67、*S. feltiae* JY90 和 *H. beicherriana* NCWZ1 等线虫。

张旭霞（2018）发现，阶段性降温驯化后，*S. litorale* 线虫在 - 20 ℃的冷冻存活率显著提高，体内可溶性糖、脂肪和海藻糖含量在驯化后增加，而蛋白质和糖原含量无显著变化。陈桂梅

（2021）分析了 *H. bacteriophora* Hb、*S. carpocapsae* All、*S. monticolum* Sm、*S. feltiae* SN 的水通道蛋白基因在冷冻胁迫下的不同转录响应。

5.3　紫外线辐射耐性及保护剂

紫外线是昆虫病原线虫防治地上害虫时最重要的影响因子。钱秀娟等（2019a）研究紫外线辐射对昆虫病原线虫存活率和致病力的影响，发现昆虫病原线虫不同品系均对紫外辐射具有一定的耐受能力。肖建飞等（2021）发现木质素磺酸钙能显著提高 *S. litorale* 抗紫外胁迫的能力。Wu 等（2023a）发现氨基化二氧化钛（Titania-NH2）纳米粒子可保护 *S. carpocapsae* 免受紫外线辐射。Ha 等（2025）发现 0.2%葡萄籽提取物与 0.1%阻燃凝胶的组合对 *S. carpocapsae* 露于 3 种波长的人工紫外线辐射（UVA、UVB、UVC）下有最好的保护效果。丁倩（2024）发现农用植物油可提高 *H. bacteriophora* Hb、*H. beicherriana* H06、*H. indica* LN2、*S. carpocapsae* All 和 *S. feltiae* SN 线虫在紫外线辐射处理下的存活率。

5.4　耐受脱水能力及机制

不同种的昆虫病原线虫，以及同种不同品系的昆虫病原线虫，耐受脱水的能力不同（冯世鹏和韩日畴，2005；颜珣和韩日畴，2010）。陈松笔等（1999）筛选获得抗干燥能力强的线虫种类。邢玉芳等（2009）测定了甘肃 8 种昆虫病原线虫的抗干燥能力。李宁等（2011）测定了 10 个昆虫病原线虫品系的抗干燥能力，*S. carpocapsae* GA 品系的存活率最高，*Heterorhabditis* sp. CZ 和 XH-9 品系则全部死亡。Ma 等（2013）发现，*S. carpocapsae*、*S. hebeiense* 和 *S. ceratophorum* 具有良好的耐脱水性。吴霞等（2019）报道，异小杆线虫抗低湿胁迫能力弱于斯氏线虫，斯氏线虫 *S. kraussei* 0657L 抗低湿胁迫能力强于测定的其他线虫，低湿胁迫对 *S. feltiae* 0619HT 和 *H. megidis* 0627M 的繁殖无显著影响。

不同昆虫病原线虫品种之间渗透压耐性存在差异，*S. carpocapsae* All 和 *S. scapterisci* SS 最耐受渗透压溶液处理（Yan *et al.*，2010，2011）。马娟等（2022）测定不同地区的昆虫病原线虫的抗干燥能力，发现 *Steinernema* sp. ZLS3、*S. carpocapsae* All 和 *S. ceratophorum* HQA87 在 25%甘油溶液中的存活率高于测定的其他线虫。

昆虫病原线虫脱水胁迫下进入休眠状态后，体表和体内发生了显著变化（陈松笔等，2001b），与耗氧量相关（陈松笔等，2001a）。不同昆虫病原线虫应对低湿胁迫的避逆策略不同，在 30%低湿环境中，*S. kraussei* 0657L 表现为干燥逃避，*H. brevicaudis* 0641TY 则表现为低湿休眠（张晓波等，2023）。*S. carpocapsae* BJ 线虫在高渗溶液中脱水后进入休眠状态，其酯酶活性降低，总糖和糖原含量均产生改变（陈松笔等，2000）。甘油处理后脱水的 *S. carpocapsae* Agriotos 合成甘油和海藻糖等保护化合物（Qiu *et al.*，2000；Qiu and Bedding，2002）。吴霞（2023）也发现，低湿胁迫会引起 *S. kraussei* 0657L 和 *H. brevicaudis* 0641TY 体内总脂肪、海藻糖和蛋白质的积累，同时能量物质与存活率和致病力之间存在着一定的相关性。

在分子响应机制方面，*S. feltiae* IS-6 线虫可通过 24%甘油溶液处理进入渗透脱水状态，UNC-87、肌动蛋白（Actin）、蛋白酶体调节颗粒（ATP 酶样）[Proteasome regulatory particle（ATPase-like）]、GroEL 伴侣蛋白（GroEL chaperonin）、GroES 共伴侣蛋白（GroES co-chaperonin）以及转座酶家族成员（Transposase family member）等蛋白的上调表达与渗透压胁迫的响应相关（Chen *et al.*，2005，2006b）。*S. carpocapsae* 的 *lea* 和 *sod-2* 基因在耐热性较弱的 MR7 品系中的表达量显著高于 All 品系，而 *t19d7* 的表达量则显著降低（Yan *et al.*，2011）。对渗透压耐性差异显著的 4 种昆虫病原线虫 *S. carpocapsae*、*S. loci*、*H. bacteriophora* 和 *H. indica* 中 *fat-2* 的表达情况分析结果显示，该基因在渗透压耐性最强的 *S. carpocapsae* 线虫中表达量最高，可能与渗透压耐性差异直接相关（Yan et *al.*，2012）。吴霞（2023）报道 *TRE* 和 *CAT* 基因能

够调控 *S. kraussei* 0657L 体内能量物质以响应低湿胁迫。黄山（2023）通过 RNA 干扰（RNA interference，RNAi）技术验证了 *CL2037* 和 *CL2161* 基因与 *S. ceratophorum* HQA-87 线虫的干燥抗性有关。研究结果表明，昆虫病原线虫对脱水响应的分子机制比较复杂，通过基因转化和添加单个基因来改善昆虫病原线虫的脱水耐受性不太可能实现。

6　昆虫病原线虫的应用

昆虫病原线虫种类会影响其对不同害虫的毒力效果，应用昆虫病原线虫时应针对特定靶标害虫筛选高毒力的品种和品系，以实现对靶标害虫的有效控制。我国学者针对我国农业中的一系列地下害虫、钻蛀害虫以及食叶害虫，筛选获得相应的高毒力昆虫病原线虫（表 1）。

表 1　昆虫病原线虫防控的主要害虫

Table 1　Major pests controlled by entomopathogenic nematodes

目标昆虫 Target insect	线虫种或品系 Nematode species/strain	参考文献 Reference
桃小食心虫 *Carposina nipponensis*	*H. bacteriophora* H06	李爱华等，2012
梨小食心虫 *Grapholita molesta*	*S. carpocapsae* All	严凯等，2017
韭菜迟眼蕈蚊 *Bradysia odoriphaga*	*H. bacteriophora* ZT，*S. carpocapsae*，*S. feltiae* SN，*H. indica* LN2	李春杰等，2013；Ma *et al.*，2013b；潘凤娟等，2013；张燕等，2014；Bai *et al.*，2016；Yan *et al.*，2019
华北大黑鳃金龟 *Holotrichia oblita*	*H. beicherriana* LF	李而涛等，2018
铜绿丽金龟 *Anomala corpulenta*	*H. beicherriana* D26-6，*S. carpocapsae*	张维伟和赵福永，2021；白勇章等，2024
暗黑鳃金龟 *Holotrichia parallela*	*H. bacteriophora* D26-6，*H. beicherriana*	李而涛等，2020；张彩铃等，2024
小云斑鳃金龟 *Polyphylla gracilicornis*	*S. longicaudum* X-7	范芳芳等，2015
白星花金龟 *Postosia brevitarsis*	*S. carpocapsae* All	李长青等，2011
小地老虎 *Agrotis ipsilon*	*S. carpocapsae*，*H. indica* LN2	Yan *et al.*，2014；武海斌等，2015b；李根等，2017；谷星慧等，2021
黄地老虎 *Agrotis segetum*	*S. glaseri* ib	张安邦等，2015
八字地老虎 *Xestia cnigrum*	*S. carpocapsae*-2	张思佳等，2013
草地贪夜蛾 *Spodoptera frugiperda*	*S. carpocapsae* All，*S. feltiae*，*H. indica*，*H. megidis* 0872L	梁铭荣等，2020；杨淋凯等，2021；蔡佳仪等，2023；Guo *et al.*，2023
斜纹夜蛾 *Spodoptera litura*	*S. longicaudum* X-7，*H. indica* 212-2	Yan *et al.*，2020；Sun *et al.*，2021
甜菜夜蛾 *Spodoptera exigua*	*H. indica* LN2，*S. carpocapsae*	刘敏等，2025
二点委夜蛾 *Athetis lepigone*	*H. bacteriophora* HB8	雷利平等，2013
番茄潜麦蛾 *Tuta absoluta*	*S. carpocapsae* All	郭文秀等，2024
舞毒蛾 *Lymantria dispar*	*S. carpocapsae* All	滑莎等，2018
腰果细蛾 *Acrocercops syngramma*	*S. carpocapsae* All	张中润等，2016
苹果蠹蛾 *Cydia pomonella*	*S. riobrave*，*S. carpocapsae*	张金花等，2024
小线角木蠹蛾 *Holcocerus hippophaecolus*	*S. carpocapsae*	路常宽等，2004
二化螟 *Chilo suppressalis*	*S. carpocapsae* N-Yz1，*S. carpocapsae* XC-4	刘琴等，2024；刘洋等，2025
腰果云翅斑螟 *Hyalospila leuconeurella*	*S. carpocapsae* All	张中润等，2017
草地螟 *Loxostege sticticalis*	*S. carpocapsae* All	李朔涵，2023

续表 1 (Table 1 continued)

目标昆虫 Target insect	线虫种或品系 Nematode species/strain	参考文献 Reference
草原毛虫 *Gynaephora alpherakii*	*S. feltiae* SN，*S. carpocapsae* All	白海涛等，2020
黄曲条跳甲 *Phyllotreta striolata*	*S. carpocapsae* All	杨凤丽等，2020；赵丽稳等，2024
红棕象甲 *Rhynchophorus ferrugineus*	*S. carpocapsae* All，*H. bacteriophora* H06	钟宝珠等，2020；Lv *et al.*，2025
茶籽象甲 *Curculio chinensis*	*S. carpocapsae* All	王轶等，2019
小蜂巢甲虫 *Aethina tumida*	*S. carpocapsae* All	韩文素等，2021
黄粉虫 *Tenebrio molitor*	*S. litorale*	詹发强等，2020
曲牙土天牛 *Dorysthenes hydropicus*	*H. bacteriphora* H06	徐常青等，2010
松褐天牛 *Monochamus alternatus*	*S. carpocapsae* All	张彦龙等，2012
核桃云斑天牛 *Batocera lineolata*	*S. carpocapsae*	陈贤群等，2016
甘薯蚁象 *Cylas formicarius*	*S. feltiae*	于海滨等，2012
臭椿沟眶象 *Eucryptorrhynchus brandti*	*S. carpocapsae* All	郑惠中，2021
白纹伊蚊 *Anopheles albopictus*	*S. abbasi*	Liu *et al.*，2020
红火蚁 *Solenopsis invicta*	*H. bacteriophora*、*S. riobrave*、 *S. carpocapsae* All	Wu *et al.*，2023b；Li *et al.*，2024c； 易松望等，2024
南瓜实蝇 *Bactrocera tau*	*S. feltiae*	Liu *et al.*，2025

根据王杰等（2021）改进。
Improved according to Wang *et al.*, 2021.

6.1　昆虫病原线虫与化学药剂共用

在害虫防治实践中，昆虫病原线虫可与兼容的化学药剂混用，以扩大防治谱或提高防治效果。我国应用昆虫病原线虫与低毒化学药剂共同防治害虫，取得较好的效果（表 2）。

6.2　昆虫病原线虫与其它微生物混用

在我国，开展了将昆虫病原线虫与其他昆虫病原如苏云金芽孢杆菌 *Bacillus thuringiensis*（Hatting *et al.*，2019）、球孢白僵菌 *Beauveria bassiana*（张伟等，2017）、绿僵菌 *Metarhizium anisopliae*（黄亚川等，2020）等协同防控害虫的研究。苏云金芽孢杆菌产生的毒素引起黏虫 *Mythimna separata* 中肠组织病变，降低黏虫的免疫力，有利于昆虫病原线虫的感染，因此两者联用对黏虫具有协同防控效果（李而涛等，2019）。PI3K/Akt/CncC 信号通路介导昆虫病原线虫和苏云金芽孢杆菌对暗黑鳃金龟 *Holotrichia parallela* 幼虫的感染（Li *et al.*，2023）。此外还发现，腐生真菌腐皮镰刀菌 *Fusarium solani* 可吸引并促进 *S. diaprepesi* 线虫感染寄主昆虫（Wu *et al.*，2018）。

6.3　昆虫病原线虫田间应用的典型案例

在我国，已利用昆虫病原线虫防治桃小食心虫（杨平等，2000）、黄曲条跳甲（Yan *et al.*，2013）、韭菜迟眼蕈蚊 *Bradysia odoriphaga*（Ma *et al.*，2013b）、小地老虎 *Agrotis ipsilon*（Yan *et al.*，2014）、华北大黑鳃金龟 *Holotrichia oblita*（Guo *et al.*，2017）、草地贪夜蛾（唐璞等，2019）等多种害虫。典型的成功案例包括利用昆虫病原线虫田间防控桃小食心虫、蛴螬和韭蛆。

6.3.1　桃小食心虫　桃小食心虫主要危害苹果、桃、杏、李、山楂、枣、石榴等，已成为我国苹果生产中发生面积最大、危害最严重的害虫之一（孙丽娜等，2018）。早在 20 世纪 80 年代，国内便应用昆虫病原线虫大面积防治桃小食心虫，防控效果显著。在山东泰安、寿光等地 5 个果园苹果生产中应用 *S. carpocapsae* Agriotes 线虫在

表 2 昆虫病原线虫与化学药剂联用防控的主要害虫

Table 2 Combination of entomopathogenic nematodes and chemicals for the control of insect pests

目标昆虫 Target insect	线虫种和品系 EPN species/strain	化学药剂种类 Chemical insecticides	参考文献 Reference
韭菜迟眼蕈蚊 *Bradysia odoriphaga*	*S. feltiae* SN	噻虫嗪 Thiamethoxam	武海斌等，2018
	S. feltiae SN	吡虫啉 Imidacloprid	Yan *et al.*，2019； 付在秋等，2020
	S. feltiae 0619HT	吡虫啉 Imidacloprid	钱秀娟等，2019b
	S. carpocapsae All	溴氰虫酰胺 Cyantraniliprole	翟婧等，2020
卵圆齿爪鳃金龟 *Holotrichia ovata*	*S. longicaudum* X-7	除虫脲 Diflubenzuron	张中润等，2006
华北大黑鳃金龟 *Holotrichia oblita*	*H. bacteriophora*	吡虫啉 Imidacloprid	Guo *et al.*，2017c
褐纹甘蔗象 *Rhabdoscelus lineaticollis*	*S. carpocapsae* All	吡虫啉 Imidacloprid	王果红等，2007
黄曲条跳甲 *Phyllotreta striolata*	*S.carpocapsae* All	溴氰虫酰胺 Cyantraniliprole	金立新等，2019
黄粉虫 *Tenebrio molitor*	*S. carpocapsae* All	茚虫威 Indoxacarb	陈瑞等，2019
红火蚁 *Solenopsis invicta*	*S. riobrave*	联苯菊酯与噻虫胺混合物 Mixture of bifenthrin and clothianidin	Wu *et al.*，2024
臭椿沟眶象 *Eucryptorrhynchus brandti*	*S. longicaudum* X-7	氯氰菊酯 Cypermethrin, 吡虫啉 Imidacloprid	郑惠中，2021
烟粉虱 *Bemisia tabaci*	*S. carpocapsae* All	柠檬烯可溶液剂 Limonene solution	陈向荣等，2021

根据王杰等（2021）改进。

Improved according to Wang *et al.*, 2021.

1.0 亿/667 m^2 剂量下对桃小食心虫的控制效果优于化学防控区（刘杰，1994；杨平等，2000）。在河北地区，*S. feltiae* Beijing 线虫在 1.0 亿/667 m^2 剂量下能够有效降低虫果率，防控效果优于化学药剂（刘新生等，1993）。刘峥等（1998）分离到一种对桃小食心虫高毒力的本土昆虫病原线虫 *Steinernema* sp.，在河南郑州、新乡、博爱等地开展 3 年的田间防控试验也表明，该线虫较常规化学药剂能够减少 22%-68%桃小食心虫的出土数量及 39%-76%的虫果数量。桃小越冬幼虫出土一般在 5 月末 6 月初，此时土壤温度和含水量均适于线虫的存活及侵染。目前，苹果产业正经历由传统果园向现代果园发展历程，桃小食心虫的防治已转套袋防治，昆虫病原线虫在现代果园中防治桃小食心虫还需进一步加强研究。

6.3.2 蛴螬 蛴螬是昆虫病原线虫最早应用及应用研究最为广泛的目标地下害虫（Glaser and Fox，1930），一系列种类或品系如 *S. glaseri*（Converse and Grewal，1998）、*S. scarabaei*（Cappaert and Koppenhöfer，2003；Koppenhöfer *et al.*，2006）、不同品系的 *H. bacteriophora*（Koppenhöfer *et al.*，2000，2002；Koppenhöfer and Fuzy，2003；Grewal *et al.*，2004）、*H. zealandica*（Grewal *et al.*，2004）等已被成功地应用于蛴螬的防治。在我国，一些本土昆虫病原线虫对蛴螬有很好的控制效果。花生田施用 *S. longicaudum* X-7、*H. bacteriophora* H06 IJ 线虫（0.5-1.0 亿/667 m^2）能够有效控制暗黑鳃金龟、华北大黑鳃金龟 *H. oblita*，使蛴螬减退率达 88%以上（Guo *et al.*，2013，2015）。烟草田中应用 *S. longicaudum* X-7 能够有效减少蛴螬虫口密度，保苗效果显著（李根，2017）。金银花田施用 *S. longicaudum* X-7 能够持续控制蛴螬危害，植株死亡率显著降低（Li *et al.*，2023）。一些环境友好型药剂如氯化烟酰类（王玉东等，2012）、昆虫生长调节剂类药剂除虫脲（张中润等，2006）与线虫混用具有协同增效作用，可提高线虫对蛴螬的防治效果。田间施用昆虫病原线虫的时间节

点非常关键，应根据当地作物蛴螬的发生危害规律，选择 1-2 龄幼虫期，采用滴灌装备将线虫悬液沿植株根茎顺流入根系土壤中发挥持续性防控作用（Guo *et al.*，2015）。

6.3.3　韭蛆　国内学者开展了大量应用昆虫病原线虫防治韭蛆（迟眼蕈蚊幼虫）的研究工作，筛选到了多种对韭蛆高毒力的线虫种类，如 *S. feltiae* 多个品系（杨秀芬等，2004；Ma *et al.*，2013）、*H. indica* LN2（孙瑞红等，2004；Ma *et al.*，2013b）、*H. bacteriophora* ZT（李春杰等，2013）等。一系列田间应用技术及配套技术的持续研究，支撑了昆虫病原线虫对韭蛆的田间成功控制。杨秀芬等（2004）对 *S. feltiae* PS4 进行田间小区试验测试，对韭蛆防治效果为 55.8%。Ma 等（2013）针对昆虫病原线虫防治韭蛆开展了系统研究，发现 *S. feltiae* JY-17 线虫对韭蛆的致死率可达 97%。赵国玉（2013）对露天栽培韭菜田中夏季应用 *H. indica* LN2 线虫对韭蛆的持续性控制效果进行了研究，发现 *H. indica* LN2 IJ 线虫按照 1.5 亿/667 m^2 施用 14 d 后韭蛆虫口密度减少 50%，与辛硫磷无显著差异，同时，线虫对韭蛆具有持续性的防治效果，直至初秋韭蛆虫口密度始终保持在 100 头/m^2 以下的较低密度。对于保护地栽培的韭菜生产，在春、秋、冬三个关键节点，施用添加 1/10 田间推荐剂量吡虫啉的 *S. feltiae* SN IJ 线虫 2.0 亿/667 m^2 表现出优于灭幼脲的防控效果，能够实现韭蛆的周年有效控制（赵国玉等，2013；Yan *et al.*，2019）。

7　昆虫病原线虫活力与环境因子的关系

7.1　昆虫病原线虫与昆虫寄主

H. bacteriophora 线虫侵染导致暗黑鳃金龟和大黑鳃金龟幼虫脂肪体和中肠细胞出现明显病变（吴文丹等，2015d）。暗黑鳃金龟的免疫相关基因 *PGRP-SC1*、*PPAE-I* 和 *GST* 参与了对 *H. beicherriana* 线虫感染的抵抗（Li *et al.*，2021b）。昆虫病原线虫可抑制水椰八角铁甲 *Octodonta nipae* 酚氧化酶系统的激活（Sanda *et al.*，2018；Sanda and Hou，2023），以及草地贪夜蛾（李而涛等，2022）和冷杉梢斑螟 *Dioryctria abietella*（聂振业等，2023）的多酚氧化酶、超氧化物歧化酶、过氧化氢酶、乙酰胆碱酯酶、谷胱甘肽 *S*-转移酶等的变化。*S. feltiae* 线虫感染大蜡螟幼虫后，昆虫的色氨酸（Trp）途径被显著激活，血淋巴中的犬尿氨酸（Kyn）和 3-羟基苯甲酸（3-HAA）含量显著升高；3-HAA 对大蜡螟幼虫高毒性（Zhang *et al.*，2022）。*S. carpocapsae* 侵染可导致榛实象甲 *Curculio dieckmanni* 幼虫相关基因和代谢物的改变（Wang *et al.*，2025）。*H. megidis* 比 *S. felitiae* 对大蜡螟幼虫表现出更强的趋性，且寄主的存在对线虫的迁移能力有影响（吴霞等，2021）。

7.2　昆虫病原线虫与活性化合物

蛔甙类线虫信息化合物具有调控线虫聚集、趋避、交配、耐受态幼虫形成及扩散传播等行为的功能（Jeong *et al.*，2005；Kim *et al.*，2009；Kaplan *et al.*，2012；Hartley *et al.*，2019；Oliveira-Hofman *et al.*，2019）。研究发现，某些蛔甙影响 IJ 的恢复、扩散和在琼脂平板和液体培养基中的产量（Kong *et al.*，2022；Wang *et al.*，2022）。此外，蛔甙和共生细菌调控大蜡螟幼虫的免疫响应（Chantab *et al.*，2024）。

研究已经发现，异戊醇对多种昆虫病原线虫具有排斥作用（Baiocchi *et al.*，2020），而寄主昆虫本身分泌的化学物质可以吸引昆虫病原线虫。红棕象甲 *Rhynchophorus ferrugineus* 利用分泌的化学信号吸引 *S. carpocapsae* 线虫（Santhi *et al.*，2021）。线虫感染致死的玉米根叶甲 *Diabrotica virgifera virgifera* 虫尸的挥发性物质对其他玉米根叶甲幼虫具有吸引作用，有利于线虫感染更多的寄主并成功繁殖（Zhang *et al.*，2019c；Santhi *et al.*，2021）。α-松油醇影响群体免疫（Social immunity），增加昆虫病原线虫对白蚁的致病性（Zeng *et al.*，2023）。甘油磷酰胆碱（Glycerophosphocholine）参与了 *S. kraussei* 0657L 的寿命调控，并通过激活胰岛素/IGF-1 信号通路和下游 PI3K/MAPK 激酶在抵抗外部应激中发挥重要作用，为提高 *S. kraussei* 的商业功效

提供了新的思路（Li *et al.*，2024d）。被昆虫病原线虫感染的昆虫尸体所释放的挥发性化合物影响了南方根结线虫的发育（Li *et al.*，2024a）。由于多重毒性作用，*S. feltiae* 线虫摄入聚苯乙烯微塑料后会损害其适合度（Li *et al.*，2024b）。绿原酸被认为可能通过胰岛素/IGF-1 信号通路提高 *S. kraussei* 的抗氧化能力并延长其寿命（陈红等，2024）。

7.3 昆虫病原线虫与环境非生物因素

田间应用昆虫病原线虫时，土壤的结构和质地、湿度、温度、田间施用剂量以及施用方法等因素直接影响昆虫病原线虫的应用效果（Půza and Mrácek，2005；武海斌等，2015c）。*S. feltiae* SN 在 15-20 ℃的温度范围内，比 *H. indica* LN2 对韭菜迟眼蕈蚊感染效果更强，表明两种昆虫病原线虫的最佳侵染温度有差异（Yan *et al.*，2019）。*Steinerenema* 线虫在 25 ℃、相对湿度为 50.5%环境中处理 9 h 后存活率仍较高，而 *Heterorhabditis* 线虫几乎没有存活（邢玉芳等，2009）。5 龄二点委夜蛾 *Athetis lepigone* 幼虫在 15%土壤含水量时对 *H. bacteriophora* HB8 线虫最敏感（雷利平等，2013），当土壤含水量为 20%时 *S. glaseri* 线虫对黄地老虎 *A. segetum* 幼虫的防治效果最好（张安邦，2015）。可通过添加抗干燥剂及抗蒸发剂以提高昆虫病原线虫防治害虫的效果（金永玲和韩日畴，2009；金永玲等，2013）。土壤质地影响昆虫病原线虫的分布、扩散和对昆虫的感染毒力（王庆雷等，1995；钱秀娟等，2005；陈书龙等，2006）。沙壤土和壤土更适合昆虫病原线虫建立种群（钱秀娟等，2014）。

8 展望

作为新型的昆虫天敌类生物农药，昆虫病原线虫及其共生细菌已经商业生产，应用于全球多种有害生物的防控。展望未来，这类制剂在我国的广泛应用仍需要高度关注如下趋势：

1）政策指引：生物农药的广泛应用离不开环境保护政策的支持。“绿水青山就是金山银山”发展理念已写进党章，在这一核心理论的指导下，我国生物农药包括昆虫病原线虫的发展前景广阔。

2）技术优化和成本控制：昆虫病原线虫保持持续商业竞争力的关键因素是基于昆虫病原线虫、共生细菌以及寄主昆虫的交互作用深入研究基础上，更优化的培养系统且更高效的贮存技术；同时，通过资源筛选、杂交、遗传改造等方法获得更耐受干燥、极端温度、紫外线等环境条件的昆虫病原线虫品系。

3）市场信誉：像其它生物农药一样，昆虫病原线虫的控制对象是害虫、植物病原等，评价其价值的关键是被保护农产品的质量和价格。消费者愿意为了健康高消费被生物农药保护的农产品。但市场上不应该出现假冒被生物农药保护的农产品，这样会动摇消费者的信心，从而摧毁被生物农药保护的农产品的信誉。这也是未来尤其需要关注的重点。

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