

应用昆虫病原线虫防控白蚁的研究现状*

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摘要 昆虫病原线虫是防治白蚁极具潜力的生物杀虫剂, 但其在白蚁防控中的应用效果有待进一步研究。本文综述了昆虫病原线虫及其共生细菌在白蚁防治中的应用研究进展, 探讨了昆虫病原线虫防治白蚁应用存在的关键问题, 并对其未来的研究方向进行展望。

关键词 昆虫病原线虫; 白蚁; 生物防治; 免疫; 防御机制

Current status of research on the use of entomopathogenic nematodes as a biological control for termites

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Abstract Entomopathogenic nematodes (EPNs) have great potential as a biological control for termites but their application requires further study. This paper reviews progress in the use of EPNs, and their symbiotic bacteria, for termite control, and the mechanisms by which EPNs control these pests. The bottlenecks, key points and future prospects for using EPNs for termite control are discussed.

Key words entomopathogenic nematode; termite; biological control; immunity; defense mechanism

白蚁分布于全球陆地面积的 50%, 是世界上农林树木、建筑结构的重要害虫 (Ahmad *et al.*, 2021)。白蚁防治的方法正逐渐由传统的化学防治转变为以安全防治、绿色防控为主 (Verma *et al.*, 2009; Ahmad *et al.*, 2021)。其中, 白蚁的生物防治是利用捕食性天敌、昆虫病原微生物、寄生螨、抗生素、生物源杀白蚁剂等, 期望成为替代或减少化学防治的新型安全防控策略 (Wang *et al.*, 2002a; Pandey *et al.*, 2012; Petráková *et al.*, 2015; Qodiriyah *et al.*, 2015; Mousavi *et al.*, 2020)。昆虫病原线虫 (Entomopathogenic

nematodes, EPNs) 因其具有能够主动搜寻寄主、杀虫谱广、不易产生抗药性、可与多种杀虫剂复配使用等优点, 已成为极具潜力的生物防治剂之一 (Bedding *et al.*, 1993; Yan *et al.*, 2019; Platt *et al.*, 2020)。早在 20 世纪 70 年代已有研究者开始利用昆虫病原线虫防治白蚁, 并发现线虫对白蚁具有较强的侵染能力, 但是野外施用防控白蚁的效果不稳定 (Fujii, 1975)。近年来, 昆虫病原线虫作为白蚁防控具有潜力的生物制剂, 相关应用研究再次被关注 (AL-Zaidawi *et al.*, 2020)。本文综述了昆虫病原线虫的防治机制、

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昆虫病原线虫在白蚁防治中的应用,以及应用昆虫病原线虫防治白蚁尚面临的免疫和栖息环境等关键问题,以期为进一步提高昆虫病原线虫防治白蚁的效果提供参考。

1 昆虫病原线虫及其侵染效率影响因素

1.1 昆虫病原线虫及其共生菌

应用于害虫生物防治的昆虫病原线虫主要为斯氏科 *Steinernematidae* 的斯氏属 *Steinernema* 和异小杆科 *Heterorhabditidae* 的异小杆属 *Heterorhabditis*。到目前为止已鉴定昆虫病原线虫 115 种,其中斯氏属 91 种线虫、异小杆属 24 种线虫 (Ali *et al.*, 2005; Shahina *et al.*, 2013)。

昆虫病原线虫通过宿主昆虫虫体的自然开口(如口、肛门、气孔等)或表皮侵入宿主 (Georgis and Gaugler, 1991; Gulzar *et al.*, 2020)。线虫侵染期幼虫 (Infective juvenile) 入侵宿主后,释放的共生细菌在昆虫血淋巴中大量繁殖,分泌毒素和次生代谢物质,分解宿主昆虫血淋巴中的营养物质,供线虫繁殖、生长发育,致使宿主昆虫患败血症,最终引起昆虫死亡 (Ciche and Ensign, 2003; Goodrich-Blair and Clarke, 2007; Liu *et al.*, 2020)。现已鉴定出昆虫病原线虫共生细菌 45 种,其中与斯氏线虫共生的嗜线虫杆菌属 *Xenorhabdus* 有 26 种,与异小杆线虫共生的发光杆菌属 *Photobacterium* 有 19 种 (Sajnaga and Kazimierczak, 2020; NCBI 数据库)。当食物匮乏或是线虫密度过高时,线虫发育成不取食的侵染期幼虫离开宿主,重新回到土壤中寻找新的寄主 (Wang and Bedding, 1996; Kaplan *et al.*, 2020)。

1.2 病原线虫侵染效率的影响因素

昆虫病原线虫对目标害虫的防效与其种类、品系、共生细菌、搜寻寄主方式及外界环境有关 (Yu *et al.*, 2006; Baimey *et al.*, 2015; Razia and Sivaramakrishnan, 2016; Iqbal *et al.*, 2020)。首

先,不同种线虫对同种害虫侵染及致死力不同,如同为异小杆属的 *Heterorhabditis bacteriophora* 和 *Heterorhabditis indica* 对韭蛆的防治效果差异显著 (孙瑞红等, 2004)。即使是同种不同品系的线虫对蛴螬的致死效果也有差异 (Sankaranarayanan *et al.*, 2019),因为不同品系线虫的共生细菌可能存在差异,其次代谢产物对害虫也可能具有不同的毒性。从小卷蛾斯氏线虫 *Steinernema carpocapsae* 的 2 个品系中分别分离到共生细菌 *Xenorhabdus nematophila* SK1 和 *Xenorhabdus nematophila* SK2,基于 GC-MS 分析分别检测出 30 种和 44 种次生代谢物,而且 SK2 毒力高于 SK1 (Hasan *et al.*, 2019),当然并不是所有的共生细菌次生代谢物对昆虫都具有杀虫活性 (Bowen *et al.*, 2000)。因此,昆虫病原线虫种属、品系与共生细菌种类之间一定程度的特异性共生关系是影响线虫杀虫毒力的重要因素 (Bedding *et al.*, 1993; 于峰, 2018)。其次,线虫对寄主攻击型 (Cruise)、中间态 (Intermediate) 和埋伏型 (Ambush) 等搜寻方式的不同也影响线虫的防效 (Kaya and Gaugler, 1993; Bal and Grewal, 2015)。小卷蛾斯氏线虫属于埋伏型,搜寻寄主能力弱,适合寄生于浅土层昆虫如桃小食心虫 *Carposina sasakii* 老熟幼虫 (杨平等, 2000);而位于深土层的昆虫如蛴螬则适合施用搜寻能力和活动能力强的攻击型线虫如格氏斯氏线虫 *Steinernema glaseri* (Guo *et al.*, 2020)。此外,线虫施用时的湿温度等环境因子也对线虫的侵染力有重要的影响。例如, *Steinernema kraussei* 和小卷蛾斯氏线虫在 25 °C 时的侵染能力高于在 15 °C 时的侵染能力 (Khan *et al.*, 2020; Julia *et al.*, 2020)。长尾斯氏线虫 *Steinernema longicaudum*、小卷蛾斯氏线虫和 *H. indica* 在 25-35 °C 的侵染能力也高于在 10-15 °C (Yan *et al.*, 2020)。小卷蛾斯氏线虫和 *H. indica* 在 40 °C 侵染能力大大下降 (Devindrappa *et al.*, 2018)。昆虫病原线虫侵染的最适合温度一般在 25-35 °C。

2 昆虫病原线虫防治白蚁的应用研究

2.1 昆虫病原线虫对白蚁致病性研究

2.1.1 不同品级白蚁对昆虫病原线虫的易感性 白蚁是由工蚁、兵蚁、繁殖蚁等多品级构成的社会性昆虫 (Rasheed *et al.*, 2019)。由于不同品级白蚁个体的先天免疫力有别而使其对昆虫病原线虫易感性有很大差异 (Mankowski *et al.*, 2005)。小卷蛾斯氏线虫和 *H. indica* 侵染台湾乳白蚁 *Coptotermes formosanus* 和菲岛乳白蚁 *Coptotermes vastator* 的工蚁和兵蚁时, 发现兵蚁更易被感染 (Mankowski *et al.*, 2005)。勇猛大白蚁 *Macrotermes bellicosus* 和西部三脉白蚁 *Trinervitermes occidentalis* 对线虫 *H. indica*、*Heterorhabditis sonorensis*、*Steinernema* sp. 的感染试验发现兵蚁比工蚁更易被感染 (Zadji *et al.*, 2014b)。此外, 北美散白蚁 *Reticulitermes flavipes* 的工蚁和若虫对线虫小卷蛾斯氏线虫和 *H. bacteriophora* 不敏感 (Manzoor, 2012)。关于繁殖蚁品级研究显示, 低浓度 *Steinernema abbasi* 和 *H. indica* 对小白蚁 *Microtermes* spp. 原始繁殖蚁有较高的感染能力 (Mohan *et al.*, 2016)。可见, 兵蚁对线虫的侵染最为敏感, 而不同种属白蚁的工蚁对线虫侵染的敏感性差异很大。

2.1.2 昆虫病原线虫对白蚁的致病性 白蚁高致病性昆虫病原线虫筛选一直是该领域白蚁生防研究的主要内容之一 (表 1)。首先, 不同线虫对同种白蚁的致病性有别。防治黑翅土白蚁 *Odontotermes formosanus* 时, 斯氏属线虫小卷蛾斯氏线虫相较异小杆属的 *H. bacteriophora* 表现出了更强的毒力 (朱建华, 2002; 于静亚等, 2018)。同样, 对成堆角象白蚁 *Cornitermes cumulans* 的侵染实验中, 斯氏属线虫也比异小杆属线虫能更有效, 其中对白蚁致死率最高的是夜蛾斯氏线虫 *Steinernema feltiae* (Souza, 2006)。然而, *S. feltiae* 能够侵染金黄异白蚁 *Heterotermes aureus* 却无法在其体内繁殖 (Yu *et al.*, 2008)。相比斯氏属线虫小卷蛾斯氏线虫 *Steinernema riobrave*, 异小杆属的 *H.*

bacteriophora 对北美散白蚁和台湾乳白蚁的致死率最高 (Wang *et al.*, 2002b)。*H. bacteriophora* 比商业化的小卷蛾斯氏线虫对差异锯白蚁 *Microcerotermes diversus* 也显示出更大的生防潜能 (Al-Zaidawi *et al.*, 2020)。

其次, 同种线虫对于不同的白蚁的侵染效果也不一样, 斯氏属线虫 *S. riobrave* 对金黄异白蚁有极高的致死率 (Yu *et al.*, 2006), 但对北美散白蚁几乎没有效果 (Wang *et al.*, 2002b)。而 *Steinernema* sp. 对勇猛大白蚁和西部三脉白蚁的侵染效果差异显著 (Zadji *et al.*, 2014b)。目前室内的研究表明, 对于高等白蚁, 斯氏属线虫防治效果优于异小杆线虫; 而对于低等白蚁, 异小杆属线虫表现出了较大的生防潜力。

2.2 昆虫病原线虫共生细菌在白蚁防治中的应用

昆虫病原线虫共生细菌的培养液可以直接用于白蚁的防治。斯氏线虫共生细菌 *Xenorhabdus steinernematis* 和异小杆线虫共生细菌 *Photorhabdus luminescens* 的细胞悬液分别对小白蚁属食菌小白蚁 *Microtermes mycophagus* 和 大白蚁属种类 *Macrotermes* spp. 有极高的致死率 (Shahina *et al.*, 2011; Iqbal *et al.*, 2020)。不仅如此, *H. bacteriophora* 的共生细菌 *P. luminescens* 的培养液也表现出对大白蚁极高的致死率 (Shahina *et al.*, 2011), *P. luminescens* 杀虫活性蛋白 *tcdA1* 和 *tcdB1* 基因与白蚁肠道细菌载体重组后, 喂食白蚁含有重组细菌的滤纸, 结果表明重组细菌具有有效且可持续的防治潜力 (Zhao *et al.*, 2008)。虽然目前昆虫病原线虫共生细菌在白蚁防治中的研究有限, 但线虫共生细菌已被证明能够通过多种形式防治害虫 (Shankhu *et al.*, 2020; Wu *et al.*, 2020), 这为今后利用昆虫病原线虫共生细菌防治白蚁的应用研究提供了参考。

2.3 昆虫病原线虫与其他杀虫剂复配应用

一些昆虫病原线虫对杀虫剂具有耐受性, 因此其与化学杀虫剂、植物源杀虫剂等混用对于害虫防治有增效作用 (Yan *et al.*, 2012; Jaffuel

表 1 昆虫病原线虫防控白蚁的研究

Table 1 Study on entomopathogenic nematodes in termite control

昆虫病原线虫 Nematode species	白蚁 Termites species	文献 References
蠹蛾新线虫 <i>Neoplectana carpocapsae</i>	台湾乳白蚁 <i>Coptotermes formosanus</i>	Fujii <i>et al.</i> , 1975
<i>Heterorhabditis</i> sp.	延伸树白蚁 <i>Glyptotermes dilatatus</i>	Danthanarayana and Vitarana, 1987
夜蛾斯氏线虫 <i>Steinernema feltiae</i>	黑胫散白蚁 <i>Reticulitermes tibialis</i>	Epsky and Capinera, 1988
夜蛾斯氏线虫 <i>Steinernema feltiae</i>	北美散白蚁 <i>Reticulitermes flavipes</i>	Mauldin and Beal, 1989
夜蛾斯氏线虫 <i>Steinernema bibionis</i>		
棉铃虫异小杆线虫 <i>Heterorhabditis heliothidis</i>		
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	好斗后琥珀白蚁	Amarasinghe and Hominick, 1993
夜蛾斯氏线虫 <i>Steinernema feltiae</i>	<i>Postelectrotermes militaris</i>	
长尾新斯氏线虫	北美散白蚁 <i>Reticulitermes flavipes</i>	Nguyen and Smart, 1994
<i>Neosteirnerma longicurvicauda</i>		
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	黑翅土白蚁	朱建华, 2002
夜蛾斯氏线虫 <i>Steinernema feltiae</i>	<i>Odontotermes formosanus</i>	
长尾斯氏线虫 <i>Steinernema longicadum</i>		
嗜菌异小杆线虫		
<i>Heterorhabditis bacteriophora</i>		
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	北美散白蚁 <i>Reticulitermes flavipes</i>	Wang <i>et al.</i> , 2002a
斯氏线虫 <i>Steinernema riobrave</i>	台湾乳白蚁 <i>Coptotermes formosanus</i>	
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		
印度异小杆线虫 <i>Heterorhabditis indica</i>		
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	台湾乳白蚁 <i>Coptotermes formosanus</i>	Mankowski <i>et al.</i> , 2005
印度异小杆线虫 <i>Heterorhabditis indica</i>	格斯特乳白蚁 <i>Coptotermes vastator</i> (=C. gestroi)	
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	成堆角象白蚁 <i>Cornitermes cumulans</i>	Souza, 2006
夜蛾斯氏线虫 <i>Steinernema feltiae</i>		
格氏斯氏线虫 <i>Steinernema glaseri</i>		
斯氏线虫 <i>Steinernema riobravus</i>		
沙地斯氏线虫 <i>Steinernema arenarium</i>		
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		
<i>Heterorhabditis</i> sp.		
斯氏线虫 <i>Steinernema riobrave</i>	黄金异白蚁 <i>Heterotermes aureus</i>	Yu <i>et al.</i> , 2006
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	扭曲颞钩白蚁 <i>Gnathamitermes perplexus</i>	
夜蛾斯氏线虫 <i>Steinernema feltiae</i>	北美散白蚁 <i>Reticulitermes flavipes</i>	
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	狭颈动白蚁 <i>Zootermopsis angusticollis</i>	Wilson-Rich <i>et al.</i> , 2007
斯氏线虫 <i>Steinernema riobrave</i>	黄金异白蚁 <i>Heterotermes aureus</i>	Yu <i>et al.</i> , 2008
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>		
夜蛾斯氏线虫 <i>Steinernema feltiae</i>		
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		
斯氏线虫 <i>Steinernema riobrave</i>	弯嘴沙白蚁 <i>Psammotermes hybostoma</i>	Ibrahim and El-Latif, 2008
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>		
<i>Heterorhabditis</i> sp.		
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		

续表 1 (Table 1 continued)

昆虫病原线虫 Nematode species	白蚁 Termites species	文献 References
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	成堆角象白蚁 <i>Cornitermes cumulans</i>	Rosa <i>et al.</i> , 2008
<i>Steinernema masoodi</i>	胖身土白蚁 <i>Odontotermes obesus</i>	Ahmad <i>et al.</i> , 2010
巴基斯坦斯氏线虫 <i>Steinernema pakistanense</i>	大白蚁 <i>Macrotermes</i> sp.	Shahina and Tabassum, 2010
斯氏线虫 <i>Steinernema riobrave</i>	黄金异白蚁 <i>Heterotermes aureus</i>	Yu <i>et al.</i> , 2010
	北美散白蚁 <i>Reticulitermes flavipes</i>	
	台湾乳白蚁 <i>Coptotermes formosanus</i>	
异小杆线虫 <i>Heterorhabditis baujardi</i>	沙白蚁 <i>Psammotermes hypostoma</i>	Elbassiouny and Abd-Elrahman, 2011
印度异小杆线虫 <i>Heterorhabditis indica</i>	黄赭无刺白蚁 <i>Anacanthotermes ochraceus</i>	
格氏斯氏线虫 <i>Steinernema glaseri</i>	北美散白蚁 <i>Reticulitermes flavipes</i>	Murugan and Vasugiet, 2011
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	北美散白蚁 <i>Reticulitermes flavipes</i>	Manzoor, 2012
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		
索诺拉异小杆线虫 <i>Heterorhabditis sonorensis</i>	勇猛大白蚁 <i>Macrotermes bellicosus</i>	Zadji <i>et al.</i> , 2014a
印度异小杆线虫 <i>Heterorhabditis indica</i>		
印度异小杆线虫 <i>Heterorhabditis indica</i>	西部三脉白蚁 <i>Trinervitermes occidentalis</i>	Zadji <i>et al.</i> , 2014b
索诺拉异小杆线虫 <i>Heterorhabditis sonorensis</i>	勇猛大白蚁 <i>Macrotermes bellicosus</i>	
<i>Steinernema</i> sp.	乳白蚁 <i>Coptotermes</i> sp.	Qodiriyah <i>et al.</i> , 2015
<i>Heterorhabditis</i> sp.	小白蚁 <i>Microtermes</i> sp.	
印度异小杆线虫 <i>Heterorhabditis indica</i>	小白蚁 <i>Microtermes</i> sp.	Mohan <i>et al.</i> , 2016
<i>Steinernema abbasi</i>		
<i>Steinernema siamkayai</i>	北美散白蚁 <i>Reticulitermes flavipes</i>	Razia and Sivaramakrishnan, 2016
巴基斯坦斯氏线虫 <i>Steinernema pakistanense</i>	<i>Odontotermis hornei</i>	
印度异小杆线虫 <i>Heterorhabditis indica</i>		
<i>Steinernema kari</i>	台湾乳白蚁 <i>Coptotermes formosanus</i>	Wagutu <i>et al.</i> , 2017
<i>Steinernema</i> sp.	黑翅土白蚁 <i>Odontotermes formosanus</i>	于静亚等, 2018
<i>Heterorhabditis</i> sp.		
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>	胖身土白蚁 <i>Odontotermes obesus</i>	Devi <i>et al.</i> , 2018
<i>Steinernema</i> sp.		
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>	象白蚁 <i>Nasutitermes</i> sp.	Neto <i>et al.</i> , 2018
格氏斯氏线虫 <i>Steinernema glaseri</i>		
<i>Heterorhabditis</i> sp.		
小卷蛾斯氏线虫 <i>Steinernema carpocapsae</i>	差异锯白蚁 <i>Microcerotermes diversus</i>	Al-Zaidawi <i>et al.</i> , 2020
嗜菌异小杆线虫 <i>Heterorhabditis bacteriophora</i>		
巴基斯坦斯氏线虫 <i>Steinernema pakistanense</i>	埃姆乳白蚁 <i>Coptotermes heimi</i>	Khanum and Javed, 2020
<i>Steinernema siamkayai</i>		
<i>Steinernema bifurcatum</i>		
<i>Steinernema maqbooli</i>		

et al., 2019; 李而涛等, 2019)。线虫与杀虫剂复配应用于白蚁防治的相关研究报道较少。有研究显示线虫小卷蛾斯氏线虫与吡虫啉混合使用

显著提高了北美散白蚁的死亡率 (Manzoor, 2012); 线虫 *Heterorhabditis* sp. 与非合成杀虫剂复配也极大地提高了 *Nasutitermes* spp. 的死亡率

(Neto *et al.*, 2018); *S. glaseri* 与植物源防治剂印楝素联合使用也有效地提高了对北美散白蚁的防效 (Murugan and Vasugiet, 2011)。昆虫病原线虫与杀虫剂复配不仅提高了害虫防治效果而且可减少杀虫剂的使用, 值得未来白蚁防治借鉴。

3 昆虫病原线虫应用于白蚁防治存在的问题

3.1 白蚁栖息环境的特殊性

昆虫病原线虫的施用方法较多, 最普遍的是野外直接喷施线虫悬浮液 (Shapiro-Ilan *et al.*, 2012)。但是, 一方面, 直接喷施的方法受外界环境影响较大, 比如外界环境干燥、高温等因素会直接影响线虫侵染能力甚至导致线虫死亡 (Shapiro-Ilan *et al.*, 2006; Hiltbold, 2015)。另一方面, 白蚁栖息环境隐秘、二氧化碳浓度高, 蚁穴内壁由粪便和唾液的混合物构成并含有抗菌物质, 不利于线虫的存活 (Chen *et al.*, 1998; Eisuke *et al.*, 2018; Tasaki *et al.*, 2020)。白蚁巢附近土壤的酸碱度也对线虫活力有所影响, 格拉塞散白蚁 *Reticulitermes grassei* 适宜生存在偏酸或中性的土壤环境中, 然而线虫则在高 pH 的土壤中较为常见 (Wu *et al.*, 2011; Cárdenas *et al.*, 2020)。可见, 白蚁自身栖息环境的特异性大多不利于直接喷施的线虫存活、侵染及持效期。有研究发现, 施用线虫感染后的大蜡螟 *Galleria mellonella* 尸体或将线虫包裹在胶囊中施用能够在一定程度上提高线虫的耐受性, 让防治效果更为持久 (谷星慧等, 2015)。因此, 应基于白蚁栖息环境及生活习性, 研发昆虫病原线虫防控白蚁的关键应用技术。

3.2 白蚁免疫防御机制的特殊性

白蚁作为社会性昆虫具有群体社会免疫与个体先天性免疫的双重防御系统来抵御外源病原体的入侵 (Liu *et al.*, 2019b)。首先, 白蚁与其它昆虫一样具有液体免疫和细胞免疫的个体免疫系统。近年来, 白蚁的免疫机制研究主要集

中于采用高通量测序技术分析寻找白蚁的关键免疫通路及免疫基因。使用真菌与细菌对白蚁进行免疫诱导后的转录组测序分析表明, 白蚁编码的大量保守免疫基因出现了显著的免疫响应, 如 *Toll-like receptor*、*caspase-1*、*Ras* 超家族, 多种抗菌肽基因表达量显著上调, 如 *prolixicin*、*cathepsin*、*Termicin* 等 (Thompson *et al.*, 2003; Abid *et al.*, 2013; Peterson and Scharf, 2016; Liu *et al.*, 2020)。同时, 不同品级和性别的白蚁应对病原体侵染时, 免疫基因的响应程度也不相同。如含有 C-type lectin 结构域的免疫识别蛋白、脂多糖结合蛋白、丝氨酸蛋白酶以及效应因子 *cathepsin*、溶菌酶等在不同的品级和性别的白蚁中表达量都存在差异 (Mitaka *et al.*, 2017); 台湾乳白蚁抗氧化防御直接相关基因中, *CAT*、*Gst*、*PrxSL*、*Cu/Zn-SOD2*、*TXN1*、*TXN2*、*TXNL1*、*TXNL2*、*TXNL4A* 和 *TPx* 在绿僵菌感染后的有翅成虫中表达量很高, 却在兵蚁中低表达 (Abid *et al.*, 2017)。在细胞免疫方面, 白蚁感染真菌后通过产生大量浆细胞或增加自由循环血细胞数量, 继而通过包被作用防御真菌 (Chouvenc *et al.*, 2009; Avulova and Rosengaus, 2011)。其次, 更为重要的是白蚁觅食、筑巢、防御等的社会性行为, 极大地提高了其对外界不利环境因素的抵御能力 (Rosengaus *et al.*, 2010; Cremer *et al.*, 2018; Liu *et al.*, 2019a)。白蚁觅食过程不可避免大量接触外界病原体, 通过避开病原体密集的地区来降低感染病原体的风险, 或者产生的抗真菌化学物质添加到筑巢材料中或利用共生微生物来抵御病原微生物 (Rosengaus *et al.*, 1998; Bulmer *et al.*, 2019)。白蚁感染病原真菌后, 在行为和生理上都发生了变化, 它们将危险信号传递给健康的个体, 或通过下颌开合及个体间的梳理行为清除被真菌感染个体的病原体 (Wilson-Rich *et al.*, 2007; Liu *et al.*, 2019b), 或将感染病原体的尸体搬离巢穴或掩埋, 从而降低病原体在群体中扩散速度 (Chouvenc and Su, 2011)。正是由于白蚁社会性群体行为防御机制, 线虫对地下白蚁的防控应用受到极大的影响 (Mankowski *et al.*, 2005; Chouvenc *et al.*, 2012)。

4 展望

目前利用昆虫病原线虫防控白蚁有潜力但仍面临着诸多挑战。首先,白蚁的双重免疫防御大大降低了线虫的实际防效。白蚁的群体免疫行为是造成线虫及其他昆虫病原微生物在实际白蚁防治应用中非常困难的关键原因之一。白蚁免疫机制的阐明尚存在大量的盲点,探究白蚁群体免疫行为的触发机制可能是未来重点突破的研究方向。例如,线虫及其制剂能够触发白蚁群体免疫,可从探究挥发物和白蚁嗅觉的关系入手展开相关研究,为线虫的筛选、改良提供方向,也为进一步开发引诱及驱避剂提供指引。

白蚁的先天免疫是防御线虫的最后一道屏障,但果蝇 *Drosophila melanogaster* 等免疫线虫的转录分析表明,传统 Toll 和 IMD 等免疫通路在对抗线虫侵染中是有限的 (Huot *et al.*, 2019)。传统 Toll 和 IMD 等免疫通路及先天免疫机制在白蚁体系中发挥怎样的作用尚未深入研究。因此,通过现代生物技术,进一步找寻白蚁免疫防御线虫的特异性信号通路、特异性靶标及作用物是促进昆虫病原线虫对白蚁防治效果的重要基础研究工作。

白蚁栖息环境不利于线虫有效侵染,因此还需解决线虫在白蚁巢中的存活与侵染的应用技术问题。通过转基因及遗传学等手段,建立或筛选高侵染性、高毒力线虫,增强线虫本身耐受性等途径增强线虫的防治效果;从应用技术上,研究开发线虫新型保护剂以延长线虫在白蚁巢中的作用时间,或分离共生细菌的毒蛋白、与其他生物防治复配使用等应用方法,为今后新型白蚁防治剂研发提供参考。

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