

二十一世纪以来中国白蚁研究进展*

曾文慧** 吴文静 李志强***

(广东省科学院动物研究所, 广东省动物保护与资源利用重点实验室, 广州 510260)

摘要 白蚁是热带和亚热带生态系统关键的分解者,也是社会生物学研究与生物质转化的模式生物,同时部分白蚁物种对社会经济和人们生活造成了严重危害。本文系统综述了 21 世纪以来我国在白蚁生态功能、社会生物学、木质纤维素代谢及白蚁防控等领域的研究进展,并展望了我国未来白蚁研究及防控技术发展的方向,旨在推动我国白蚁相关领域的技术进步及白蚁防控的绿色与智能化转型,为我国白蚁防治与开发利用提供理论支撑与技术参考。

关键词 白蚁; 社会生物学; 木质纤维素降解; 共生微生物; 害虫防治

Progress in termite research in China in the 21st century

ZENG Wen-Hui** WU Wen-Jing LI Zhi-Qiang***

(Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Institute of Zoology,
Guangdong Academy of Sciences, Guangzhou 510260, China)

Abstract Termites are key decomposers in tropical and subtropical ecosystems, as well as model organisms in sociobiology and biomass conversion. However, certain termite species pose a severe threat to socioeconomic development and people's livelihood. This paper systematically reviews advances in research on termites in China in the 21st century, covering ecological functions, sociobiology, lignocellulosic metabolism, and management strategies. Future directions for termite research and control in China are also discussed, with an emphasis on promoting technological innovation and facilitating environmentally-friendly, rational, termite management. This work provides theoretical support and technical references for both the control, and sustainable utilization, of termites in China.

Key words termites; sociobiology; lignocellulose degradation; symbiotic microorganisms; pest control

白蚁 (Isoptera) 作为典型真社会性昆虫的代表类群,具高度分化的品级系统和复杂的协作行为,在热带和亚热带生态系统中发挥着重要的生态功能,是地球上最成功的纤维素降解者,能够将 65%-99% 的木质纤维素转化为可利用能量,加速生态系统物质循环、能量流动 (Khan and Ahmad, 2018)。然而,约 10% 的白蚁物种被列为害虫,其通过蛀食木材和危害非纤维素材料,每年造成全球数十亿美元的经济损失 (Scharf, 2015; Mogilicherla *et al.*, 2023)。我国白蚁资源丰富,

亦是受其危害最严重的国家之一。白蚁的相关研究受到了国内外学者的广泛关注。

进入 21 世纪以来,我国白蚁研究也取得了显著进展。白蚁分类学研究从多种技术手段上探索新的分类方法,开始聚焦我国分类学问题的厘定;在社会生物学方面,组学大数据分析、RNA 干扰等主流技术已全面应用于围绕白蚁生存策略、繁殖、品级分化及社会免疫为主的调控机制研究,并对白蚁与共生微生物协同降解机制也开展了较为深入的研究。在防治技术层面,目前替

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**第一作者 First author, E-mail: Zengwh@giz.gd.cn

***通讯作者 Corresponding author, E-mail: lizq@giz.gd.cn

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代持久性有机污染物 (Persistent organic pollutants, POPs) 的毒土预防及白蚁饵剂监控装置成为主要的防治方法。与此同时, 天然杀虫剂、纳米载药、缓释系统及智能监测装置的创新研究也已不断发展, 我国白蚁治理正在向绿色化、精准化方向逐步转型。同时, 我国白蚁分类有待持续系统修订、白蚁生态适应性及生态功能研究仍存在局限性、白蚁绿色防控技术的应用缺乏突破, 传统化学防治现状也亟需技术更新、迭代。本文综述了本世纪以来我国在白蚁多样性、社会生物学、木质纤维素代谢及绿色防控技术等多个领域的研究进展。

1 白蚁多样性与生态功能

我国白蚁分类研究始于 20 世纪 60 年代, 2000 年出版《中国动物志: 昆虫纲·第十七卷·等翅目》。但是, 白蚁分类依据的外部形态量度性状具较大局限性, 我国学者积极探索消化道内部形态 (高超等, 2011)、表皮碳氢化合物含量 (张红兵等, 2005)、DNA 序列多态性 (邢连喜等, 2001) 及少数分子标记序列、线粒体基因组信息 (周家怡等, 2025) 等, 结合传统形态开展白蚁分类及系统发育研究, 不断有白蚁同物异名、隐存种或新记录种的报道 (Wu *et al.*, 2019a; Ke *et al.*, 2024), 并仍有待继续系统解决。目前按最新分类系统和分类研究我国有白蚁 7 科 476 种。同时, 白蚁分布 (特别是乳白蚁、散白蚁) 正逐渐北扩 (李小荣等, 2014), 目前仅黑龙江、青海、宁夏、内蒙古、新疆 5 个省 (自治区) 无白蚁分布的公开报道。

虽然白蚁在全球生物的地球化学循环和生态系统功能中发挥重要作用, 但全球气候变化、大规模森林破碎化通过影响种间竞争而加剧白蚁危害 (Wu *et al.*, 2024a)。土地利用及生态类型差异显著影响白蚁物种、功能的多样性 (Li *et al.*, 2016b; Liu *et al.*, 2019c)。研究发现, 温度、地表湿度、土壤 pH 值、植被指数、凋落物量、地形等是白蚁多样性的重要环境因素 (Li *et al.*, 2016b; Thant *et al.*, 2023), 其中温度和土壤因子是形成白蚁形态量度性状区域分布格局的关键

驱动力 (Liu *et al.*, 2022)。白蚁是热带地区木质纤维素降解最主要的无脊椎动物贡献者, 其活动极大地改善了土壤特性及生物群落组成 (Njoroge *et al.*, 2025; Thant *et al.*, 2025; Wu *et al.*, 2025)。

2 白蚁社会生物学

2.1 生态适应及筑道、觅食

白蚁生态适应性强, 涉及行为、生理等调节机制。群体规模是种间竞争、格斗取胜的主要因素, 常见白蚁台湾乳白蚁 *Coptotermes formosanus*、黑翅土白蚁 *Odontotermes formosanus*、黑胸散白蚁 *Reticulitermes chinensis* 数量相当时, 土白蚁工蚁的斗争能力明显强于另两种白蚁的工蚁, 土白蚁可能在其群体建立中占据优势 (陈艳等, 2007)。此外, 白蚁在面临威胁时能迅速启动精细化应急行为, 如台湾乳白蚁工蚁形成单向逃逸流, 而兵蚁则通过攻击行为保护群体 (Wang *et al.*, 2016)。节律调控基因 (如 *Cry2* 与 *Per1*) 参与了黑胸散白蚁和黑翅土白蚁的昼夜节律调控, 其中 *Cry2* 与 *Orco* 还协同通过光敏性介导地磁场定向行为 (Gao *et al.*, 2021, 2023), 以及通过去饱和酶基因 (如 *Cfor-desatA2-b*) 调控脂肪酸合成影响交哺行为及耐旱性 (Xu *et al.*, 2024a)。对于白蚁同巢个体的识别, 化学感受基因 *Orco* 与神经传导基因 *5-HTT* 被发现共同介导黑翅土白蚁个体间识别, 其表达沉默会导致工蚁攻击同巢个体 (Sun *et al.*, 2019)。

白蚁的筑道行为对其饵剂研发有着重要的指导作用。对筑道基质的精准选择与利用, 保障了白蚁群体在复杂环境中的资源获取与生存优势。白蚁挖掘隧道受基质类型、温湿度等因素的显著影响。其中, 黑翅土白蚁在砂壤土中 28 °C 下表现最优的挖掘效率 (Xu *et al.*, 2019), 而台湾乳白蚁和黑胸散白蚁在黏土与壤土中的穿透速度显著高于砂土 (厉嘉辉等, 2019)。当泥被通道被破坏时, 白蚁优先利用黏土颗粒进行快速修复, 呈现三阶段逃逸模式, 并同步修复通道, 这种高效响应能力与其对黏土基质的偏好密切相关 (Xiong *et al.*, 2018)。

白蚁的觅食行为是一个多因素调控的复杂过程。首先,食物成分及取食环境均能影响白蚁的摄食选择,例如,小米粉添加 10 %白砂糖对黑翅土白蚁有诱食效应(黄求应等, 2005); 1.5%浓度的二氧化碳可增加对台湾乳白蚁的引诱,适量茶多酚可提高对苯二酚对台湾乳白蚁的诱食效果(张世军和李志强, 2017; 候亚会等, 2018); 在干燥条件下,聚丙烯酸钠等保水材料可提升台湾乳白蚁的取食行为,而聚丙烯酰胺/凹凸棒石复合材料能促进其觅食(Xie *et al.*, 2019a, 2019b)。其次,林木挥发物及微生物代谢物也可能引起白蚁觅食响应,松木 α -蒎烯和 β -蒎烯可抑制台湾乳白蚁的聚集行为,而含氧萜烯衍生物则表现出引诱效应(宋灿灿等, 2019); 密粘褶菌 *Gloeophyllum trabeum* 腐木提取物能显著增强黑翅土白蚁的踪迹活性(丁芳等, 2015), 木霉 *Trichoderma* spp. 代谢产物则可诱导台湾乳白蚁和黑翅土白蚁聚集(Zhang *et al.*, 2023)。Wen 等(2014)揭示了黑翅土白蚁分泌的(3Z)-十二碳-3-烯-1-醇与(3Z,6Z)-十二碳-3,6-二烯-1-醇构成变化的踪迹信息素系统。嗅觉系统在白蚁觅食中发挥关键作用,尖唇散白蚁 *Reticulitermes aculabialis* 的嗅觉蛋白对长链烃类和萜类挥发物具有特异性亲和特性(Yang *et al.*, 2025); 黑翅土白蚁神经肽 Y 基因 *NPY* 级联下调化学感受基因 *Orco* 的表达可损害其觅食嗅觉响应; 黑胸散白蚁蛋白激酶基因 *PKG* 沉默会破坏其对信息素的追踪能力而影响觅食成功率(Xu *et al.*, 2022, 2024b); 能量代谢基因 *IDH* 被发现能通过调控脑部 ATP 供应调控台湾乳白蚁觅食决策(Xu *et al.*, 2021)。以上研究呈现出白蚁通过整合环境信号、化学通讯与基因表达,从个体到群体的觅食调控网络。

2.2 繁殖与品级分化

白蚁繁殖与品级分化机制一直是社会性演化的研究热点。白蚁的繁殖始于分飞行为,白蚁分飞后线粒体 ATP 供应能力下降,飞行肌逐步退化解体,其特有的背侧板肌(II-tpm5 与 III-tpm5)调控脱翅(Zhang *et al.*, 2021)。黑胸

散白蚁分飞后配偶定位受副腺蛋白(Accessory gland protein, ACP)琥珀酰化修饰调控,通过 β -丙氨酸代谢通路修饰位点靶向干预抑制繁殖(Liu *et al.*, 2024)。两型钩白蚁 *Ancistrotermes dimorphus* 雌性腹板腺则合成(3Z,6Z)-十二碳-3,6-二烯-1-醇吸引配偶(Wen *et al.*, 2015)。白蚁生殖策略多样,黑胸散白蚁原始繁殖蚁(Primary reproductive)依靠脱水减重抗寒,存在着糖脂代谢转换机制,以提高工蚁密度来增加交哺频率是其提高产卵量与生物量积累的策略之一(Bai *et al.*, 2021; Li *et al.*, 2021)。面对配偶缺失,截头堆砂白蚁 *Cryptotermes domesticus*、圆唇散白蚁 *Reticulitermes labralis*、黑胸散白蚁等低等白蚁可快速分化形成补充繁殖蚁(Secondary reproductive)。截头堆砂白蚁具备转化成多种翅芽长度补充繁殖蚁的能力;黑胸散白蚁的补充繁殖蚁相较原始繁殖蚁和脱翅繁殖蚁有更快的产卵速度和更为持久的产卵周期;圆唇散白蚁的工蚁还具有逃避型较攻击型更易分化的特点,且为依靠数量优势提升群体繁殖力(张小晶等, 2015; Bai *et al.*, 2022; Wu *et al.*, 2024b, 2024c)。同时,近源杂交也是白蚁补充繁殖策略之一:在实验室条件下实现了黄胸散白蚁 *Reticulitermes flaviceps* 和黑胸散白蚁的杂交并产生后代(Wu *et al.*, 2019e);即使尖唇散白蚁和黄胸散白蚁的受精卵在关键发育阶段存在显著差异(Peng *et al.*, 2023),尖唇散白蚁雌性仍倾向于与黄胸散白蚁雄性进行种间交配(Wu *et al.*, 2024c)。此外,圆唇散白蚁工蚁主动搬运柱隔孢菌 *Fibulorhizoctonia* sp. 至卵堆,工蚁缺失后菌萌发并致死白蚁卵,提示真菌参与了白蚁繁殖调控(Ye *et al.*, 2019a)。

白蚁品级分化的多型现象及机制是白蚁社会生物学的重要方向。黑翅土白蚁幼蚁、工蚁、兵蚁可据触角感器来区分,其表皮碳氢化合物组分含量具品级特异性,其下唇腺结构也随品级有别,工蚁腺泡发达,兵蚁腺囊转化为防御器官(杨锦锦等, 2015; 张新慰等, 2015; 徐立军等, 2019)。散白蚁工蚁和兵蚁性腺发育差异显著,其中尖唇散白蚁工蚁卵子发生停滞无卵黄形成

(朱蓉等, 2009; 王云霞等, 2011); 圆唇散白蚁工蚁向补充繁殖蚁转化存在性别差异, 雌性需经两次蜕皮进入“前补充繁殖蚁”阶段, 而雄性则无需蜕皮直接交配 (Su *et al.*, 2017b)。围绕保幼激素 (Juvenile hormone, JH) 调控通路的品级分化与表型可塑分子机制研究, 一定程度上揭示了低等白蚁品级分化的多层次调控。台湾乳白蚁工蚁向前兵蚁转化中, 脂肪体发育相关代谢通路的变化与补充繁殖蚁分化时的能量分配机制相似 (Du *et al.*, 2020a, 2020b), 同时 miRNA 调控核糖体生物合成通路影响白蚁表型 (Du *et al.*, 2024)。黑胸散白蚁胰岛素信号通路 (Insulin signaling pathway, IIS) 在维持繁殖蚁长寿中起关键作用 (Haroon, 2022), 间接调控糖酵解酶-磷酸果糖激酶参与了各品级的能量代谢和行为可塑性 (Hassan *et al.*, 2021b)。圆唇散白蚁依靠 Ras-MAPK 通路调控了 JH 受体 *Met* 的表达, 促进了工蚁生殖器官 (如卵巢) 发育分化成繁殖蚁; 而表皮蛋白 RR 亚家族基因调控了翅型分化 (Su *et al.*, 2016b; Ye *et al.*, 2019b)。尖唇散白蚁兵蚁的特异性蛋白基因 *RaSpl* 通过结合 JH III 调控 *Met/Kr-h1* 信号级联通路 (Wu *et al.*, 2022), 其工蚁头部内表皮特异表达, 其中 *SgAbd* 等基因高表达与其环境适应性相关 (Rasheed *et al.*, 2019; Ye *et al.*, 2021)。双凹新白蚁 *Neotermes binovatus* 工蚁富集代谢与感器发育基因且宿主-鞭毛虫共表达强烈 (Huang *et al.*, 2025b)。

2.3 社会与先天免疫

白蚁进化出社会行为与生理免疫相结合的社会免疫防御体系。我国的研究涉及群体免疫行为、先天性免疫的生化与分子机制及共生微生物等领域。

梳理行为 (Allogrooming) 是白蚁抵御病原菌的重要社会行为, 该行为频率/时长在病原胁迫下显著增强。金龟子绿僵菌 *Metarhizium anisopliae* 的侵染可促进黑胸散白蚁个体间相互理毛频率升高清除体表孢子降低死亡率, 同时先天免疫基因表达下调, 提示社会行为可替代部分生理免疫成本 (Liu *et al.*, 2015, 2019a; Hassan *et al.*, 2021a)。化学感受在调控白蚁免疫行为上

起着重要的介导作用。麦角甾醇是触发台湾乳白蚁工蚁梳理行为增强的关键化学信号 (Chen *et al.*, 2023d), 并进一步由气味结合蛋白 CforOBP7 通过高亲和力结合白蚁尸体挥发物质-油酸介导乳白蚁掩埋响应 (Li *et al.*, 2024a), 有效阻止病原扩散。黑翅土白蚁嗅觉受体基因 *OforOrco* 介导了沙雷氏菌胁迫下的梳理行为, *OforOrco* 的沉默显著降低该行为频率从而提高了感病白蚁死亡率 (Lu *et al.*, 2024)。其次, 群体品级结构亦影响免疫效率。台湾乳白蚁高兵蚁比例激发工蚁无品级偏向性梳理行为, 群体倾向于牺牲部分被感染工蚁并上调先天性免疫水平以维持群体健康 (Zeng *et al.*, 2022); 尖唇散白蚁的梳理清洁主要由 4 龄以上工蚁承担, 食物以层叠式交哺方式传递 (邢连喜等, 2014); 兵蚁受保幼激素调控抑制 *RaSpl* 基因的表达, 从而激活报警信息素分泌等途径影响其撞头、撕咬等防御行为。 (Li *et al.*, 2024b)。此外, 其他免疫防御生态研究发现, 木霉兼具吸引台湾乳白蚁聚集、拮抗绿僵菌侵染及改变病原规避行为的三重生态功能 (Wen *et al.*, 2020); 法氏嗜渣螨 *Acarus farris* 寄生导致台湾乳白蚁增强报警振动和理毛的行为频率, 进而导致白蚁能量消耗, 加速宿主死亡 (Chen *et al.*, 2022b)。

白蚁先天免疫中氧化还原酶的作用受到较多的关注。台湾乳白蚁通过表达过氧化氢酶 (Catalase, CAT)、谷胱甘肽 S-转移酶 (Glutathione S-transferase, GST) 等 17 种抗氧化基因, 分泌萘、正己酸等挥发性有机化合物, 共同抑制病原真菌的孢子萌发 (Hussain *et al.*, 2017); 抑制过氧化氢酶基因表达引起抗菌肽基因表达、酚氧化酶活性的下调, 显著增加乳白蚁对绿僵菌的易感性 (Zeng *et al.*, 2024), 抑制酚氧化酶原 (Polyphenol oxidase, PPO) 基因 (如 *OfPPO*) 也可显著提高细菌感染致死率 (Wang *et al.*, 2022)。黑胸散白蚁经绿僵菌诱导亦可激活超氧化物歧化酶 (Superoxide dismutase, SOD) 和过氧化氢酶活性, 上调酚氧化酶、转铁蛋白及抗菌肽基因表达 (Liu *et al.*, 2015); 主动免疫中硒、钙、铬水平及硒蛋白 T 基因 (*SELT*) 显著

下调, 其中 *SELT* 与转谷氨酰胺酶基因 *TG* 共同驱动了黑胸散白蚁的免疫响应 (Zhao *et al.*, 2020)。病理学研究显示, 黑翅土白蚁经绿僵菌侵染被破坏了肌肉、脂肪组织及血淋巴系统, 并表现出血淋巴细胞钙离子浓度升高 (Dong *et al.*, 2009)。此外, 肠道微生态研究显示, 局部肠道免疫也发挥了重要的白蚁防御作用: 黑翅土白蚁感染罗伯茨绿僵菌 *Metarhizium robertsii* 后肠道菌群多样性先降后升, 动态重塑协助免疫稳态恢复 (Wu *et al.*, 2021); 抗生素清除其共生菌则导致 *APOA2*、*Calpain-5*、*Hsp70* 等基因表达紊乱, 显著削弱白蚁防御能力 (Tang *et al.*, 2023; Hassan *et al.*, 2024); 漆酶基因 *Cflac1* 沉默也扰乱肠道氧化还原稳态, 相应地降低了台湾乳白蚁对绿僵菌的抗性 (曾文慧等, 2024)。

RNA 干扰、组学等分子生物学技术为白蚁免疫机制解析, 及靶向免疫的防控提供了新策略。台湾乳白蚁基因组筛查拓展了免疫基因库, *CfPGRP-SC1/CfSCR3/CfHemocytin* 等基因表达抑制可显著提升白蚁对绿僵菌的敏感性 (Chen *et al.*, 2023b)。黑胸散白蚁对粘质沙雷氏菌 *Serratia marcescens* 侵染的免疫响应基因富集于吞噬、自噬、内吞作用及 Toll、IMD、黑化通路; 蛋白质组学分析发现其主动免疫涉及 12 种应激响应蛋白、6 种免疫信号蛋白及 2 种效应分子; 病毒基因组研究发现其携带病毒 RCBsV 与 RCBV, 降低其丰度能严重干扰白蚁正常的社会性行为 (Liu *et al.*, 2015; Luo *et al.*, 2022; Huang *et al.*, 2025a)。RNA 干扰 (RNA interference, RNAi) 技术是近年来白蚁分子通路研究的最常用手段, 研究发现黑胸散白蚁 *GNBP2* 基因下调能够削弱了白蚁对病原菌的免疫响应, 觅食核糖体蛋白 *RPL23* 的抑制可限制 *GNBP1*、*GNBP2*、酚氧化酶及凋亡基因 (*TNF- α* 、*caspases*) 等多个免疫通路关键基因的表达 (Zhou *et al.*, 2021b; Yu *et al.*, 2024); 干扰胰岛素受体底物 *IRS* 引发糖脂代谢紊乱, 减弱白蚁梳理行为并抑制抗菌肽基因表达, 最终黑胸散白蚁巢群抗真菌能力降低 (Zhou *et al.*, 2024b)。黑翅土白蚁抗菌肽基因 *Oftermicins* 的表达抑制可显著增加粘质沙雷

氏菌对土白蚁的致死率 (Feng *et al.*, 2022)。脂多糖结合蛋白 *CfLBP* 对 IMD 通路调控, 可显著降低台湾乳白蚁对病原菌的防御能力 (Chen *et al.*, 2023c)。此外, 非编码 RNA 也调控白蚁的免疫反应, Liu 等 (2023) 通过上调黑胸散白蚁 miR-7885-5p 和 miR-252b 靶向抑制多个免疫反应来提升真菌对白蚁的毒性; 台湾乳白蚁经典免疫与凋亡相关通路基因的多个 miRNA 被挖掘, 如 miR-120 靶向 *Draper* 基因 (张泓等, 2024)、miR-571 可抑制 *POP5* 及其下游丝氨酸蛋白酶基因、miR-701 靶向 *Toll4* 抑制抗菌肽合成 (Chen and Li, 2025a, 2025b)。

3 白蚁木质纤维素代谢

白蚁肠道被誉为高效降解木质纤维素的“世界上最小的生物反应器” (Brune, 1998), 其内丰富的微生物群落可降解食物中 65%-87% 的半纤维素和 74%-99% 的纤维素 (Watanabe and Tokuda, 2010)。2000 年以来, 我国研究逐渐从单独挖掘白蚁木质纤维素降解资源, 转向跨学科的仿生研究与资源化应用, 内容涵盖低等与高等白蚁的共生消化机制、木质纤维素酶资源以及肠道微生物的开发与利用。

3.1 低等白蚁的宿主-鞭毛虫-细菌共生消化系统

低等白蚁依赖其肠道内由宿主-鞭毛虫-细菌/古菌构成的高度协同共生系统, 实现了对木质纤维素的有效降解。 (Noda *et al.*, 2007)。围绕白蚁肠道共生系统高效转化降解木质纤维素的策略和机制, 国内外学者进行了多层次的研究。白蚁前肠和中肠主要起摄食、储藏、磨碎食物及部分消化食物的作用, 后肠由 P1、P2、P3、P4、P5 组成可吸收食物残渣的水分和无机盐也是消化木质纤维素主要场所, (杨红等, 2006; 羊桂英等, 2020)。微电极技术研究显示, 白蚁肠道内环境维持着相对稳定的中性 pH;。中肠具备富氧环境是修饰木质素的重要场所; 后肠囊形胃的氧、氢浓度和氧化还原电位呈辐射状分布, 氧浓度在肠壁最高、肠腔中心最低, 氢浓度则相反, 使多种微生物异质性分布有序降解木质纤维素

(Brune *et al.*, 1995; Ebert and Brune, 1997; Schmitt-Wagner and Brune, 1999; Kappler and Brune, 2002; Ke *et al.*, 2010)。肠道微环境的精细分区,促进了低等白蚁内源与外源酶系在空间和功能上的协同分工:宿主白蚁提供内源性糖苷水解酶(Glycoside hydrolases, GH)(如GH1、GH9等)以及多种辅助氧化还原酶(如漆酶、过氧化物酶、血蓝蛋白等),这些酶类在前肠和中肠的富氧环境中参与木质素的初步修饰与纤维素的初步水解(Qiu *et al.*, 2015; Geng *et al.*, 2018a)。而在后肠的厌氧环境中,鞭毛虫成为纤维素与半纤维素降解的关键执行者,其表达的GH5、GH7、GH45等纤维素酶以及GH10、GH11等半纤维素酶,能高效分解木质纤维素多糖(Xie *et al.*, 2012)。此外,共生细菌进一步丰富了酶系的多样性,编码包括GH3、GH5、GH6等纤维素酶,以及GH10、GH26、GH53等半纤维素酶,协同完成对木质纤维素的多层次降解(Watanabe and Tokuda, 2010; Zhang *et al.*, 2024)。这种多源、分区、协同的酶系统,构成了白蚁高效降解木质纤维素的核心机制。

结合分离培养、显微观察和高通量测序等技术研究白蚁肠道微生物多样性,研究人员逐步揭示了肠道微生物的类群、丰度和分布特征。原生动物主要隶属于真核生物副基体门(Parabasalia)的4个目(Trichomonadida、Trichonymphida、Spirotrichonymphida、Cristamonadida)和前轴柱门(Preaxostyla)的1个目(Oxymonadida)(羊桂英等, 2020),其多样性受白蚁种类、品级、食物等多种因素的影响。例如,台湾乳白蚁体内的3种鞭毛虫*Pseudotrichonympha grassii*、*Holomastigotoides mirabile*和*Spirotrichonympha leidyi*的平均数量分别为780、1 630和2 950只(谢磊等, 2011)。双凹新白蚁*Neotermes binovatus*工蚁和兵蚁均发现Cristamonadida、Trichomonadida、Tritrichomonadida和Oxymonadida各目的鞭毛虫,工蚁的鞭毛虫丰度显著高于兵蚁(Huang *et al.*, 2025b)。细菌主要为拟杆菌门(Bacteroidaceae)、螺旋体门(Spirochaetes)、变形菌门(Proteobacteria)、厚

壁菌门(Firmicutes)、放线菌门(Actinobacteria)、迷踪菌门(Elusimicrobia)等,及以产甲烷菌为代表的古细菌(孙新新等, 2017)。细菌多分布于后肠,以螺旋体门为主;前肠、中肠也共生着多样化的细菌群落,以变形菌门和厚壁菌门为主,拟杆菌门相对丰度也较高,其中前肠有候选门_TM6(Candidate phylum_TM6)、装甲菌门(Armatimonadetes)和大量木聚糖分解菌,中肠则有大量染料脱色菌(Dar *et al.*, 2022, 2024)。

共生微生物功能及与宿主互作机制的解析不断深入。首先,木质纤维素转化降解的过程逐步明晰。白蚁进行木质纤维素预处理,鞭毛虫是降解主力主导淀粉和蔗糖代谢途径,共生原核生物进一步代谢参与氨基酸合成、核苷酸代谢、维生素合成和碳代谢等过程,合成必需氨基酸、维生素等,为白蚁提供营养和能量(Xie *et al.*, 2012; Liu *et al.*, 2016; Alom *et al.*, 2024),其中柠檬酸菌属的菌株(*Citrobacter* sp.)具有固氮活性(梅建凤等, 2002)。利用热裂解气相色谱质谱联用、固态/液态核磁共振、高效阴离子交换色谱等技术,更详细地描绘了其分子过程:白蚁上颚将食物研磨为细小颗粒,增大共生微生物和酶类接触面积,与唾液中的宿主酶(如内切葡聚糖酶)混合进入前肠,由漆酶、过氧化物酶等降解修饰;随后进入中肠,由活性氧介导进一步解聚木质素,通过断裂部分醚键(β -O-4)使木质素-多糖复合体松动而不破坏芳香环,脱除甲氧基($-\text{OCH}_3$)和氧化侧链,解除木质素和半纤维素间的疏水作用,断裂木聚糖和纤维素间的氢键,从而暴露多糖;进入后肠后,多糖与共生微生物分泌的酶系接触,被水解为葡萄糖和木糖,由肠上皮细胞吸收,而修饰后的木质素则随粪便排出,从而通过低能耗的木质素局部修饰实现纤维素的高效利用(多糖消化率74%-99%)(Ke *et al.*, 2010; 谢蓉蓉等, 2015; Geng *et al.*, 2018a; Li *et al.*, 2023a)。其次,进一步探究了共生系统对环境胁迫的动态响应。如食物成分影响,木质素含量高的食物促进螺旋体门、拟杆菌门核心菌群(如*Candidatus Azobacteriodes*)增殖以降解木质素,而纤维素富集时,拟杆菌门(如*Dysgonomonas*

属、弧菌属) 丰度增加 (Su *et al.*, 2017a; 曾文慧等, 2017b; Alom *et al.*, 2024); 温度影响, 台湾乳白蚁在 28 °C 时鞭毛虫活性最佳, 但高温下宿主与共生体纤维素酶基因表达互补, 维持消化效率 (Zeng *et al.*, 2016a); 低毒物质、抗生素等胁迫下, 非优势类群 (如 *Dysgonomonas*) 增殖协助解毒并维持纤维素酶活性 (曾文慧等, 2017b; Zeng *et al.*, 2021), 或通过不同种类鞭毛虫的消长变化及宿主内源酶的补偿机制, 维持系统稳定 (Zeng *et al.*, 2016b)。

低等白蚁的三重共生系统通过宿主预处理、鞭毛虫主导降解及细菌代谢支持, 实现木质纤维素高效利用。组学技术揭示了肠段特化、代谢互补和环境响应的分子基础, 为仿生开发木质纤维素转化技术提供了新思路。

3.2 高等白蚁的宿主-细菌共生消化系统

高等白蚁在进化过程中丢失了鞭毛虫, 演化为以宿主自身酶系和细菌共生为核心的多样化木质纤维素降解策略。白蚁不同品级和龄期 (幼蚁、老熟工蚁、兵蚁、若蚁等) 肠道菌群存在显著差异, 反映其分工、发育和食物变化 (Li *et al.*, 2016a)。根据食性的不同, 高等白蚁可分为木食性、土食性/腐食性和培菌性白蚁三大类, 高等白蚁的肠道结构和微生物组成与低等白蚁不同, 其肠道结构更为复杂且更长 (Hongoh, 2011; Brune, 2014; Mikaelyan *et al.*, 2015; 梁世优等, 2019)。高等木食性白蚁中肠至囊形胃间的部分区域 pH 呈碱性, 部分近中性; 土食性白蚁取食高度腐朽的木头或含有机质的土壤, 后肠 P1 和 P3 均膨大, pH 波动较大, 氢浓度总体低于其它类型白蚁; 培菌白蚁取食木材、草、枯枝落叶等并培养真菌, 肠道结构和理化环境与低等食木白蚁相似, 中肠氧浓度相对较高, P3 氢浓度相对较高 (Li *et al.*, 2012; Brune, 2014)。

高等白蚁共生微生物的核心功能是协同降解木质纤维素并维持系统稳定, 其群落结构是理解功能的基础。不同食性白蚁的菌群差异显著: 高等木食性白蚁肠道中, 优势菌群为螺旋体门、纤维杆菌门 (Fibrobacteres) 和 TG3 菌门 (TG3

phylum), 菌群多样性高于低等白蚁 (Brune and Dietrich, 2015; Su *et al.*, 2015, 2016a); 土食性白蚁木质纤维素降解能力略低, 优势菌群为厚壁菌门、放线菌门, 有许多耐碱性的梭菌 (Schmitt-Wagner *et al.*, 2003; Köhler *et al.*, 2008; 孙新新等, 2017; Xie *et al.*, 2024a, 2024b); 培菌白蚁与菌圃微生物、肠道菌群构成三重共生关系, 肠道优势菌以拟杆菌门和厚壁菌门细菌为主, 变形菌门的紫细菌, 螺旋体占比较小, 菌圃在有活蚁时以蚁巢伞属 *Termitomyces* spp. (俗称鸡枞菌) 真菌为主, 废弃后炭角菌 *Xylaria*、念珠菌 *Candida*、毕赤酵母 *Pichia*、木霉菌 *Trichoderma* 等成为优势类群, 菌圃细菌以厚壁菌门、拟杆菌门、变形菌门为主, 而菌圃不同状态 (新鲜、成熟、废弃) 及基质会显著影响细菌群落结构和多样性 (Long *et al.*, 2010; 钱茜等, 2011; 李丹红等, 2017; 孙新新等, 2017; 梁世优等, 2019; Liang *et al.*, 2020; 张硕等, 2020; 尚华蓉等, 2022; Sun *et al.*, 2024)。在共生系统维护方面, 肠道和菌圃中的放线菌 (如 *Amycolatopsis*、*Streptomyces*) 能产生抑制炭角菌等竞争性真菌或病原体的活性物质, 保护白蚁的食物源 (Nagam *et al.*, 2021; Chen *et al.*, 2023a)。菌圃中的草酸营养菌 (Oxalotrophic bacteria) 能降解真菌产生的草酸, 将其转化为方解石, 通过草酸盐-碳酸盐途径 (Oxalate-carbonate pathway) 维持菌圃内微生态稳定 (Sun *et al.*, 2024)。

针对高等白蚁及其与共生微生物分工协作的研究, 同样聚焦于木质纤维素的降解领域。培菌白蚁降解主力是蚁巢伞, 幼蚁对木质素进行初步修饰, 生成衍生化合物后与半纤维素、纤维素等一同排入菌圃, 继而蚁巢伞分泌高活性的氧化酶, 通过芬顿反应 (Fenton chemistry) 破坏木质素屏障, 并利用多种酶系剪切多糖长链或主链, 随后工蚁取食被降解的菌圃进行二次消化, 由白蚁及其肠道菌群提供内切葡聚糖酶、 β -葡萄糖苷酶、 β -甘露糖苷酶等下游降解酶系共同完成消化利用 (Pan *et al.*, 2009; 杨芳等, 2012; Liu *et al.*, 2013, 2019b; Zhang *et al.*, 2014; 宁娜等, 2015; Li *et al.*, 2017, 2020; 梁世优等, 2019; Schalk *et al.*,

2021; Ahmad *et al.*, 2022, 2025)。木食性高等白蚁肠道菌群的功能、消化系统研究较少,在商城奇象白蚁 *Mironasutitermes shangchengensis* 中预测拟杆菌门菌发挥了重要作用 (Su *et al.*, 2015); 短角球白蚁 *Globitermes brachycerastes* 中发现具多重活性的 β -木糖苷酶(兼具 β -葡萄糖苷酶和 α -阿拉伯呋喃糖苷酶活性) (Liu *et al.*, 2018)。木材经象白蚁 *Nasutitermes* sp. 肠道消化后, β -芳基醚 (β -aryl ethers)、苯基香豆素 (Phenylcoumarans)、树脂醇 (Resinols) 和二苯并二氧辛 (Dibenzodioxocins) 等主要碳-碳键结构几乎完全消失, 甲氧基 (Methoxyls) 显著减少, 粪便中木质素含量减少 6.1%, 表明其采用解聚木质素大分子的策略, 区别于低等白蚁仅断裂部分醚键释放多糖的策略 (Li *et al.*, 2023a)。但是, 多种高等白蚁与肠道菌群的分工互作机制和木质纤维素的转化过程尚待阐明。

固氮对取食寡氮的白蚁尤为重要, 高等白蚁因食性分化而固氮能力有别。一般认为培菌白蚁和土食性白蚁的固氮能力较弱, 因培菌白蚁的菌圃能为白蚁提供含氮丰富的食物, 土食性白蚁取食的土壤含有较丰富的氮元素, 故固氮需求低 (王亚召等, 2016; 孙新新等, 2017)。但在黑翅土白蚁中也分离到具有固氮活性的肺炎克雷伯菌 *Klebsiella pneumoniae*, 能在厌氧条件下产生大量的氨, 补充白蚁氮营养 (Wu *et al.*, 2014); 从象白蚁中分离培养的几株梭菌也显示出固氮活性, 而未能纯培养的菌群中还有很多潜在固氮菌 (李丹红等, 2017)。

3.3 白蚁木质纤维素酶基因功能

白蚁高效降解木质纤维素的消化系统依赖于宿主分泌的内源性酶与共生微生物分泌的外源性酶的复杂协同作用。该领域研究始于木质纤维素酶活性的系统筛查。通过比较不同白蚁物种及其不同品级、不同肠道区段中各种木质纤维素酶的活性, 揭示了其功能上的空间分工和品级分工, 如 β -葡萄糖苷酶活性在黑翅土白蚁头部、台湾乳白蚁中肠、黄胸散白蚁后肠活性最高; 木聚糖酶在乳白蚁和散白蚁的后肠、土白蚁和大白蚁

的中后肠活性最高; 漆酶在乳白蚁和散白蚁均检测到; 外切- β -1,4-葡聚糖酶的总活性水平在黄翅大白蚁 *Macrotermes barneyi* 中高于台湾乳白蚁; 土白蚁工蚁的内切- β -1,4-葡聚糖酶活性高于兵蚁和真菌 (Mo *et al.*, 2004; Deng *et al.*, 2008; Zeng *et al.*, 2012; Li *et al.*, 2013; 宁娜等, 2015)。明确共生真菌参与木质素降解, 共生真菌的粗漆酶在低 pH 值和高温度下表现出高活性 (Pan *et al.*, 2009); 以及环境因素对酶活性有显著影响 (刘瑞娟等, 2012)。另外, 研究发现白蚁肠道真菌辅助酶家族可通过氧化切割参与白蚁纤维素降解 (Yu *et al.*, 2025), 白蚁巢产酶菌株 *Bacillus siamensis* YC-9 能产生蛋白酶、淀粉酶、纤维素酶、果胶酶等多种工业酶 (Wang *et al.*, 2021), 以及黑胸散白蚁肠道的酵母 *Candida pseudorhagii* SSA-1542T 能产生高活性木聚糖酶, 表现出高木聚糖分解活性以及 D-木糖发酵能力 (Ali *et al.*, 2017)。进一步通过酶动力学分析了白蚁纤维素酶 (β -葡萄糖苷酶、内切- β -1,4-葡聚糖酶、漆酶等) 最适温度、pH 值和底物 (Xue *et al.*, 2008; Shi *et al.*, 2010; Zhou *et al.*, 2010; 许利霞等, 2012), 木质素以及若干单糖/糖衍生物 (如 D-果糖、L-山梨糖) 对白蚁水解酶分泌的诱导效应 (曾文慧等, 2011), 以及不同物种水解酶与底物的结合模式 (Qi *et al.*, 2016), 筛选优良产酶菌株、酶活条件、酶基因 (高云航等, 2013; Mao *et al.*, 2025)。

组学技术的发展不仅深化了对白蚁及其共生微生物消化酶基因资源的认识, 更已深入到从宏基因组或分离菌株中规模化筛选、表征具有工业应用潜力的新型木质纤维素酶。例如, 木食性短角球白蚁肠道菌群含能将多糖解聚成可发酵的糖类的木聚糖消化酶基因簇, 其组成酶之间表现出功能互补机制 (Liu *et al.*, 2019c); 培菌性白蚁肠道的拟杆菌含丰富的 β -葡萄糖苷酶基因 (Liu *et al.*, 2011; Zhang *et al.*, 2014; Gao *et al.*, 2016)。在此基础上, 开展了木质纤维素酶的克隆、纯化、表达、最佳活性条件筛选及工程化改造, 如 β -葡萄糖苷酶、漆酶等白蚁内源性消化酶 (Feng *et al.*, 2015; Liu *et al.*, 2017a; 曾文慧等,

2017a; Geng *et al.*, 2018b; Zhou *et al.*, 2019; Mao *et al.*, 2025) 及木聚糖酶、木质素过氧化物酶等共生物酶 (Wang *et al.*, 2012; Han *et al.*, 2013; 高云航等, 2014; 刘晓静等, 2015; Bai *et al.*, 2016) 的克隆、纯化和表征; 内切 β -1,4-葡聚糖酶、 β -葡萄糖苷酶、 β -1,3(4)-葡聚糖酶等基因的异源表达 (Ni *et al.*, 2005, 2007b, 2014; Li *et al.*, 2020; 苏丽娟等, 2020); 利用不同白蚁酶基因共表达、重组表达 (高山象白蚁 *Nasutitermes takasagoensis* 纤维素酶 *NtEG* 基因), 技术优化酶的性能, 如热稳定性、pH 适应性、比活性等 (Ni *et al.*, 2007a, 2007b; 林丽华等, 2009; 刘慧琳等, 2011; Qian *et al.*, 2015; Zhang *et al.*, 2018; 杜娇等, 2019)。利用 RNAi 等手段抑制纤维素代谢相关基因的研究, 进一步证明了这些基因对白蚁正常生理的重要性 (Liu *et al.*, 2017b; Wu and Li, 2018; 候亚会等, 2019; Wu *et al.*, 2019c)。基因组比较分析表明, 白蚁碳水化合物活性酶 (Carbohydrate active enzymes, CAZymes) 基因在种间高度保守, 但 GT1、GH1 和 AA3 等基因家族存在扩张现象 (He *et al.*, 2023)。

4 白蚁共生微生物利用

4.1 固体废弃物的生物降解

针对有机污染物 (如染料、多环芳烃、塑料、农药) 和木质纤维素废弃物, 研究人员从白蚁肠道筛选高效降解菌株, 构建人工菌群, 用于生物降解。例如白蚁共生微生物 *Sterigmatomyces halophilus*、*Meyerozyma caribbica*、*Meyerozyma guilliermondii* 等酵母, 可通过单菌株或多菌株构建多元菌群, 高效脱色降解多种偶氮染料 (如 RB5、AO7), 耐受高盐环境, 并降低产物毒性 (Al-Tohamy *et al.*, 2020, 2021, 2023; Ali *et al.*, 2022b; Elsamahy *et al.*, 2023); 细菌菌群 SSA-6 (含 *Meyerozyma guilliermondii*、*Acidisoma tundrae*、*Vanrija humicola* 等) 和 CTB-4 (含 *Burkholderia*、*Xanthomonas*、*Shewanella*、*Pseudomonas*) 能有效降解木质纤维素 (如木屑、秸秆) 和杂酚油污染物, 显著提高后续厌氧消化

产甲烷效率 (Ali *et al.*, 2019, 2021); 肠道来源的酵母和细菌 (如 *Candida guilliermondii*、*Sterigmatomyces halophilus*、*Bacillus cereus*、*Pseudomonas aeruginosa*) 显示出对低密度聚乙烯的降解能力 (Ali *et al.*, 2024)。

4.2 杀菌活性物质筛选

白蚁肠道是新型抗菌、抗真菌活性物质的丰富来源, 具有开发生物杀菌剂的潜力。如从白蚁或其巢穴分离的共生放线菌 *Streptomyces* spp. (如 BYF-112、T33、T37、YH01、T12、BYB02 等菌株) 能产生放线菌素 D、四环素 D、抗生素 Resistomycin、Roseoflavin 等多种活性化合物, 对植物病原真菌 (*Magnaporthe grisea* 等) 和人类病原细菌 (*Staphylococcus aureus* 等) 具有显著抑制活性 (Zhang *et al.*, 2013, 2020; Yin *et al.*, 2019; 张萍华等, 2021; Zhou *et al.*, 2021a; 吴炜城等, 2022; Wu *et al.*, 2024b)。暹罗芽孢杆菌 *Bacillus siamensis* YC-9 能有效防治黄瓜枯萎病, 其产生的 C-15 surfactin 是关键抗菌物质 (Zhou *et al.*, 2022)。

4.3 共生系统仿生与生物能源开发

借鉴白蚁消化系统的结构, 模拟白蚁前肠和中后肠的分区处理, 研究人员开发了两段式微反应器系统, 显著提高小麦秸秆的水解效率 (Xia *et al.*, 2022)。分离白蚁肠道中能高效发酵糖类产醇或积累油脂的菌株, 如 *Lactococcus* sp. X1 能发酵葡萄糖、木糖及二糖生产 L-乳酸, 预处理玉米芯, 以及分泌维生素 C 等营养因子 (Li *et al.*, 2023b); 仿生肠道褶皱状结构构建的负载纤维素酶的柔性微反应器模型, 可用于生产葡萄糖 (Lin *et al.*, 2024)。模拟白蚁口器和共生真菌互作, 开发结合球磨和类芬顿反应的预处理系统, 能有效促进木质素解聚和后续酶解 (Lin *et al.*, 2025)。模拟白蚁前肠高效降解木质素过程, 构建固定化漆酶和可回收香草醛的微反应器系统, 能有效保持漆酶活性, 增加纤维素可及性, 实现高纤维素转化率和葡萄糖产率 (Lin *et al.*, 2023)。

借鉴白蚁肠道多菌协同降解木质纤维素的

模式, 人工模拟微生物群落用于生物能源转化, 如 SSA-6、CTB-4 等联合体模拟了肠道微生物在降解、发酵和解毒方面的分工协作, 实现木质纤维素到生物能源(甲烷、乙醇)或化学品的转化 (Ali *et al.*, 2019, 2021)。利用白蚁肠道高效产油酵母菌株 *Meyerozyma caribbica* SSA1654, 可将木质纤维素水解糖或芳香族化合物转化为脂质, 脂质积累率高达 47.25%, 用于生产生物柴油 (Ali *et al.*, 2022a); 链霉菌属 *Streptomyces* sp. MS-52 菌株能有效降解小麦秸秆产糖, 并进一步发酵转化为生物乙醇 (Danso *et al.*, 2022)。

5 白蚁绿色防控技术

5.1 天然白蚁防控活性物质挖掘

随着环保意识的增强, 一些传统化学杀虫剂因对非靶标生物的危害及环境污染问题正逐渐被限制使用, 环境友好、高效的白蚁防治剂越发被关注。21 世纪以来, 我国学者在真菌、细菌、植物精油及矿物材料等天然杀白蚁活性物质的挖掘与应用方面展开研究工作。

昆虫病原微生物中, 除传统的绿僵菌菌株之外, Dong 等 (2007) 从黑翅土白蚁体表分离的绿僵菌新变种 *Metarhizium anisopliae* var. *dcjhyium* 在孢子浓度为 3×10^8 个/mL 时, 接种 3 d 后可致白蚁 100% 死亡。细菌代谢产物同样是天然杀虫物质的重要来源, 如从美国扁柏 *Chamaecyparis lawsoniana* 中分离的内生芽孢杆菌 *Paenibacillus aliginolyticus*, 其代谢物诺卡酮 (Nootkatone)、 τ -桉叶醇 (τ -muurolol) 等表现出显著的抗菌和杀白蚁活性 (Ruan *et al.*, 2024); 另有研究从黑翅土白蚁中分离的粘质沙雷氏菌分泌的金属蛋白酶对白蚁表现出强毒性, 揭示了细菌蛋白在白蚁毒理机制中的关键作用 (Fu *et al.*, 2021a)。

矿物材料中, 干硅藻被发现对黑胸散白蚁具有杀虫效果, 且能显著抑制白蚁的筑道行为 (Gao *et al.*, 2018)。此外, 生物炭作为土壤改良剂, 在高添加量 (> 10%) 时可通过改变土壤 pH、湿度及微生物组成对台湾乳白蚁产生驱避作用,

显示出预防白蚁的应用潜力 (Chen *et al.*, 2022c)。

植物源杀虫物质始终是绿色杀白蚁剂研发的重要来源。植物次生代谢物氧化苦参碱及马缨丹提取物通过抑制白蚁的生理代谢过程, 显示出良好的杀虫潜能 (谷岱霏等, 2017; 孙骊珠等, 2017)。杉木 *Cryptomeria fortunei* 叶片与心材精油对黑胸散白蚁具有显著毒杀活性 (Xie *et al.*, 2014); 薄荷属植物 (如柠檬薄荷 *Mentha citrata*、胡椒薄荷 *Mentha piperita*) 精油及其主效成分 (香芹酮、薄荷醇) 能够协同调控解毒酶系统并抑制神经靶标, 从而发挥毒杀效应 (Wu *et al.*, 2023), 同属的留兰香 *Mentha spicata* 精油及其成分香芹酮则经由诱导氧化应激与细胞凋亡途径, 对白蚁产生神经毒性及细胞毒性的双重效应 (Xie *et al.*, 2024c); 香紫苏 *Salvia sclarea*、迷迭香 *Rosmarinus officinalis* 等精油及其单体化合物 (丁香酚、百里香酚) 亦表现出强效熏蒸活性, 其作用机制与酯酶和谷胱甘肽 S-转移酶活性升高及乙酰胆碱酯酶抑制密切相关 (Yang *et al.*, 2023); 香茅 *Cymbopogon citratus* 精油中的柠檬醛可通过破坏白蚁体壁几丁质结构显著削弱其爬行与抓附能力 (Jin *et al.*, 2022)。此外, 广玉兰 *Magnolia grandiflora* 的营养成分可抑制黑翅土白蚁工蚁发育, 其机理可能与前列腺素 A3 (PGA3) 过量合成及钙离子浓度升高相关 (Zhou *et al.*, 2024a)。

5.2 缓释与纳米载药技术

智能纳米农药 (Intelligent nanopesticides) 是当前绿色、可持续农药剂型研究的新兴领域。纳米载药及相关缓释技术在我国白蚁防治领域也逐渐凸显其潜力。

纳米递送可有效降低农药使用剂量及对环境的负面影响。例如 Ma 等 (2022) 将高效氯氰菊酯 (β -cypermethrin, β -CYP) 负载于 ZIF-8 金属有机框架, 制备了 pH 响应型纳米递送系统 (β -CYP/ZIF-8) 有潜力应用于台湾乳白蚁绿色防控。类似地, 姜精油和罗勒精油的纳米乳剂对黑翅土白蚁的致死效果远超普通精油 (Nasser *et al.*, 2024b)。针对白蚁消化的特异缓释技术也

有进展,如 Wu 等 (2024f) 开发的纤维素酶响应型控释制剂,在纤维素酶触发下精准释放药剂,对黄胸散白蚁的杀虫效果优于等剂量氟虫腈,且对非靶标生物的毒性降低 6.5 倍以上;吡虫啉 (Imidacloprid, IMI) 与金属有机框架 (UiO-66) 和木质素磺酸钠 (Sodium lignosulfonate, SL) 的复合物 (IMI@UiO-66@SL),在酸性和漆酶富集环境中表现出高效释放特性 (Wu *et al.*, 2025b)。缓释技术同样在木材防腐领域发挥重要作用。海藻酸钠与钙离子交联包封桉树油 (EO@SA-Ca) 的复合体系显著提升了木材的耐腐蚀性和抗白蚁性能,质量损失率降低至 0.85% (Wang *et al.*, 2025a)。将昆虫病原线虫与金属有机框架材料及海藻酸钠制备成复合微球,不仅延长了线虫的存活率,还对白蚁的致死效果高达 85% (Chen *et al.*, 2021)。微生物合成的纳米制剂也表现出较好的杀白蚁效果,帚状赛多孢菌 *Scedosporium apiospermum* 生物合成的氧化锌 (ZnONPs)、二氧化钛 (TiO₂NPs) 和壳聚糖纳米颗粒 (CsNPs) 在 1 000 µg/mL 浓度下对黑翅土白蚁的致死率接近 100% (Nasser *et al.*, 2024a)。

此外,基于 RNAi 的靶向防治一直受限于 RNA 合成成本及易降解性难以应用于白蚁防控。利用纳米载药技术推进 RNAi 靶向害虫防治,近年来已成为一条极具潜力的研究路径。国内白蚁防治领域也开始有相关报道:由工程菌表达的 dsRNA (如 dsRcOrco-HT115),并制备成壳聚糖-dsRNA 纳米复合物,不仅大大降低了 dsRNA 的合成成本也极大提升了其稳定性 (Jiang *et al.*, 2023); Liu 等 (2023) 通过纳米递送 GST/SOD 酶基因 miRNA 以及 miR-7885-5p/miR-252b 模拟物达到显著增强真菌对黑胸散白蚁的致死效果。

5.3 不同杀虫机理联合

基于不同杀白蚁作用机理有效成分的复合应用,不仅能产生协同增效作用,更可提升天然杀虫物的杀虫效能,减少化学农药用量。首先是天然杀虫物与传统农药的联用,土壤真菌代谢产物乙基 2,4-二氧代戊酸酯可通过触发台湾乳

白蚁的聚集行为,显著增强氟虫腈的防治效果,为基于行为调控的联合防治策略提供了思路 (Javaid *et al.*, 2025)。其次,天然杀虫物之间也可进行协同增效的复配:粘质沙雷氏菌与金龟子绿僵菌复合剂在防治黑翅土白蚁中表现出显著的协同杀虫效果 (Fu *et al.*, 2021b);植物源 ATP 酶抑制剂 α-松油醇与昆虫病原线虫小卷蛾斯氏线虫 *Steinernema carpocapsae* 联用,通过抑制白蚁的免疫防御机制,显著提升了线虫对台湾乳白蚁的毒力 (Zeng *et al.*, 2023)。此外, Xiong 等 (2025) 利用 dsRNA 靶向抑制昆虫生长调节剂 RH-5849 诱导的相关抗性基因,显著提高了 RH-5849 的对台湾乳白蚁的致死效果。这些研究不仅揭示了多种有效成分联合使用的协同机制,也为白蚁的综合治理提供了多样化的技术路径,未来需进一步优化并开展野外验证。

5.4 白蚁的综合治理

白蚁危害波及范围极广,自建筑构件的蛀蚀、文物古迹的损毁、水利设施的渗漏,至农林作物的减产乃至电缆电线的侵蚀,造成巨大的经济损失,甚至引发安全事故。我国白蚁防治早期主要依赖化学药剂灭治,80 年代初期至 20 世纪末提出“以防为主,综合防治”,进入 21 世纪转向基于环保型白蚁监测控制系统的“预防为主、防治结合、综合治理”阶段,实施白蚁区域控制,在提升效果的同时显著降低环境影响。

5.4.1 白蚁监控的数智化 传统的白蚁监测与防控主要通过诱杀法实施,需要定期人工检查及更换饵剂。随着信息技术的进步,我国逐渐发展出有线及无线监测技术,并进一步集成升级为白蚁智能监测预警系统。该系统集成新型传感、物联网、移动网络、大数据管理和地理信息等技术,实现“互联网+白蚁防治”的综合治理模式,提升了预防、灭治、监控一体化的效率,正开始应用于我国房屋建筑、水利工程、古树名木等的白蚁预防和治理实践。

白蚁的隐蔽性和长期破坏性使得高效监测技术至关重要。通过不断优化饵块体积和材料进而优化诱捕站提高监测效果 (Dong *et al.*, 2011;

曹婷婷等, 2018), 以及研制探底雷达利用高密度电阻率法探测土壤电阻异常从而识别堤坝白蚁巢穴, 已被用于巢穴二维/三维成像识别 (Yang *et al.*, 2009; 杨秀好等, 2012; 臧德记等, 2015)。国家知识产权局数据库的公开专利信息显示, 随着电子信息技术发展, 白蚁监测设备开始集成电子传感与自动报警功能。基于白蚁取食饵料、活动引起的振动、电磁及环境变化的智能化监测技术主要包括: (1) 通过重力变化或饵料断裂等感知白蚁活动; (2) 通过白蚁取食导致电阻/光敏电阻变化、电路通断、触点开关或磁控开关等触发报警; (3) 应用红外、声波/声频、重量/重力、气压、压力、二氧化碳浓度等传感器监测环境变化, 判断白蚁活动强度、数量或饵料被取食情况; (4) 采用智能识别技术, 通过红外摄像头或影像识别获取白蚁图像, 判断进入对象及确认灭杀效果。同时, 物联网传输技术的应用, 实现了长待机和远距离双向数据通信, 主要包括: (1) 在饵料中嵌入无线射频识别 (Radio frequency identification, RFID) 标签, 白蚁取食导致标签损坏, 通过无线信号检测标签状态变化; (2) 通过霍尔传感器监测饵料状态, 利用窄带物联网 (Narrow band internet of things, NB-IoT) 远程传输信息, 或集成 RFID 和 NB-IoT 通讯模块的电路控制盒实现远程智能监测; (3) 采集装置内部图像直观显示白蚁, 结合温湿度传感器和远距离无线电 (Long range radio, LoRa) 模块实现点位数据的远距离实时传输; (4) 采集装置白蚁活动影像, 结合温湿度传感器数据和定位系统, 通过通用分组无线业务 (General packet radio service, GPRS) 实现远程实时报警。此外, 白蚁为害检测技术也已从人工检查, 延伸至对白蚁危害特征 (如木质构件内部损伤) 的智能诊断。针对木材内部空洞与结构损伤检测的应用基础研究, Chen 等 (2022a) 基于敲击声随内部空洞体积变化的机理, 开发了一种基于深度神经网络 (Deep neural network, DNN) 的方法识别木结构空洞的严重程度; Guo 等 (2022) 提出基于锆钛酸铅 (Lead zirconate titanate, PZT) 主动传感与本征多尺度熵分析的智能木材损伤监测技术, 利用变

分模态分解 (Variational mode decomposition, VMD) 处理收集到的响应信号, 再结合多尺度样本熵 (Multiscale entropy, MSE) 提取定量损伤指标, 最终由卷积神经网络 (Convolutional neural network, CNN) 实现损伤智能诊断, 提升木结构健康监测的精度与可靠性。

白蚁监控系统自动化程度对其持续有效运行至关重要, 如药剂余量自动检测、识别白蚁活动信号后自动投放或灭杀、以及自动清理等功能。人工智能与物联网技术的融合也开始应用到我国白蚁综合治理领域。例如, AI 驱动的视觉识别技术取得革新, Jiang 等 (2025) 报道了一种改进的 MCD-YOLOv8 模型, 通过蒙特卡洛注意力机制 (Monte carlo attention, MCA) 和轻量化模块 (Dimension-aware selective integration, DASI) 提升复杂环境下土白蚁痕迹识别能力; 王一非等 (2025) 提出的 ACP-YOLOv5s 模型引入自适应颜色感知模块, 在泥被、泥线与背景色混淆场景下精度达 91.2%, 显著优于主流模型。

随着白蚁监测技术的信息化与自动化发展, 多源融合应用性研发成为必然。Li 等 (2025) 提出集成物理传感器框架、人工智能算法分析生物特征与无人机影像的智能监测系统。目前在重要堤防、古建筑、历史文化名镇等地开始示范应用白蚁远程实时自动化监测预警系统。该系统集成了白蚁检测仪、信号采集监测基站、数据库、电脑管理平台及手机 APP 技术进行自动监测, 当白蚁侵入监测点后, 系统触发预警机制, 实时上报位置信息; 基站汇总各监测点信号后转发至云端数据库, 数据处理后实时推送至后台管理平台及管理人员 (周乾, 2019; Zhang *et al.*, 2022; 黄院生和黄若迪, 2023)。在堤坝白蚁防治实践中, Wang 等 (2025b) 基于白蚁生物学特性构建了由前端诱捕监测层、中间传输存储层、中心处理预警层组成的三层监测预警系统, 结合电磁感应非环路穿透技术、远程传感 GPS 定位、物联网和云端分析, 尝试对白蚁活动的实时、自动化、高精度监测与预警。

5.4.2 害堤白蚁的危害防治技术 害堤白蚁以土栖性的黑翅土白蚁、黄翅大白蚁为主, 汛期水

位提高,会造成跌窝、渗漏、管漏、滑坡甚至垮坝等险情。早期广东省提出“三环节八程序”的白蚁防治质量保证体系,后经各地不断完善。害堤白蚁危害管理的重心是巢穴的精准定位与长效阻隔,综合防治的技术核心是白蚁监测。

巢穴定位早期主要依赖人工巡查,后续研究采用探地雷达法和高密度电阻率法等综合物探技术对堤坝白蚁巢穴进行探测,通过分析地下介质波速差异实现蚁巢定位,可提升检测效率(陆俊等, 2015);或者融合多种地球物理勘探技术优势,提出堤坝蚁巢“探查-处治-监控”全过程技术框架(高长胜等, 2024; 谭磊等, 2024)。但是,害堤白蚁巢穴的精准定位仍有待技术攻关、深入验证。预防阻隔是害堤白蚁防控的重要手段,主要的屏障技术方法:(1)毒土法,设置隔离防护沟,构建毒土屏障或者物理屏障隔离坝体和白蚁,如使用含 20%氰戊菊酯的杀虫浆液灌浆形成毒土柱(贺海洪等, 2008; 赵卫全等, 2025);(2)食盐法,在堤坝防渗黏土中加入 0.8%的食盐阻止白蚁穿越(陈来华等, 2011);(3)生态控制法,及时清理蚁患区和蚁源区白蚁喜食食物,并在蚁源区种植对白蚁有驱避作用的植物形成生态屏障。

在害堤白蚁的早期治理中,挖巢法因工程量巨大且会破坏堤坝结构,现已较少采用。目前的主流方法是结合化学诱杀与压力灌浆,并在浆液中掺入菊酯类或吡虫啉等药剂。然而,现有药剂对生态环境和饮用水源仍存在安全风险,亟需开发新型绿色环保浆液或白蚁防治剂,例如在泥浆中掺入流动性强、无毒的硅酸钠水溶液(赵卫全等, 2025),或白蚁分飞季结合灯光诱杀,亦可利用植物、微生物等生物控制手段作为辅助措施调控白蚁种群(高长胜等, 2024)等等。

5.4.3 房屋及木构件的白蚁防治技术 房屋建筑白蚁防治包括预防处理和灭治处理。钢筋混凝土结构并未能从根本上消除白蚁对房屋建筑的危害。对于建筑木构件的防护,使用含丙环唑、苯并异噻唑啉酮(Benzisothiazolin, BIT)及高效氯氟氰菊酯的水基微乳剂处理,可使埋地木材在半年内免遭白蚁蛀蚀(张斌等, 2021)。

自 2001 年中国严格限制氯丹、灭蚁灵使用后,不断筛选和优化出新的环保型替代药物,白蚁饵剂监控系统、白蚁监测喷粉控制系统得到应用推广,如房屋通过地上型监测盒检测散白蚁活动后,投放氟铃脲或氟虫腈饵剂,能显著降低白蚁数量与木材损耗,甚至阻断分飞行为(Liang *et al.*, 2010)。白蚁预防的物理屏障技术,例如采用特定粒径(1.36-2.58 mm)的砾石砂构建屏障阻断白蚁危害(Li *et al.*, 2011),但目前仍难以成为我国房屋建筑白蚁预防的主要措施。2025 年实施的新版《房屋白蚁防治技术标准》(JGJ/T245-2024)核心是建立覆盖建筑全生命周期的“预防-治理”全链条管理体系,白蚁监控技术体系在此标准中得到进一步规范。

6 展望

白蚁是重要的生态系统分解者,也是重要的经济和资源昆虫,有害白蚁危害隐蔽、广泛且严重。新世纪以来,我国白蚁研究在多个领域取得显著进展,但是在全球气候变化持续加剧、我国城市化进程加快和新质生产力加速发展的背景下,我国白蚁研究正迎来新的挑战 and 更高的要求。我国白蚁研究未来将在如下方面得到关注:

(1)在白蚁分类、系统学研究上,结合现有外部形态特征、内部形态特征、分子特征数据进一步得到应用,特别是线粒体全基因组与核基因联合,重点开展系统性分类修订、属内和属间的系统发育关系分析、特征演化研究。

(2)在白蚁多样性及生态功能上,随着国家公园的立法、生物多样性保护加强,我国白蚁区系、不同时空尺度白蚁生态功能的研究将进一步得到关注。例如,白蚁对生态系统功能维持的贡献,对土壤节肢动物群落、保护地动植物组成的影响,以及物种多样性、功能多样性、种群遗传结构等对生态环境变化的响应或适应性研究。

(3)在白蚁社会生物学方面,作为最原始的真社会性昆虫,白蚁因隐蔽生活而研究难度大,随着分子生物学技术的应用,白蚁生存策略、品级分化、社会免疫及其协同调控网络将得到更好的揭示,从表型、行为、基因表达、化学通讯及

微生物互作等多个层面, 加快理解昆虫社会性进化与适应。

(4) 在白蚁资源开发利用方面, 多组学技术融合将进一步促进白蚁-微生物共生机制的研究, 从静态鉴定走向动态功能解析, 系统揭示白蚁-鞭毛虫/真菌-细菌在降解木质纤维素过程中的互作网络、代谢物交换及调控机制, 碳氮循环、能量流动以及关键酶系的协同表达等过程, 为资源化利用奠定基础, 包括开发仿生反应器、构建人工功能菌群用于木质纤维素利用、新能源生物炼制, 以及挖掘食药价值。

(5) 在白蚁监测技术方法上, 智能传感与物联网技术的引入将进一步提升白蚁危害监测预警的实时性与准确性, 甚至通过图像识别和行为分析算法, 可自动判别白蚁活动与危害等级。白蚁智能监测装置及智能监测系统还有技术问题有待完善, 但必将得到进一步推广应用。

(6) 在白蚁防治技术与区域治理方面, 白蚁防治技术多学科交叉、多技术融合、综合治理体系的构建是未来发展一个侧重点。白蚁防治、控制装置正朝着精准化、绿色化与智能化方向转型, 例如环保技术联合、小分子靶向药剂研发、纳米缓释载体包裹等的应用研究与系统评估。同时, 白蚁区域治理的理念将得到进一步加强, 在一定范围内实施综合治理, 甚至纳入我国南方建筑设计与城市运维标准。

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