

二十一世纪中国亚洲玉米螟研究进展*

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摘要 亚洲玉米螟 *Ostrinia furnacalis* 是中国玉米生产的首要害虫, 近年来随耕作制度变革和全球气候变暖为害持续加重, 严重威胁中国玉米的安全生产。进入 21 世纪, 中国对亚洲玉米螟的研究取得了显著进展。在基础研究方面, 解析了性信息素的合成路径、调控机制和感受机理; 揭示了其滞育调控机制; 系统解析了其先天免疫系统, 包括模式识别受体、关键信号通路及效应因子, 为开发靶向生物农药提供了分子基础; 明确了玉米对亚洲玉米螟的防御机制; 揭示了其对 Bt 杀虫蛋白的抗性机制。在应用技术方面, 构建了以农业防治为基础、多种绿色技术协同的综合防控体系。本研究综述系统总结了我国在亚洲玉米螟研究领域的最新进展, 为持续推进其绿色可持续治理奠定了坚实的理论基础。

关键词 亚洲玉米螟; 滞育; 性信息素; 免疫; 防御; 抗性机制; 防控技术; 进展

Progress in research on the Asian corn borer (*Ostrinia furnacalis*) in China since the beginning of the 21st century

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Abstract The Asian corn borer, *Ostrinia furnacalis*, is the primary insect pest of corn in China. The damage to corn crops caused by this species has continued to intensify in recent years due to changes in farming practices and global warming, and poses a serious threat to corn production. Since the beginning of the 21st century, significant progress has been made in research on the Asian corn borer in China. With respect to the sex pheromones of this species, their synthesis pathway, regulatory mechanisms, and perception mechanisms have been elucidated. Its diapause regulation mechanisms have also been revealed, and its innate immune system, including pattern recognition receptors, key signaling pathways, and effector molecules, have been systematically analyzed, providing a molecular basis for the development of targeted biopesticides. The mechanisms used by corn to defend against the Asian corn borer have also been clarified, and the mechanisms underlying its resistance to Bt insecticidal proteins have been uncovered. An integrated pest management system has been established, based on agricultural control and the synergy between various environmentally-friendly techniques. This paper systematically summarizes the latest advances in research on the Asian corn borer in China, providing a solid theoretical foundation for the environmentally-friendly and sustainable management of corn crops.

Key words *Ostrinia furnacalis*; diapause; sex pheromone; immune; defense; resistant mechanism; control measures; progress

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亚洲玉米螟 *Ostrinia furnacalis*, 属鳞翅目草螟科 (以下简称玉米螟), 是我国玉米上最重要的害虫, 我国昆虫学者对亚洲玉米螟开展了大量研究工作, 取得了重要进展。王振营等 (2000) 综述了 20 世纪中国玉米螟的研究历史与现状, 特别是 20 世纪 80 年代后在玉米螟人工饲养技术、优势种鉴定与分布、生物学和生态学、抗螟品种鉴定与利用、毒理和抗药性、天敌种类和应用、产量损失与经济阈值、预测预报和关键防治技术研究的现状和取得的进展。进入 21 世纪, 随着科学进步和新技术在昆虫学研究领域的应用, 中国玉米螟研究取得显著进展, 本文从亚洲玉米螟发生现状、滞育调控机制、免疫反应、寄主互作、Bt 抗性和抗药性机制以及绿色防控技术等多个方面对研究进展进行了综述。

1 亚洲玉米螟发生现状

进入 21 世纪, 随着玉米播种面积的增大, 耕作制度变革、品种更换和全球气候变暖, 亚洲玉米螟发生世代数增加, 大发生频率周期明显缩短, 为害加重, 为害玉米果穗, 诱发和加重玉米穗腐病的发生, 籽粒中真菌毒素含量增加, 严重影响玉米的品质 (Li et al., 2023 a, 2023b)。由于亚洲玉米螟对玉米安全生产的重要性, 2023 年农业农村部将亚洲玉米螟列为《一类农作物病虫害名录》中华人民共和国农业农村部公告第 654 号, 2023)。

1.1 发生为害现状

2003 年以来, 全国玉米螟的发生呈持续上升趋势, 常年发生面积在 2 000 万 hm^2 以上, 2012 年总体偏重发生, 全国发生面积达 2 426 万 hm^2 (刘杰和姜玉英, 2014)。2013-2018 年, 全国玉米螟年发生面积稳定在 2 300 万 hm^2 (全国农业技术推广服务中心-病虫测报网, 2013-2018. <https://www.natesc.org.cn/htm>)。亚洲玉米螟为害对玉米产量造成严重影响, 据统计 2006-2015 年 10 年间, 经防治后平均每年挽回产量损失 488.73 万吨, 每年仍可造成实际损失 207.26 万吨 (刘万才等, 2016)。

1.2 发生世代和分布变化

20 世纪 80 年代, 新疆伊犁河谷仅有欧洲玉米螟 *Ostrinia nubilalis* 分布 (周大荣等, 1988), Wang 等 (2017) 首次报道了亚洲玉米螟在伊犁河谷地区出现, 伊犁河谷成为亚、欧两种玉米螟混生区, 亚洲玉米螟已逐渐取代欧洲玉米螟, 成为该区的优势种, 并首次在自然界中发现了亚洲玉米螟和欧洲玉米螟之间的杂交个体, 两者之间出现了基因渗透现象, 随后的研究进一步确认了亚、欧两种玉米螟在该区同域共生 (Li and Yang, 2022; 丁新华等, 2023)。到目前为止, 亚洲玉米螟在我国除西藏和青海没有分布外, 其他省 (直辖市、自治区) 均有分布。随着农业种植结构的调整, 甜、糯等鲜食玉米种植面积扩大, 且分期播种和反季节种植, 为亚洲玉米螟提供了适宜寄主和繁殖场所, 取食甜玉米的亚洲玉米螟幼虫较普通玉米存活率高 3-7 倍, 发育历期提前 4-6 d, 甜玉米且更能吸引亚洲玉米螟产卵 (何康来等, 2002), 导致亚洲玉米螟世代重叠, 为害加重。气候变暖导致亚洲玉米螟发生世代增加, 黑龙江省齐齐哈尔、哈尔滨等地由 1 代区变为 1、2 代混合发生区 (王连霞, 2016; 刘兴龙等, 2023)。吉林省伊通县和集安市玉米螟由 1 代区变为 1.5 代区, 原为 2 代区的双辽市和梨树县已变成 2 代为主兼 2.5 代发生区 (鲁新等, 2015)。辽宁省沈阳市由 2 代区转变为 2、3 代混生区 (张柱亭等, 2014) 此外, 气候变暖播种期提前, 玉米生育期相应提前, 品种生育期延长, 玉米螟营养条件得到改善。如吉林省中部主推品种生育期多在 130 d 左右, 玉米螟可完全发育成 2 代 (鲁新等, 2005)。亚洲玉米螟在东北春玉米区世代数的增加, 直接导致该区玉米螟为害加重 (王振营和王晓鸣, 2019)。

2 亚洲玉米螟性信息素组分鉴定与调控机制

20 世纪 70 年代, Klun 等 (1980) 首次发现其亚洲玉米螟雌蛾释放特异挥发性化合物对雄蛾具有定向吸引作用, 由此开启了亚洲玉米螟性

信息素系统研究。历经数十年探索,亚洲玉米螟性信息素在组分鉴定、感受机制及田间应用方面取得显著进展,已成为我国首批产业化的绿色防控技术之一。

2.1 组分鉴定与调节机制

20 世纪 80 年代, Klun 等 (1980) 首次从美国夏威夷亚洲玉米螟种群雌蛾性腺中分离出顺/反-12-十四碳烯醇乙酸酯 (Z12-14:Ac/E12-14:Ac), 确定其 1:1 比例为关键活性组分。程志青等 (1980) 对中国广东阳山种群的鉴定显示, Z/E12-14:Ac 为主成分 (47:53), 并存在微量十四碳醇乙酸酯 (14:Ac)。杜家纬等 (1986) 也发现亚洲玉米螟性信息素中 3 个主要成分: 十四碳醇乙酸酯 (14:Ac), 顺-12-十四碳烯醇乙酸酯 (Z12-14:Ac) 与反-12-十四碳烯醇乙酸酯 (E12-14:Ac), 但比例为 26:32:42。近年来对新疆亚洲玉米螟种群研究表明, Z12-14:Ac 占 E/Z 总量的 60.46%, 14:Ac 占三元混合物的 25.00%, 且比例呈正态分布, 提示地理种群间性信息素可能存在差异 (Deng *et al.*, 2023), 其他地区种群性信息素比例差异也陆续有报道 (蓝陈仪航等, 2023)。而欧洲玉米螟的性信息素主要成分 (Z/E11-14:Ac) 和亚洲玉米螟性信息素类似, 仅仅是双键位置不同, 但这两个近缘种存在基因渗透现象 (Wang *et al.*, 2017)。

秆野螟属 *Ostrinia* 昆虫通过选择性表达不同的 D11-去饱和酶基因来产生物种特异性的性信息素, 亚洲玉米螟通过沉默 D11-去饱和酶基因并启用 D14-去饱和酶, 形成独特的性信息素合成路径 (Fujii *et al.*, 2015)。转录组比较发现并验证了 Δ 14-去饱和酶 (Des-14) 和脂肪酸还原酶 FAR14 在信息素腺体中特异高表达, 且 PBAN 神经肽通过与其受体 PBANR 结合, 触发 Ca^{2+} 内流, 激活下游信号级联, 促进信息素合成 (Yao *et al.*, 2021)。而性信息素比例的调控, 是通过脂肪酸还原酶基因 *pgFAR* 的编码区突变来改变其底物专一性, 从而决定了各物种雌性性信息素中不同组分及其精确比例 (Lassance *et al.*, 2013)。

2.2 感受机制与神经编码

扫描电镜与单感器记录表明, 亚洲玉米螟雄性触角上存在 4 种类型毛感器 (A-D 型), 其中 A-C 型对 Z/E12-14:Ac 敏感, 而 D 型特异性响应 Z12-14:Ac (Takanashi *et al.*, 2006; Liu *et al.*, 2018), 此功能分离策略保障了组分比例识别精度。性信息素的初级识别是通过性信息素结合蛋白将性信息素运送到受体蛋白, 体外结合试验发现, 性信息素结合蛋白 (OfurPBP3) 可高效转运主成分 Z12/E12-14:OAc 至受体 (Zhang *et al.*, 2017a)。非洲爪蟾卵母细胞表达系统验证发现, Or4 受体对 Z/E12-14:OAc 均产生强电流响应, 而 Or6 受体主要响应 E12-14:OAc (Liu *et al.*, 2018)。

3 亚洲玉米螟滞育调控机制

近年来, 围绕亚洲玉米螟的光温调控机制、气候变暖响应、种群内变异及人工调控应用等方面展开了研究。

3.1 滞育类型与化性的关系

亚洲玉米螟的化性 (每年发生世代数) 随纬度降低呈递增趋势, 在中国高纬度的黑龙江黑河 (50°14'N) 仅发生 1 代, 而热带地区的海南乐东 (18°10'N) 可发生 7 代 (Liu *et al.*, 2023), 在云南省高海拔地区以老熟幼虫滞育越冬, 每年发生 4-5 代; 低海拔地区部分幼虫不滞育, 每年发生 5-7 代 (太红坤等, 2016)。亚洲玉米螟属于兼性滞育昆虫, 末龄幼虫必须在短日照和低温诱导下进入滞育, 越冬后才能继续发育, 热带地区不具备滞育条件, 幼虫不滞育可正常发育 (Liu *et al.*, 2023, 2025a)。中国东北同一生态区内 3 种生物型共存, 通过对东北种群室内多代分离筛选, 能分离出明显特征的不同生物型种群 (Liu *et al.*, 2023)。

3.2 滞育的光温调控

光周期和温度是诱导亚洲玉米螟滞育的核心环境信号, 其响应机制呈现出显著的地理种群分化和遗传多样性。不同化性种群的滞育诱导临

界光周期 (Critical photoperiod, CLP) 存在明显差异。高纬度一化型种群的 CLP 较长 (鲁新和周大荣, 2000), 确保其在日照变短的秋季顺利滞育, 而低纬度多代型种群的 CLP 较短, 保证了更高世代的延续。温度对光周期具有很强的补偿效应, 亚洲玉米螟的滞育诱导受光周期与温度共同调控, 表现出典型的具有温度补偿作用的“长日型”反应模式, 临界光周期随地理纬度北移而增长 (郭建青等, 2013)。在 16 h 长日照下, 多化性品系 18 °C 时滞育率可达 6%, 而在 28 °C 时降至 0.5% 以下 (Liu *et al.*, 2023)。

3.3 滞育调控机制

亚洲玉米螟滞育幼虫通过降低含水量、提高脂肪含量、降低呼吸速率和增加耐缺氧能力以增强耐寒性, 而血淋巴出现特异滞育关联蛋白 (Diapause-associated protein, DAP), 可能具有储氮与抗冻双重功能 (Zhao *et al.*, 1994)。不同地理种群幼虫脂肪含量在 45%-70% 之间, 呈纬度递减趋势; 高纬度种群过冷却点显著低于低纬度种群, 与脂肪含量呈负相关, 与含水量呈正相关 (刘宁等, 2005; 涂小云等, 2015)。不同纬度亚洲玉米螟幼虫发育时间和蛹重也存在显著差异, 高纬度种群幼虫发育时间短, 体重较高, 而低纬度种群幼虫发育时间长, 体重较小 (Fu *et al.*, 2022)。这些生理变化是滞育适应性进化的重要机制, 有助于幼虫在严寒冬季存活。

亚洲玉米螟的滞育遗传有很多报道, 通过遗传杂交实验来分析杂交后代的滞育表现, 可进一步明确滞育和性别的关系。将长光照条件下长光照反应的南昌种群和短光照反应的哈尔滨种群进行杂交, 发现哈尔滨种群的临界光周期明显长于南昌种群的临界光周期, 而杂交 F₁ 代临界光周期介于两者之间, 表明临界光周期是由多基因控制, 并发现父本对临界光周期的影响比母本大 (黄丽莉, 2013)。将极高滞育率的哈尔滨种群, 高滞育率南昌种群分别和基本不滞育的乐东种群进行杂交, 证实亚洲玉米螟的滞育和父本的性别连锁, 且性状呈显性 (Xia *et al.*, 2012; Fu *et al.*, 2015; Huang *et al.*, 2020)。

进一步的基因组分析表明, 亚洲玉米螟北方种群的遗传多样性、基因组杂合率要高于南方种群, 并且定位到主效控制滞育的 *period (per)* 基因 (彭炎, 2024)。通过构建南北方亚洲玉米螟种群的泛基因组图谱, 发现南方种群 *FTZ-F1* 基因的一个 225 bp 插入 SV 显著抑制其转录活性, 延迟幼虫发育, 而北方种群无此插入, 发育加快 (Peng *et al.*, 2024)。也有报道表观遗传机制在滞育调控中起着重要作用, 通过对亚洲玉米螟幼虫进行 CHIP-seq、WGBS 和 RNA-seq 等多组学联合分析发现, H3K9me3 与 H3K27me3 在滞育启动前后显著变化, 表观修饰抑制剂处理可显著改变滞育率, 提示组蛋白甲基化与 DNA 甲基化共同调控滞育关键基因表达 (Lv *et al.*, 2024)。最新的研究表明, 亚洲玉米螟的滞育是由 *Cycle* 基因 C 亚型特异的 N 端外显子碱基缺失引起, 敲除亚洲玉米螟 *CycC* 基因后, 其在短日照下进入滞育的比例显著下降, 表明 *CYC-C* 的缺失会严重破坏滞育的启动 (Zheng *et al.*, 2025)。

总之, 亚洲玉米螟滞育是其适应纬度环境梯度与季节性气候的关键策略, 由光周期 (CLP 梯度) 与温度 (补偿效应) 协同调控, 是生理适应 (代谢抑制/抗寒增强) 与多层级遗传调控 (多基因控制/表观修饰/关键基因 *CycC* 等) 共同构成越冬生存保障机制。

4 亚洲玉米螟的免疫反应

先天免疫是昆虫适应复杂环境的关键, 也是害虫绿色防控的重要研究方向。亚洲玉米螟在其生命周期的不同阶段都会受到各种病原微生物和寄生物体的侵害。与其他昆虫相似, 亚洲玉米螟的先天免疫反应包括体液免疫 (Humoral immunity) 和细胞免疫 (Cellular immunity)。体液免疫包括抗菌肽 (Antimicrobial peptides, AMPs) 的产生、活性氧和一氧化氮的产生以及由酚氧化酶激活系统 (PPO-AS) 介导的黑化反应。细胞免疫主要通过血细胞参与的细胞吞噬 (Phagocytosis)、包裹 (Encapsulation) 和结节形成 (Nodulation) 等过程清除异物。二者相关联系、相互协作, 通过一系列的模式识别受体

(Pattern recognition receptors, PRRs) 可以特异性识别来自于不同病原微生物的病原相关分子模式 (Pathogen-associated molecular patterns, PAMPs) 从而激活下游信号通路, 启动先天免疫系统以清除病原物。

由于亚洲玉米螟人工饲养技术成熟, 实验操作简便, 近年来关于其先天免疫方面的研究成为研究热点, 在模式识别受体、免疫信号通路、体液免疫和细胞免疫等方面取得一定进展。

4.1 模式识别受体

亚洲玉米螟对入侵微生物的识别是通过 PRRs 识别特定 PAMPs 而启动。在亚洲玉米螟体内已发现多种模式识别受体, 包括 β -1,3-葡聚糖识别蛋白 (β -1,3-glucan recognition proteins, β -GRPs)、肽聚糖识别蛋白 (Peptidoglycan recognition proteins, PGRPs) 和 C-型凝集素 (C-type Lectins, CTLs)。Of β GRP3 在抵御细菌感染中至关重要, 能激活 PPO 通路 (Wu *et al.*, 2018); OfPGRP-S 可结合金黄色葡萄球菌 *Staphylococcus aureus* 和苏云金芽孢杆菌 *Bacillus thuringiensis*, 并增强酚氧化酶活化, 参与 PPO 途径 (Sun *et al.*, 2014); OfPGRP-A 和 OfPGRP-B 分别识别革兰氏阳性菌和阴性菌, 推测分别参与 Toll 通路和 Imd 通路 (Wang *et al.*, 2022)。在亚洲玉米螟转录组中鉴定到 14 个 CTL 基因, 发现 OfIML-4 可促进细胞凝集、吞噬作用、包裹化与 PO 活化, 并显著增强亚洲玉米螟抗真菌免疫 (Shen *et al.*, 2018; Li *et al.*, 2025a)。

4.2 免疫信号通路

免疫信号通路是连接病原体识别和免疫反应的中间过程。在亚洲玉米螟中主要存在 IMD、Toll、JNK/MAPK 等免疫信号通路。亚洲玉米螟 OfRelish 的激活可诱导多种抗菌肽基因表达, 表明 OfRelish 是 IMD 途径的关键组成部分 (Chen *et al.*, 2021)。虽然在亚洲玉米螟 Toll 信号通路的研究中, Toll-Spätzle 受体尚未系统解析, 但研究发现作为 Toll 样通路的重要接头蛋白, OfMyD88 在 Bt 感染中显著上调并促进抗菌肽产生, 表明 OfMyD88 通过 Toll 信号通路参与防御 Bt 的入侵

(Alradi *et al.*, 2022)。除上述经典通路外, 研究发现 JNK/MAPK 对亚洲玉米螟免疫反应有调节作用, 在受到 Cry1Ab 杀虫蛋白刺激时, OfERK 基因显著上调 (Li *et al.*, 2024a)。此外, 磷脂酶 A2 (Phospholipase A2, PLA2) 能调控亚洲玉米螟抗菌肽的表达和黑化反应, 表明二十碳烷醇信号通路也参与了亚洲玉米螟的先天免疫反应 (Ji *et al.*, 2022)。最新研究还发现 OfEiger 也是一种重要的昆虫免疫调节因子, 可协同调节 IMD、Toll、NO 和 MAPK 信号通路 (Bi *et al.*, 2025)。

4.3 体液免疫

亚洲玉米螟的体液免疫是在 PRRs 识别 PAMPs 后, 激活上述免疫信号通路, 通过激活不同的转录因子来调控 AMPs 的表达, 从而杀灭病原物的过程。目前已在亚洲玉米螟中鉴定到 7 个不同基因家族的 AMPs: 天蚕素 (Cecropins)、溶菌酶 (Lysozymes)、攻击素 (Attacins)、防御素 (Defensins)、葛佬素 (Gloverins)、Lebocins 和 Moricins (Zhang *et al.*, 2013; Liu *et al.*, 2014)。当亚洲玉米螟受到不同病原体的入侵时会激活不同类型抗菌肽的表达。

黑化反应是亚洲玉米螟体内一项重要的体液免疫。当 PRRs 识别 PAMPs 后可启动丝氨酸蛋白酶级联反应, 催化 PPO 水解为有活性的酚氧化酶 (Phenoloxidase, PO), 进而启动黑色素的产生。Ofserpin1 作为丝氨酸蛋白酶抑制因子, 能够通过抑制 PAP 活性调控 PPO 激活系统, 从而实现对亚洲玉米螟免疫反应的负调控 (Zhang *et al.*, 2016; Feng *et al.*, 2008, 2018)。SP13 和 SP105 均与丝氨酸蛋白酶抑制剂 serpin-3 形成 SDS 稳定的复合物, 并且抑制其激活酚氧化酶原 (Chu *et al.*, 2015, 2017)。SP7 能被丝氨酸蛋白酶抑制剂 serpin-3 和 serpin-4 有效调控 (Zhang *et al.*, 2022)。

此外, Liu 等 (2025b) 发现 OfApoLp-III 参与调节 PPO-AS, 并通过调节 PPO2 和一氧化氮合酶 (Nitric oxide synthetase, NOS) 表达来减少一氧化氮 (Nitric oxide, NO) 的产生, 以应对各种细菌感染。研究还发现, 亚洲玉米螟需要

NO 和钙调磷酸酶 (Calcineurin, CanA) 来对抗细菌感染, 且通过实验证明 CanA1 介导了 NO 信号和 IMD 通路之间 AMP 的产生 (Chen *et al.*, 2022)。

4.4 细胞免疫

目前对亚洲玉米螟细胞免疫的研究还较少。细胞免疫主要是由血淋巴细胞介导完成的。利用体外培养的亚洲玉米螟血细胞系, 建立了分别富含浆细胞和颗粒细胞的两个亚系, 对比分析发现两种细胞在延展、吞噬和包囊等反应中行为差异明显, 表明两种细胞可能采用不同的策略来清除异物 (Hu *et al.*, 2021)。细胞免疫同样受到体内信号调控网络的影响。PLA₂ 在多方协调免疫信号通路的同时, 也对细胞免疫产生影响, 研究发现使用 PLA₂ 抑制剂处理亚洲玉米螟可使血细胞的结节、包囊和黑化等先天免疫反应能力显著下降, 而重组 OfPLA2 在 Ca²⁺ 存在下能部分恢复细胞免疫功能。由此可见, 体液与细胞免疫在分子水平共同作用, 构筑起亚洲玉米螟抵御病原的防御体系 (Ji *et al.*, 2022)。

昆虫病原微生物可被昆虫免疫系统识别, 进而激活昆虫自身天然免疫系统以抵御其侵染。因此, 昆虫自身的免疫反应能力影响着生物防治的效果。为更好地利用病原微生物防治亚洲玉米螟, 寻找优秀的免疫靶标基因至关重要。目前通过转录组测序, 围绕亚洲玉米螟免疫相关基因的筛选与鉴定工作取得诸多进展 (Liu *et al.*, 2014; Chen *et al.*, 2019; Zhou *et al.*, 2022; Qiao *et al.*, 2023), 这些成果为挖掘潜在的免疫靶标基因, 并研发以 RNAi 为靶点的新型绿色农药制剂防治亚洲玉米螟提供了理论依据。

5 玉米对亚洲玉米螟的防御机制

玉米在与亚洲玉米螟长期的协同进化中形成了复杂精细的防御机制, 包括组成型防御 (Constitutive defenses) 和诱导型防御 (Induced defenses)。

5.1 组成型防御

组成型防御是玉米固有的抗性基础, 依赖于

物理屏障和组成型抗虫化学物质 (郭井菲等, 2014)。物理防御方面, 玉米抗螟性与叶片硬度、厚度、表皮毛等物理性状高度相关 (武德功等, 2018), 针对玉米螟高龄幼虫钻蛀茎秆为害的特点, 玉米穗上节、穗节、穗下节的表皮穿刺强度是决定茎秆对玉米螟钻蛀抗性的核心物理性状 (Guo *et al.*, 2022)。化学防御方面, 苯并恶嗪酮类化合物 (Benzoxazinoids) 及其衍生物是最重要的组成型抗虫次生代谢物 (Wouters *et al.*, 2016), 其中以丁布 (DIMBOA) 研究最为深入。丁布通过直接抑制亚洲玉米螟取食和干扰消化酶系统发挥抗虫作用 (Yan *et al.*, 1999)。早期研究发现, 玉米心叶期 DIMBOA 含量与亚洲玉米螟的食叶级别呈显著负相关 (王蕴生等, 1985)。宋鹏飞等 (2014) 进一步证实不同玉米品种的丁布含量差异显著, 且与抗螟性呈正相关。田间对京科 968、先玉 335、郑单 958 等主栽品种的研究, 均验证了丁布在玉米抗螟性中的核心作用 (Guo *et al.*, 2019; 刘树楠等, 2019)。然而, 防御通常伴随着生长和产量的降低, 即“此消彼长”的平衡 (Defense-growth trade-offs) (Züst and Agrawal, 2017), 这在一定程度上解释了兼具优异抗螟性与高产潜力的品种相对稀缺的原因。然而, Guo 等 (2022) 在对 10 个抗螟和感螟自交系的系统研究中并未观察到玉米对玉米螟的抗性、耐害性和其生长间的权衡, 表明玉米可通过基因型特异的代谢重组 (如 Bxs 积累与激素动态平衡) 协调防御与生长, 这为培育兼具抗虫性与高产潜力的玉米品种奠定了重要理论基础。

5.2 诱导型防御

诱导防御是植物-昆虫互作领域的研究热点, 它仅在受到害虫取食或相关刺激时才会被触发。在玉米应对玉米螟取食的诱导防御研究中, 茉莉酸 (JA) 信号通路在其中占据核心调控地位 (Yang *et al.*, 2015; Zhang *et al.*, 2015; Guo *et al.*, 2019)。玉米对玉米螟的诱导防御包含直接与间接防御, 直接防御主要通过调控苯并恶嗪酮类物质动态变化来抑制玉米螟生长发育 (Huang *et al.*, 2006), 其中以 HDMBOA-Glc 为标志性物质

(Guo *et al.*, 2017, 2019); 间接防御主要通过释放萜烯等挥发性物质, 通过吸引玉米螟天敌昆虫, 如腰带长体茧蜂 *Macrocentrus cingulum* 保护玉米降低螟害 (Guo *et al.*, 2019)。萜烯类物质在植物与害虫的互作中发挥着多样化的作用。如 DMNT 在拟南芥中能够驱避小菜蛾 *Plutella xylostella* (Chen *et al.*, 2021), 但在玉米中, 却与 TMTT 共同成为吸引玉米螟幼虫的信号物质 (Zhao *et al.*, 2024a)。这种功能差异揭示了植物化学防御机制的复杂性。需要强调的是, 玉米田间抗螟性鉴定的结果正是这种复杂性的体现, 综合反映了玉米的组成抗性与诱导抗性的共同作用 (Guo *et al.*, 2022)。

随着玉米遗传转化技术的完善和生物信息学等学科的发展, 一系列与玉米抗虫性状相关的关键遗传位点及调控基因已被鉴定 (Tang *et al.*, 2019; Niu *et al.*, 2023; Chen *et al.*, 2024; Zhao *et al.*, 2024b), 主要聚焦于调控苯并恶唑啉类物质 (Gao *et al.*, 2019; Zhang *et al.*, 2020) 和萜烯类物质 (Li *et al.*, 2015) 合成的基因, 为玉米抗虫分子育种提供了潜在靶点。在玉米-害虫的长期协同进化过程中, 玉米螟也进化出了相应的反防御策略, 例如形成谷胱甘肽 S-转移酶 (GST) 家族成员介导的丁布解毒机制 (Chen *et al.*, 2025) 等。

5.3 球孢白僵菌与环境因子对玉米抗螟性的调控

玉米对玉米螟的防御能力受到生物及环境因子的显著影响, 国内研究主要聚焦于生防真菌 (特别是昆虫病原真菌) 及 CO₂ 等环境因子。球孢白僵菌 *Beauveria bassiana* 通过内生定殖启动玉米防御响应 (Bing and Lewis, 1991), 直接驱避玉米螟幼虫取食并抑制其生长发育 (隋丽等, 2020, 2023)。球孢白僵菌与棘孢木霉 *Trichoderma asperellum* 联合处理玉米种子, 可协调玉米的抗氧化剂系统和茉莉酸 (JA) 信号途径, 提升玉米防御酶活性, 抑制幼虫自身的免疫相关基因表达, 增强对害虫的防治效果, 提高玉米产量 (Batoool *et al.*, 2020a, 2020b, 2022)。球孢白僵菌可通过两种方式降低玉米螟对玉米的危害: 一

是定殖玉米后改变玉米挥发物组成以吸引玉米螟成虫产卵, 同时降低植株氮含量抑制幼虫存活, 形成“陷阱效应” (Zhu *et al.*, 2023); 二是通过间接诱导植物间通讯, 当未被其定殖的玉米遭受草地贪夜蛾 *Spodoptera frugiperda* 取食时, 会释放植醇诱导邻近植株产生针对玉米螟的防御反应 (Batoool *et al.*, 2025)。

环境因子同样显著影响玉米的诱导防御过程。例如, 温度和 CO₂ 浓度的升高可通过增强 JA 信号通路、防御酶活性及酚类物质积累等途径, 提高玉米对玉米螟的防御能力 (Xie *et al.*, 2022)。CO₂ 浓度升高可正向调控球孢白僵菌介导的玉米抗螟性。在此条件下, 该虫生真菌不仅能更有效减轻玉米螟为害, 还能维持植株氮含量, 最终提升玉米的生物量和产量 (Sui *et al.*, 2024)。充分说明在虫生真菌等生物因子与 CO₂ 等非生物因子的影响下, 田间玉米的防御机制更为复杂。

6 亚洲玉米螟对 Bt 杀虫蛋白及杀虫剂的抗性机制

6.1 对 Bt 杀虫蛋白的抗性机制

亚洲玉米螟对 Bt 杀虫蛋白的抗性机制主要涉及三方面:

中肠代谢酶介导的抗性 中肠代谢酶的变化会影响杀虫蛋白的活化从而导致抗性的产生, Xu 等 (2015) 发现亚洲玉米螟 Cry1Ab 抗性品系中肠解毒及代谢酶转录水平降低, 导致水解原毒素的能力减弱, 这可能是其产生 Bt 抗性的机制之一。Cry1Ac 抗性品系细胞色素 P450 单加氧酶 (P450) 基因显著上调, 可能通过增强毒素的降解或者修饰来降低活性, 甚至可能影响相关基因的表达, 共同参与抗性的形成 (Zhang *et al.*, 2017b)。

受体结合能力降低介导的抗性 Bt 抗性的关键因素包括受体的变异和基因表达调控的改变 (Jurat-Fuentes *et al.*, 2021)。Cry1Ab 通过 ABCC2 和 Cadherin+ABCC3 两条功能冗余的杀虫通路发挥作用, 而 Cry1F 仅依赖 ABCC2 通路,

揭示了亚洲玉米螟对 Cry1Ab 抗性风险低而对 Cry1F 抗性风险高的分子遗传机理 (Wang *et al.*, 2025)。CRISPR/Cas9 技术也证实 ABCC2 是 Cry1F 的功能受体 (Wang *et al.*, 2020)。钙黏蛋白 (CAD) 通过结合区域突变及转录水平下调参与对 Cry1Ac 的抗性 (Jin *et al.*, 2014), 但 CAD 不能直接介导 Cry1Ac 在细胞膜上形成孔道 (Jin *et al.*, 2021); 另外, APN1、APN3 等亦与 Cry1Ab/Cry1Ac 抗性相关 (Zhang *et al.*, 2017b)。比较研究发现, Cry1Ah 抗性品系刷状缘膜囊泡 (BBMV) 与 Cry1Ah 的结合能力降低, 定量实验鉴定出多个可能与抗性相关的受体基因 (APN、ALP、ABCC3 等) 表达量下调, 这些变异可能影响受体的识别和特异性结合 (Shabbira *et al.*, 2019, 2020)。

免疫防御系统介导的抗性 昆虫可通过免疫系统调控对 Bt 的耐性。比如玉米螟取食 Bt 玉米以后, 其体内的羧酸酯酶 (CarE) 活性加速毒素降解 (Shi *et al.*, 2011)。Cry1Ah 可诱导玉米螟产生酚氧化酶并影响微生物群落的组成提高免疫能力 (Prabu *et al.*, 2020)。肠道共生菌通过激活 Toll/IMD 信号通路诱导宿主产生抗菌肽, 强化免疫防御, 降低对 Cry1Ac 的敏感性 (Li *et al.*, 2025b)。尿苷二磷酸葡萄糖醛酸转移酶 (UGTs) 的糖基化反应可减轻有毒物质的影响。林雅玲等 (2023) 通过 RNAi 沉默 UGT 基因可降低玉米螟对 Cry1Ie 的抗性, 实现抗性逆转。Prabu 等 (2022) 在 Cry1F 抗性品系中发现四跨膜蛋白 CD63 显著上调, RNAi 沉默 CD63 后可恢复对 Cry1F 的敏感性。

6.2 亚洲玉米螟对杀虫剂的抗性机制

目前, 我国针对玉米螟抗药性的系统监测仍较有限。研究表明, 山西省多地种群已对多种常用杀虫剂产生低到中等抗性水平。山西大同种群对茚虫威中等抗性 ($RR=40.6$), 长治种群对溴氰虫酰胺为低抗 ($RR=8.0$), 但两地种群对辛硫磷仍敏感 (蔡冬敏, 2023)。新疆地区亚洲玉米螟抗性发展较为显著, 2018 年昌吉、伊宁等种群对氯虫苯甲酰胺、溴氰虫酰胺等几种常规药剂抗性

倍数在 3.67-20.17, 属中等水平; 至 2019 年, 昌吉种群对溴氰虫酰胺抗性急剧升高至 1 429 倍 (支昊宇等, 2021a)。室内筛选试验表明, 亚洲玉米螟对常规杀虫剂虽具抗性发展潜力, 但进程较缓, 如丁硫克百威 LC_{50} 致死剂量连续筛选 10 代后, 抗性倍数仅为 5.4 (林荣华等, 2008)。

多种解毒酶在玉米螟对杀虫剂的抗性中发挥重要作用, 包括羧酸酯酶 (CarE)、P450、谷胱甘肽 S-转移酶 (GST)、多功能氧化酶 (MFO) 等。相较敏感种群, 新疆玉米螟田间种群的 CYP450、GST 和脂酶 (EST) 活力普遍升高 (支昊宇等, 2021b)。特定杀虫剂暴露也可诱导酶活性变化, 如红绶曲霉与四唑虫酰胺处理能提高玉米螟幼虫体内 CarE、GST、SOD、CAT 等活性 (袁梓涵等, 2024)。杀虫剂还可通过干扰玉米螟生理过程发挥作用, 例如酰胺类化合物可上调肌质网/内质网 ATPase 基因表达, 导致 Ca^{2+} 持续释放和肌肉强直收缩而致死 (Cui *et al.*, 2017)。靶点位点不敏感性是另一重要抗性机制。鱼尼丁受体 (RyR) 表达量的上调可能与玉米螟对酰胺类化合物的敏感性下降有关 (Cui *et al.*, 2013)。

7 亚洲玉米螟防控技术进展

进入 21 世纪, 我国亚洲玉米螟防控技术体系已从单一的化学防治发展为以农业防治和生态调控为基础、多种绿色技术协同应用的综合防控体系。

7.1 农业防治与生态调控技术

玉米机械化收获时将秸秆粉碎, 秸秆中越冬的亚洲玉米螟幼虫死亡率达 87.9%-95.5%, 有效降低了越冬幼虫基数 (陈继光等, 2016)。

玉米与匍匐型绿豆间作, 显著提高了玉米螟赤眼蜂对亚洲玉米螟卵的寄生率 (周大荣等, 1997), 玉米螟赤眼蜂被匍匐型绿豆叶片挥发性气味所吸引从而提高了寄生率 (Bai *et al.*, 2011)。玉米与甘蔗、谷子、绿豆、大豆、花生或向日葵间作, 亚洲玉米螟的为害明显减轻 (鲁新等, 2007; 田耀加等, 2012; 陈斌等, 2015; Li *et al.*, 2022a)。在常规播期玉米田内小面积晚播同品种玉米作

为诱集田集中防治,显著减轻了常规播期大田玉米二代玉米螟发生和为害(鲁新等,2007)。

7.2 理化诱控技术

亚洲玉米螟性信息素对 2 代成虫具有显著诱集作用,玉米螟卵量减少 67.5%,百株虫量减少 66.5%(吴祖幸等,2013)。性信息素作为迷向剂能够干扰玉米螟成虫交配,降低交配率。二元混合物(Z-12-14:Ac : E-12-14:Ac $\approx$ 1 : 1) ≥ 6 mg,或任一单组分约 5 mg,可完全阻断玉米螟雄蛾交配行为(Chen *et al.*, 2017);正十四烷基乙酸酯对当地种群具有行为调节功能,三元混合物诱捕效果更优(Deng *et al.*, 2023)。性诱剂与杀虫灯结合起来,可明显提高诱杀效果(赵秀梅等,2014)。

7.3 生物防治技术

20 世纪 70 年代起,利用赤眼蜂防治亚洲玉米螟已在东北春玉米区得到广泛应用,进入 21 世纪后,随着赤眼蜂生产和释放技术的改进,特别是“公共植保、绿色植保”理念的提出,以及政府对绿色防控技术的支持,应用面积明显增加(Wang *et al.*, 2014)。如 2004 年以来,吉林省政府每年拿出专项资金对粮食主产区实施生物防螟重大技术推广项目补贴,2012 年以来,吉林省每年应用赤眼蜂防治玉米螟面积均稳定在 230 万 hm^2 左右,约占玉米种植面积的 55%(张俊杰等,2015)。李敦松等(2013)利用无人机释放赤眼蜂防治玉米螟,开创无人机释放赤眼蜂的先河,植保无人机释放赤眼蜂,显著提高了释放效率和防治效果,近年来已得到广泛应用。植保无人机释放松毛虫赤眼蜂 *Trichogramma dendrolimi* 防治亚洲玉米螟,防治效果达 76.4%-81.2%(杜文梅等,2023)。

生物农药在玉米螟的防治中发挥着重要作用,球孢白僵菌除直接侵染害虫外,还可通过在玉米植株内生定殖诱导玉米产生系统抗性,控制亚洲玉米螟(冯树丹等,2017; Batool *et al.*, 2020, 2022a, 2022b),利用球孢白僵菌浸种或通过滴灌根部,可明显减轻亚洲玉米螟为害(Batool *et al.*,

2022a; Feng *et al.*, 2023)。载菌技术的突破使赤眼蜂携带球孢白僵菌孢子量达到 3.6×10^4 孢子/蜂,协同防控效果提升 24.5%(杨芷等, 2020a, 2020b)。使用植保无人机联合喷施球孢白僵菌和金龟子绿僵菌,防治二代亚洲玉米螟防治效果好(张云月等,2022)。

7.4 绿色化学防治技术

化学防治技术向高效、低毒、精准的方向发展。增效剂实现农药减量 15%-30%而不降低防效(Li *et al.*, 2023c)。分子生物学技术的创新应用为亚洲玉米螟绿色防控开辟了新途径。病原相关蛋白 1 (PR1) 等关键分子靶标的揭示为 RNA 农药开发奠定基础(Zhang *et al.*, 2015, 2025a; Wu *et al.*, 2016);配合新型递送系统有望实现 RNA 干扰技术的高效应用(Li *et al.*, 2025c)。几丁质酶抑制剂等新型化合物在极低浓度下表现优异防效(Shen *et al.*, 2019; Lu *et al.*, 2021; Liang *et al.*, 2024; Zou *et al.*, 2024)。纳米材料如氧化石墨烯的应用及智能递送系统实现了环境响应精准释药、药剂稳定性和释放效率提升(Wang *et al.*, 2019, 2023; 杨君等, 2020; Zhang *et al.*, 2025b)。

7.5 转基因抗虫玉米产业化

He 等(2003)在中国最早报道转 *cry1Ab* 基因玉米在整个玉米生长期可有效控制亚洲玉米螟为害。Bt 杀虫蛋白在玉米不同生育期不同组织的时空表达量与亚洲玉米螟幼虫死亡率呈显著正相关(王冬妍等,2004)。近年来,我国转基因抗虫玉米研发取得突破性进展,自主研发的转 *cry1Ab* 基因玉米(如 DBN9936)可使玉米螟幼虫数量下降 95%以上(孙丹丹, 2021; Yang *et al.*, 2023; He *et al.*, 2025)。多基因叠加技术日趋成熟,转 *cry1Ab/cry1Ac* 基因玉米 ZZM030 对玉米螟具有良好防效(刘晓贝等, 2020);转双价(*cry1Ab+vip3Aa*)及三价(*cry1Ab/cry2Aj/vip3A*)基因的抗虫玉米品种在玉米主产区对玉米螟等害虫的控制效果表现优异(Li *et al.*, 2022b, 2024b)。2023 和 2024 年先后有两批共 63 个转

基因抗虫玉米品种通过审定, 产业化进程加快, 为亚洲玉米螟防控提供了新的技术措施。

21 世纪以来, 我国对亚洲玉米螟的研究已从传统的生物学、生态学防治深入到基因组学、分子免疫学、化学生态学和基因工程等前沿领域, 揭示了其滞育、免疫、抗性 etc 内在机制, 以及与环境、寄主的互作关系。这些研究为以生态调控、生物防治、理化诱控和转基因技术为核心的绿色综合防控技术体系的建立与发展, 为保障我国玉米安全生产提供了坚实的科技支撑。

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