

中国入侵昆虫预防与控制研究进展*

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摘 要 在全球经济一体化、农业结构调整以及全球气候变化等因素的影响下, 我国正面临着严峻的生物入侵问题。外来入侵昆虫是我国生物入侵的重要组成部分, 阐明其传入至成灾的发生过程与机制, 研发快速高效的防控技术体系具有重要意义。本文综述了近 20 年来我国在外来入侵昆虫的生物学特性、种群遗传分化、种间互作与生态适应方面取得的重要研究成果, 以及在入侵昆虫早期快速检测、田间监测与高效防控技术的研发与应用方面取得的进展, 并提出入侵昆虫学科未来发展的方向与思路。旨在为进一步分析新时代背景下入侵昆虫的发生机制奠定基础, 对丰富和完善入侵昆虫可持续控制的策略和措施也具有指导意义。

关键词 生物入侵; 遗传分化; 种间互作; 生态适应; 预防控制

Research progress on prevention and control of invasive insects in China

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Abstract Increasing economic integration, crop structure adjustment, and global climate change have led to China becoming one of many countries that has been severely affected by invasive species. The majority of invasive species in China are invasive insects. It is important, therefore, to clarify the factors that affect their abundance, and to develop efficient methods of prevention and control for these pests. This article provides an overview of progress in research on the biological characteristics, genetic differentiation, interspecies interactions and ecological adaptation, of invasive insects, as well as their early detection, field monitoring and prevention and control technology in China over the past 20 years. Perspectives and directions for future research on invasive insects are also discussed. Information in the factors affecting the occurrence of invasive insects, prospects for improving current control strategies and tactics for preventing biological invasions, are also provided.

Key words biological invasions; genetic differentiation; interspecies interaction; ecological adaptation; prevention and control technology

作为经济全球一体化快速发展的国家之一, 由于商品贸易、国际旅游以及交通运输的快速增长, 我国正面临着严峻的生物入侵问题。20 世

纪以来, 大规模的生物入侵集中发生在农田、森林、草原、岛屿、湿地、河流、海洋和自然保护区等 (Yan *et al.*, 2017)。自 2001 以来, 我国科

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研人员在全国范围内逐步开展了广泛的外来入侵物种调查。Xu 等 (2012) 编制了我国外来入侵物种名录, 共列出了 488 种生活在陆地、内陆水域和海洋生态系统中的入侵物种, 包括 171 种动物、265 种植物、26 种真菌、3 种原生生物、11 种原核生物和 12 种病毒。直至 2016 年末, 我国至少存在 610 种外来入侵物种, 其中 50 种被列为全球最具危害的 100 种外来入侵物种 (ICUN)。外来入侵物种每年在我国造成的直接经济损失高达 170 亿美元, 同时严重破坏了多种生态系统以及生物多样性 (Wan *et al.*, 2017)。因此, 生物入侵被认为是我国最大的生物安全问题之一, 近几十年来, 受到我国政府和学术界的高度重视。

随着外来入侵物种数量日益增多, 入侵机制越来越复杂, 危害面积逐步增加, 防控难度日趋加大。从 21 世纪开始, 我国各部委逐渐加大了对生物入侵研究的投入。国内学者也围绕入侵生物学的三大科学问题: 入侵性、可入侵性与控制力开展了深入细致的研究, 取得了一系列创新性成果。外来入侵昆虫是我国生物入侵的重要组成部分, 阐明其传入至成灾的发生过程与机制, 研发快速高效的防控技术体系具有重要意义。因此, 本文总结了近 20 年来我国在外来入侵昆虫的生物学特性、种群遗传分化、种间互动与生态适应方面取得的重要研究成果, 以及在入侵昆虫早期快速检测、田间监测与高效防控技术的研发与应用方面取得的显著进展, 并提出入侵昆虫学科未来发展的方向与思路。

1 入侵昆虫的基础研究

1.1 生物学特性

1.1.1 寄主范围 寄主范围的宽窄决定了昆虫到达新生境后能否找到充足的资源以满足自身生长以及种群发展的需要。寄主范围广、食性杂通常是外来昆虫成功入侵的重要因素。扶桑绵粉蚧 *Phenacoccus solenopsis* Tinsley 的寄主种类包括 57 科 207 种, 随着调查的深入, 寄主范围还在不断扩大 (Fand and Suroshe, 2015), 在我国主要寄主超过 160 种 (Tong *et al.*, 2019)。

西花蓟马 *Frankliniella occidentalis* (Pergande) 也为杂食性害虫, 可在 60 多个科、500 多种植物上取食。桔小实蝇 *Bactrocera dorsalis* Hendel 作为全球危害最为严重的 5 种实蝇之一, 寄主范围也超过 250 种 (Aketarawong *et al.*, 2014)。总体来看, 宽广的寄主范围促进了入侵昆虫的定殖与扩散, 然而有些昆虫从原产地入侵到新的栖息地后, 寄主范围反而变窄。例如, 马铃薯甲虫 *Leptinotarsa decemlineata* (Say) 在原产地美国的寄主种类超过 20 种, 但传入我国后寄主范围明显缩小, 在新疆仅有 6 种, 其中以马铃薯 *Solanum tuberosum* L. 最为偏好, 正是由于这一食性改变, 导致该甲虫入侵后对我国马铃薯产业造成毁灭性的经济损失。这可能与生态环境变化 (如种植模式、气候因子等) 相关, 也进一步说明入侵昆虫具有较强的寄主适应性进化能力。

1.1.2 繁殖能力 入侵昆虫往往具有较高的繁殖能力, 如烟粉虱 *Bemisia tabaci* (Gennadius)、红火蚁 *Solenopsis invicta* Buren、马铃薯甲虫、扶桑绵粉蚧等单雌产卵量可达几百上千头。除此之外, 生殖方式多样化也是其成功入侵并快速扩张的重要因素, 多种入侵昆虫兼具两性生殖与孤雌生殖两种模式, 如扶桑绵粉蚧、西花蓟马 (Tong *et al.*, 2019)。稻水象甲 *Lissorhoptrus oryzophilus* Kuschel 雌虫在原产地主要选择两性生殖, 而入侵我国后, 所有雌性个体均为孤雌生殖, 这极大地加快了其在中国的定殖与扩散 (Jiang *et al.*, 2007)。不同昆虫雌虫交配次数也不相同, 在入侵过程中所起的作用也不同。多次交配雌虫能够从中获得更多的营养物质以提高他们繁殖能力, 如草地贪夜蛾 *Spodoptera frugiperda* (Smith) (Johnson, 1987)。然而, 交配次数并非越多越好。水椰八角铁甲 *Octodonta nipae* (Maulik) 再交配次数达到 15 次时, 其雌虫产卵量最大, 卵的孵化率与种群增长率也最高, 当再交配次数增加至 20 次时, 产卵量与孵化率都显著降低, 且雄虫寿命显著缩短 (Li *et al.*, 2014a)。相反, 桔小实蝇雌虫则通过交配抑制 (单次交配) 来提高其后代数 (Wei *et al.*, 2015a)。不同的交配策略可能与入侵昆虫的资源分配权衡 (Trade-off) 密切相关。还有一些入侵昆虫具有很强的

后代保护能力,能在恶劣环境条件下控制自身的产卵行为直至条件改善,以保证后代的存活率(Jiang and Cheng, 2003a; Lu and Peng, 2017)。

1.1.3 迁飞力 迁飞强弱是决定入侵昆虫快速扩散的重要因素之一,红脂大小蠹 *Dendroctonus valens* LeConte 具有很强的迁飞能力,它在北美的飞行距离已超过 16 km/年 (Smith, 1971),进入我国后,其飞行距离可增加至 35 km/年以上(张历燕等, 2002)。这一优势使红脂大小蠹成虫能够成功入侵到我国大部分地理区域,甚至能够翻越吕梁与太行山等屏障(张历燕等, 2002)。草地贪夜蛾也是一种典型的迁飞型入侵害虫,每晚可飞行 100 km 以上,雌成虫在产卵前的迁飞距离可达 500 km,这有效促进了草地贪夜蛾种群的扩散 (Westbrook et al., 2016; Day et al., 2017)。有报道称草地贪夜蛾成虫在 30 h 内可从美国密西西比州迁飞至加拿大南部,迁飞距离长达 1 600 km (Rose et al., 1975)。昆虫的迁飞能力主要由其自身条件,以及环境因子决定。例如,迁飞能力可能与温度、食物、寄主植物、种群密度,以及生殖状态密切相关。

1.2 种群遗传分化

1.2.1 入侵来源 明确外来昆虫的入侵来源对解析其入侵机制以及制定防控策略,如早期监测预警与天敌引种等具有重要意义。然而,当前我国学者对于入侵昆虫的入侵来源分析仅集中在几种昆虫。Chu 等 (2011) 确定我国 Q 型烟粉虱起源于西地中海地区,可能是摩洛哥和/或西班牙,而非东地中海地区。分布在我国西北与东北地区的苹果蠹蛾 *Cydia pomonella* (L.) 的遗传结构具有明显差异,推测其入侵来源可能不同 (Li et al., 2015; Chen et al., 2017)。Men 等 (2013) 和 Li 等 (2015) 发现西北地区与东北黑龙江的苹果蠹蛾可能分别来源于中亚与俄罗斯远东地区。王帅宇 (2010) 利用群体遗传结构分析表明,亚洲和欧洲南美斑潜蝇 *Liriomyza huidobrensis* Blanchard 种群可能起源于南美洲,而我国的三叶斑潜蝇 *Liriomyza trifolii* (Burgess),除广西种群外,均可能来源于我国台湾或欧洲地区,但对于广西种群的起源地仍无法确定。红火蚁在我国

的入侵来源则相对复杂,何晓芳等 (2006) 研究显示,红火蚁可能直接从靠近阿根廷的南美地区传入我国香港,并以此作为起源地传播到我国其他地区。另外的研究则认为,广东吴川的红火蚁可能起源于美国南部(曾玲等, 2005; Yang et al., 2012)。Ascunce 等 (2011) 也支持我国红火蚁种群可能来源于美国南部。由此我们推测,外来入侵昆虫可能在起源地即发生种群遗传分化,因此,起源与入侵种群的遗传结构和/或多样性密切相关。

1.2.2 入侵路径 入侵路径研究也是制定害虫管理策略的基础,并对入侵昆虫的风险评估具有重要意义。遗传结构分析发现,我国 B 型与 Q 型烟粉虱均可能通过多次入侵事件进入我国(褚栋等, 2012; Li et al., 2017)。而我国红棕象甲 *Rhynchophorus ferrugineus* Fabricius 种群既可能来源于多次入侵事件,也可能来自源于同一事件中多个单倍型的入侵 (Wang et al., 2015a)。Qin 等 (2018) 推测入侵非洲和夏威夷的桔小实蝇种群由南亚种群单一入侵而来,且南亚可能也是其他亚洲种群的来源地。然而,桔小实蝇向北入侵进入我国华中地区则可能经历了多次、反复入侵过程,这可能与水果贸易相关。除此之外,入侵路径与种群定殖后的扩散分布也密切相关。邵敬国等 (2008) 研究表明,红火蚁在我国广泛的地理分布可能与其多次入侵事件有关。苹果绵蚜 *Eriosoma lanigerum* (Hausmann) 已在我国多个地区发生,而其传播扩散途径仍不明确, Zhou 等 (2015) 研究表明,近期在新疆建立的苹果绵蚜种群可能并非由我国北方的“超级群体”传入,而是具有多个传入来源。以上证据显示,我国入侵昆虫的传入扩散途径是复杂多样的,仍有很多昆虫的入侵路径不尚明确,直接制约了我们对入侵昆虫早期预警与风险分析策略的制定。

1.3 种间互作

1.3.1 竞争取代 昆虫之所以能够成功入侵到世界各地并造成严重危害,与其具有强有力的竞争能力息息相关,比如资源竞争、干涉竞争等。研究表明,入侵 B 型烟粉虱与本地温室粉虱 *Trialeurodes vaporariorum* (Westwood) 相比具有

更高的植物有毒次生物质降解能力,其有利于 B 型烟粉虱对寄主资源的利用,从而竞争取代温室粉虱种群 (Peng *et al.*, 2013)。在我国大陆,无论在个体水平还是群体水平上,红火蚁与绝大多数本地蚂蚁相比,均表现出竞争优势 (Chen *et al.*, 2011; 高燕等, 2011), 如限制土著蚂蚁利用蜜露资源 (Huang *et al.*, 2010; Zhou *et al.*, 2014a), 限制其觅食行为与活动 (Wu *et al.*, 2014), 同时自身表现出更快速的食物搜索与招募能力 (Lu *et al.*, 2012)。除资源获取、搜寻与抢夺等方面,资源变质也是入侵昆虫资源利用竞争的重要方式,它通过降低或改变现有资源质量,以限制其他物种(如天敌昆虫)的生长发育,从而提高其竞争力 (Feng *et al.*, 2015; Zhou *et al.*, 2016a)。除了资源竞争外,干涉竞争也是入侵种成功取代本地种的关键,如格斗干涉、生殖干涉等。我国学者发现,当入侵 B 型烟粉虱与土著烟粉虱处于同一生态位时,会发生“非对称交配互作现象”,即雄性 B 型烟粉虱能干扰土著烟粉虱的交配,反之则没有影响。这一现象显著加快了入侵烟粉虱的竞争取代速度 (Liu *et al.*, 2007)。

1.3.2 协同互作

1.3.2.1 与病毒的协同互作 作为病毒传播的媒介昆虫, B 型烟粉虱参与了双生病毒的复制、转运与传播 (Wei *et al.*, 2014), 而病毒则增强了烟粉虱在寄主植物上的生存表现。与本地烟粉虱 Asia II 3 相比, B 型烟粉虱在感染中国番茄曲叶病毒 (Tomato yellow leaf curl China virus, TYLCCNV) 与烟草曲茎病毒 (Tobacco curly shoot virus, TbCSV) 的寄主上取食时,其繁殖力与寿命显著增加 (Jiu *et al.*, 2007)。随后,我国学者发现, TYLCCNV 可能是通过抑制茉莉酸介导的寄主植物防御反应,从而间接地使 B 型烟粉虱受益,比如 TYLCCNV 中的 β C1 蛋白能够抑制植物萜类物质的合成 (Zhang *et al.*, 2012; Luan *et al.*, 2013b)。同时, Luan 等 (2013a) 还发现,取食带毒植物的 B 型烟粉虱体内氧化磷酸化通路基因和解毒酶基因表达下调。由此说明,病毒可能通过抑制植物的防御反应,从而改变入侵昆虫在“生长与防御”资源分配中的权衡。入侵昆虫用于应对植物防御的能量分配减少,间

接提高了其在生存表现上的资源利用。

1.3.2.2 与共生菌的协同互作 越来越多的证据表明,共生微生物促进了昆虫生物入侵的发生。Xu 等 (2015b) 发现,肠道细菌协助红脂大小蠹释放信息素马鞭草烯酮,从而调控其入侵我国后对寄主的最适选择。此外,红脂大小蠹蛀道内的共生菌还可以帮助其降解植物防御物质柚皮素,从而提高其寄主适合度 (Cheng *et al.*, 2018)。由此说明,共生菌能够有效促进入侵种寄主适应。除此之外,共生菌还参与调控入侵种与本地种之间的资源竞争。在面对红火蚁的竞争压力时,黑头酸臭蚁 *Tapinoma melanocephalum* Fabricius 肠道共生菌类群会发现相应变化,以帮助其改变营养生态位,从而避开与红火蚁竞争原本偏好的蜜露等糖类物质而偏向于取食更多的动物尸体等高蛋白食物 (Cheng *et al.*, 2019)。共生菌类型也可能与入侵昆虫的定殖与传播扩散密切相关, *Hamiltonella* 仅存在于两种入侵烟粉虱中 (B 和 Q 型) (Bing *et al.*, 2013)。Himler 等 (2011) 证实,感染 *Rickettsia* 的烟粉虱产卵量增大,后代存活率升高,发育加快,以及雌性比例显著增加。这可能是由于内共生菌与烟粉虱宿主之间存在水平基因转移,从而提升其自身代谢与营养获取的需求 (Luan *et al.*, 2015; Rao *et al.*, 2015; Zhu *et al.*, 2016)。

1.3.2.3 与伴生菌的协同互作 昆虫伴生菌的变异可能也与其成功入侵息息相关。例如,入侵我国的红脂大小蠹伴生菌数量与种类与其北美本地种群相比具有明显差异 (Lu *et al.*, 2008, 2009), 尤其是其伴生真菌长梗细帚霉 *Leptographium procerum* 变异形成中国独特单倍型,该单倍型对油松的致病力明显高于北美本地种的 *L. procerum* 单倍型 (Lu *et al.*, 2010)。然而,伴生菌 *L. procerum* 对红脂大小蠹的作用并非总是正向的,它会与红脂大小蠹幼虫争夺糖类资源,从而导致幼虫生长速度减慢 (Wang *et al.*, 2013)。但 Zhou 等 (2016b) 证实共生细菌能够调节 *L. procerum* 对松醇与葡萄糖的消耗顺序,从而减轻 *L. procerum* 对红脂大小蠹幼虫的拮抗作用。研究结果表明,入侵昆虫-共生菌-伴生菌-寄主植物是一个复杂的协同互作网络,从而保证了物种之间

的资源利用稳定与平衡,对入侵昆虫的定殖与扩张具有重要意义。

1.3.2.4 与其他物种的协同互动 一些外来入侵昆虫自身,以及与本地昆虫,与其他入侵昆虫也可能具有协同互动效应。如红火蚁工蚁之间的相互清洁行为能显著提高其自身的存活率(Qiu *et al.*, 2014)。松材线虫幼虫分泌的蛔甙(Ascarosides)既能加快松墨天牛 *Monochamus alternatus* Hope 发育进程,又能吸引自身幼虫进入天牛气门,从而促进其种群扩散(Zhao *et al.*, 2016)。红脂大小蠹和本地种黑根小蠹 *Hylastes parallelus* Chapuis 能释放共同的聚集信息素而产生协同危害(Lu *et al.*, 2007),且它们具有不同的取食分布,避免了资源竞争(吴建功等, 2002)。入侵种扶桑棉粉蚧与红火蚁,以及黑头酸臭蚁也具有协同互作的关系。扶桑棉粉蚧为红火蚁和黑头酸臭蚁提供蜜露资源(Zhou *et al.*, 2012, 2014a, b),红火蚁与黑头酸臭蚁则通过抑制或削弱天敌减少其对扶桑棉粉蚧的寄生或捕食(Zhou *et al.*, 2014a, b, 2016a; Cheng *et al.*, 2015; Feng *et al.*, 2015)。此外,红火蚁还能缓解其他植食性昆虫,如美洲棘蓟马 *Echinothrips americanus* Morgan 与扶桑棉粉蚧的竞争(程寿杰等, 2013)。

1.4 生态适应

1.4.1 温度适应性 随着全球气候变暖的加剧,温度胁迫成为昆虫成功定殖的关键屏障,而入侵昆虫往往具有较高温度适应能力。如 B 型烟粉虱与红火蚁均具有很强的耐高温适应力与热激耐受性(Cui *et al.*, 2008; Xu *et al.*, 2009; Gao *et al.*, 2015),推测可能与热抗性基因的表达变化相关(Lv and Wan, 2008; Mahadav *et al.*, 2009)。而烟粉虱、苹果绵蚜和扶桑棉粉蚧等的耐寒能力很强,能在我国大部分地区安全越冬。有些昆虫还能通过滞育现象有效提升其对极端高低温的适应性,如稻水象甲、苹果蠹蛾与马铃薯甲虫等(Jiang *et al.*, 2004; 杨瑞, 2008)。另外,昆虫不同龄期的温度适应策略也不相同,如桔小实蝇,其卵对高温具有较高耐受性(李柏树等,

2013),而蛹期,尤其是越冬前期对低温的适应性更强(Wang *et al.*, 2014b),且幼虫的寄主植物影响其后代抗寒力(任璐等, 2006),这一温度适应机制可能与其体内氧化还原酶、抗氧化酶等密切相关(Jia *et al.*, 2011; Gao *et al.*, 2013; Wei *et al.*, 2015b)。有趣的是,同种昆虫不同地理种群的温度适应性也可能不同,如红棕象甲在上海与福州的温度适应阈值以及最适生长温度均具有明显差异(Peng *et al.*, 2016)。

1.4.2 抗药性 20 世纪 90 年代末,我国农药进入高速发展阶段,当前年产量可达 370 万吨,消费量达 1.8 万吨(Pan *et al.*, 2019)。大量农药使用导致入侵昆虫产生严重的抗药性,如马铃薯甲虫、桔小实蝇等(Jiang *et al.*, 2010; 王志田等, 2010; Jin *et al.*, 2011; Zhang *et al.*, 2014b)。入侵昆虫抗性进化可能与其解毒代谢增强、敏感性下降、消化代谢升高等相关(Shen *et al.* 2012; Huang *et al.*, 2013; Hu *et al.*, 2014; Jiang *et al.*, 2014)。抗药性增强还可促进物种之间的竞争替代,入侵烟粉虱(B 和 Q 型)的抗药性明显高于本地粉虱,促进了其对本地粉虱的竞争替代。其中, Q 型烟粉虱的抗药性明显高于 B 型烟粉虱(Luo *et al.*, 2010; Pan *et al.*, 2015),室内与大田试验均证实,杀虫剂的广泛施用加快了入侵 Q 型烟粉虱在我国对 B 型烟粉虱的竞争替代(Sun *et al.*, 2013)。

1.4.3 其他适应性 外来昆虫入侵到新环境,很可能面对食物不充足的情况,较强的抗饥饿能力可能是影响其种群成功定殖的重要因素。在剥夺食物资源的情况下,扶桑棉粉蚧若虫可存活 5 d 左右,成虫存活的时间更长,平均可达 9 d,且饥饿 4 d 对其成虫繁殖力没有显著影响(郑婷等, 2011; Tong *et al.*, 2019)。这一适应性促进了扶桑棉粉蚧的成功定殖与扩散。桔小实蝇对湿度的适应范围较宽,干燥不会影响其幼虫化蛹(Xie and Zhang, 2009),且蛹比幼虫的湿度耐受性更强,可以在 10%-60% 的湿度范围内存活和发育(Hou *et al.*, 2006; 任璐等, 2007)。不同地理种群的稻水象甲对水稻耕作制度,如水肥管理的适应性并不相同,在美国,延迟水稻浸水时间

可以减少稻水象甲卵的沉积, 从而减轻危害 (Huang *et al.*, 2017), 但入侵我国后, 并未发现这一现象, 反而是苗期施氮量对稻水象甲繁殖具有显著影响 (Jiang and Cheng, 2003b)。

2 入侵昆虫的应用研究

2.1 检疫检测

口岸检验检疫是预防外来生物入侵的第一道防线, 而开发快速检测识别技术是提高检验检疫效率的关键。Wang 等 (2019) 获得一对特异性 CO I 引物能够从 21 种近缘种中快速、灵敏的鉴定出木薯绵粉蚧 *Phenacoccus manihoti* Matile-Ferrero。张桂芬等 (2012) 采用 SS-PCR 技术, 获得一对特异性引物, 可用于美洲斑潜蝇 *Liriomyza sativae* (Blanchard) 的快速识别与鉴定。利用 CO II TS1 与间接 ELISA 方法同时鉴定三叶斑潜蝇发现, 以 CO I 作为条形码序列鉴定效果更好, 而 ELISA 方法更适用于样本量较大的田间样品 (郭伟等, 2013)。当前, 基因组学与分子生物学技术的快速发展, 为入侵物种的快速鉴定提供了更有力的数据支撑, 有效促进了 CO I、SCAR 分子标记、MGB 探针, 以及 DNA 芯片等一系列分子鉴定技术的开发与应用。

2.2 农业防治

入侵昆虫的农业防治措施包括调整寄主作物种植期, 选择不敏感作物轮作, 清除作物残茬, 采取合理水肥管理, 以及选择抗性作物品种等。例如, 选择适宜的马铃薯种植期与非寄主作物轮作能够提高马铃薯甲虫越冬成虫的死亡率与延长越冬成虫的出现时间 (Guo *et al.*, 2017)。郭利娜等 (2011) 研究也证实, 第一代马铃薯甲虫幼虫在轮作马铃薯田的密度仅为连作马铃薯田的 29%-84% (平均 65%)。水旱作物轮作也能有效控制稻水象甲为害, 且轮作面积越大防效越好 (刘志峰等, 2016)。水肥管理策略对不同入侵昆虫的影响也不相同, Bi 等 (2005) 证实过量施用氮肥将显著增加烟粉虱种群数量, 从而加剧危害。然而, 增加施肥却能通过提高植物抗性从而减少马铃薯甲虫危害 (郭利娜等, 2011; 郭

文超等, 2014)。

2.3 化学防治

2.3.1 化学农药 随着社会经济的发展, 以及可持续生态环境建设的迫切需求, 越来越多的对环境友好的病虫害防治措施逐步出现, 但化学农药依然是最经济有效的技术手段之一。筛选低毒高效的药剂是科学用药的基础。我国学者针对多种入侵昆虫进行了化学农药筛选与控制效应评估, 并逐步运用于生产实践。例如, 在实验室和田间条件下, 评估了氟磺胺、吡虫啉与毒死蜱等多种杀虫剂对红火蚁的防治效果 (李惠陵等, 2007), 随后发现, 亚致死剂量的吡虫啉能够显著降低红火蚁蚁后生殖能力, 从而导致成年工蚁和蛹的出现时间显著推迟, 对蚁巢早期的建立有很大影响 (Wang *et al.*, 2015b)。基于红火蚁的社会性特征, 毒饵也是控制其危害的有效手段, 黄田福等 (2007) 发现将毒饵与接触性杀虫剂相结合, 可大规模杀灭 94% 的红火蚁种群。此外, 我国学者还成功筛选出了多种高效、低毒的新烟碱类杀虫剂, 如乙酰胺类和吡虫啉类杀虫剂, 通过拌种或喷施方法能够有效控制马铃薯甲虫的越冬成虫或第一代幼虫 (郭建国等, 2010a, b; 付文君等, 2013)。刘中芳等 (2016) 研究发现, 240 g/L 氟啶虫腈悬浮剂 5 000 倍液对苹果绵蚜持续控制效果较好, 适用于绵蚜发生盛期。欧善生等 (2009) 发现, 田间施用 500 倍 3% 的阿维菌素苯甲酸酯和 45% 的马拉硫磷, 对红棕象甲的防治效果分别可达 93.4% 和 84.5%; 并且发现熏蒸法比其他方法更有效, 推荐在野外使用 (刘丽等, 2011)。

2.3.2 植物源农药 植物源杀虫剂被看作是环境友好的化学制剂, 在入侵昆虫防控中的应用越来越广泛。植物挥发物或提取物对红火蚁有较高效的毒杀或趋避作用 (Tang *et al.*, 2013; Wang *et al.*, 2014a, 2014b), 如非洲山毛豆与青蒿挥发物对红火蚁工蚁具有高效的毒杀作用, 分别可达 95% 和 80% (Li *et al.*, 2014b; Zhang *et al.*, 2014a), 辣椒与杜仲的精油提取物对红火蚁具有强烈的趋避效应 (Wang *et al.*, 2014a, 2014c)。杠柳毒苷对红火蚁也具有很高的控制活性, 可对

其中肠上皮细胞造成严重伤害 (Li and Zeng, 2013)。油松释放的(+)-3-萜烯是红脂大小蠹的最佳引诱剂 (Sun *et al.*, 2004), 目前, 在我国各红脂大小蠹入侵地区, (+)-3-萜烯已成功应用于红脂大小蠹的诱集防控 (Sun *et al.*, 2004; Liu *et al.*, 2006)。植物源农药虽然具有对环境污染小、抗药性产生难、成本低等特点, 但仍存在效应缓慢、控制范围狭窄、残效期短、稳定性较差, 以及易受到环境因素制约等劣势, 这直接限制了其在生产实践中的广泛应用。

2.4 生物防治

2.4.1 天敌昆虫 在我国, 入侵昆虫的生物防治研究也取得了一系列重要的进展, 如烟粉虱、椰心叶甲 *Brontispa longissima* (Gestro)、桔小实蝇等。据统计, 烟粉虱在我国的寄生性与捕食性天敌分别有 56 与 54 种 (Li *et al.*, 2011), 其中 10 余种寄生性与捕食性天敌目前已商品化应用 (Wan and Yang, 2016; Wang and Yang, 2017)。天敌对烟粉虱的控制效应往往不是由单一天敌种类所决定, 不同天敌间通常形成复杂的协同互作网络。例如, 海氏桨角蚜小蜂 *Eretmocerus hayati* (Zolnerowich & Rose) 与浅黄恩蚜小蜂 *Encarsia sophia* (Girault & Dodd) 联合释放, 可以有效增强控制效应 (Xu *et al.*, 2015a, 2016; Huang *et al.*, 2016)。另外, 丽蚜小蜂 *Encarsia formosa* Gahan、浅黄恩蚜小蜂与异色瓢虫 *Harmonia axyridis* (Pallas) 联合释放, 以及东亚小花蝽 *Orius sauteri* (Poppius) 与丽蚜小蜂联合释放均能够显著增强它们对烟粉虱的控制效应 (李姝等, 2014; Tan *et al.*, 2016)。除此之外, 天敌昆虫的联合释放也应用于其他昆虫中, 以提升控制效应。吴正伟等 (2015) 研究表明, 赤眼蜂和周氏啮小蜂 *Chouioia cunea* Yang 联合释放能够有效防治苹果蠹蛾。但椰心叶甲的生物防治比较例外, 当前, 椰心叶甲啮小蜂 *Tetrastichus brontispae* F. 与椰甲截脉姬小蜂 *Asecodes hispinarum* Bouček 已经成功工厂化生产以及田间释放应用, 其单一释放的寄生率分别可达 100% 与 90%, 但是同时寄生效率并不稳定 (Lu and Peng, 2017), 两种

寄生蜂之间是否存在寄生干涉及其机制如何还有待进一步研究。

2.4.2 昆虫病原微生物 白僵菌 *Beauveria bassiana* 与绿僵菌 *Metarhizium anisopliae* 是常见的昆虫病原真菌, 逐步应用于入侵昆虫的生物防治。室内试验证实, 白僵菌对桔小实蝇成虫、稻水象甲成虫与烟粉虱若虫表现出较高毒力 (章玉苹等, 2010; Xia *et al.*, 2013; 徐进等, 2013)。白僵菌控制稻水象甲的大田试验也开始进行 (徐进等, 2015)。绿僵菌也逐步应用于椰心叶甲、稻水象甲、水椰八角铁甲等生物防治。我国学者对椰心叶甲的高效绿僵菌菌株进行了筛选, 并研发出大批量生产技术以及制剂类型, 大田试验显示, 施用绿僵菌一周后, 椰心叶甲的死亡率可达 80% (秦长生等, 2008)。除此之外, 还有多种昆虫病原微生物在我国开展应用, 刘晓燕等 (2010) 从红火蚁工蚁上分离获得一株淡紫色拟青霉菌 *Paecilomyces lilacinus* (Thom) Samson, 其对红火蚁工蚁的致死率可到 70%, 但长期持续控制效应并不稳定, 可能由于协同进化的产生导致红火蚁防御体系的形成 (Qiu *et al.*, 2014, 2016)。粉虱座壳孢 *Aschersonia aleyrodalis*、蜡蚧轮枝菌 *Verticillium lecanii* 以及玫烟色棒束孢 *Isaria fumosorosea* 对烟粉虱也有较好的防治效果 (邱宝利等, 2003; 田晶等, 2014)。昆虫病原线虫也是一种极具潜力的昆虫致病微生物, 小卷蛾斯氏线虫 *Steinernema carpocapsae* 能够抑制水椰八角铁甲的细胞免疫, 可作为一种极具潜力的生物防治剂 (Sanda *et al.*, 2018)。夜蛾斯氏线虫 *Steinernema feltiae* 与异小杆线虫 *Heterorhabditis bacteriophora* 分别对稻水象甲幼虫与成虫具有高致死力 (孙文鹏等, 2006)。然而, 受温度、湿度等环境因素的制约, 病原微生物对昆虫的田间防治效果通常较慢, 且不稳定。在大田应用中往往需要和其他物质联合使用, 才能发挥其控制效应。近年来的研究表明, 玫烟色棒束孢与噻虫嗪或吡虫啉、白僵菌与非离子表面活性剂联合使用对烟粉虱控制具有协同增效作用 (Mascarin *et al.*, 2014; Zou *et al.*, 2014)。樊江斌等 (2015) 发现添加低剂量的氧化铁, 能

够显著增强和提升颗粒体病毒在田间的活性与持久性,从而提高其对苹果蠹蛾的控制效果。此外,颗粒病毒与线虫混合或轮换使用对于防治苹果蠹蛾具有明显效应(Lacey *et al.* 2004)。

3 发展方向

综上所述,近年来我国学者在外来入侵昆虫的研究领域取得了一系列重要进展,尤其是在解析入侵昆虫的生物学特性、生态适应性进化、以及昆虫种内/间的竞争互作机制方面取得重大突破,同时对于入侵昆虫的综合防控技术研发也逐步深入。尽管如此,我国生物入侵防控发展仍然任重道远。习近平总书记首次将生物安全纳入新时代国家安全观范畴,其中生物入侵则是生物安全领域的重要组成部分。为此,我国政府成立了专门的部门,从政策研究、法律法规体系建设、以及项目设置等方面,指导和支持了我国生物入侵研究的发展,以及防控策略的制定。在此大背景下,也在全球经济一体化、农业结构调整以及全球气候变化等因素的影响下,我国生物入侵研究,尤其是入侵昆虫研究将迈入一个全新的时代,未来的发展方向主要包括以下几个方面:

基于多层次、多维度的生态因子,如景观生态因子、区域生态因子、以及全球生态因子(如全球气候变化),解析其对外来物种的传入、定殖、扩散的影响,这将有利于制定各国之间、地区之间、省市之间入侵昆虫传入与扩散的早期预警与风险分析策略,也能进一步明确外来入侵昆虫的遗传分化特性、生态适应机理,以及种群扩张行为与机制等。

新一代测序技术和生物信息学的发展加速了昆虫基因组的研究,这不仅有助于解决学界广泛关注的种群遗传和进化生态等问题,也促进了我们对害虫适应性和致害性变异机理有了更新更全的认识,为害虫治理提供了新的机遇和挑战。当前,入侵昆虫的基因组测序研究也日益发展,截止 2018 年 12 月,已有 67 种入侵昆虫完成了基因组测序(黄聪等, 2019),如苹果蠹蛾(Wan *et al.*, 2019)、烟粉虱(Xie *et al.*, 2017)等。这为我们解析害虫的入侵机制,开发新型防

控技术提供了新的思路和研究方向。一是可以利用全基因组重测序方法补充分子标记技术遗传信息不全的缺点,全面深入的解析入侵昆虫的遗传结构与分化特征,从而明确其入侵来源与路径。二是从全基因组层面,利用 RNAi 或 CRISPR/cas9 等分子生物技术解析入侵昆虫-植物互作、入侵昆虫抗药性、以及入侵昆虫发育、繁殖以及免疫的分子机制等,从而为抗性育种、抗药性治理,以及行为调控提供数据支撑。

抗药性的快速发展导致化学农药的控制效应逐步降低,而天敌昆虫、病原微生物以及生物农药受环境因子制约通常田间应用效应也较低。因此,开发新型友好的入侵昆虫防治技术,如遗传调控、生物农药基因改造等,是未来入侵昆虫治理的发展趋势。近年来,基于基因组大数据的支持,遗传调控技术在害虫防治方面取得了一定进展,在入侵昆虫防治方面也展现出良好前景。在全基因组范围内筛选昆虫生长发育的关键基因,采用性别控制开关,通过遗传转化手段改变自然种群性别从而实现种群数量逐步下降。生物农药基因改造方面,利用 RNAi 技术改造微生物农药。将害虫的靶标基因 dsRNA 表达原件转入到微生物(如 Bt)中,构建具有 RNAi 杀虫活性的微生物。

随着全球经济发展,入侵生物扩散速度越来越快,扩散途径更加复杂。传统的物理或化学诱集监测无法精准快速的获取信息,使早期预警与风险分析的准确性受到限制。未来应该充分利用物联网、大数据等现代信息技术,如整合卫星遥感数据、无人机遥感数据、物联网观测数据、地面调查数据、气象数据、环境数据等多源数据,基于 AI 数据处理,构建实时监测、早期预警、预测预报和应急防控指导等综合智能信息化平台,从而全面提高害虫监测预警的准确性和时效性。

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