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农田重金属沿植食性昆虫 – 天敌昆虫传递及对害虫生物防治的影响

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摘要: 农田重金属污染是全球农业面临的重要环境问题之一。重金属经植物吸收富集, 由植食性昆虫取食并积累而产生上行效应, 影响天敌昆虫的生长发育、生殖能力以及行为, 进而影响天敌对害虫的控制作用。本文系统总结了农田生态系统中重金属沿植食性昆虫传递对天敌昆虫的影响, 分析了农田重金属污染对害虫生物防治的直接与间接影响效应, 发现重金属胁迫一般会导致天敌昆虫生长发育延缓、生殖力降低、捕食量减少等, 直接影响害虫生物防治效果; 但也可能导致害虫毒物兴奋效应产生和抗性能力增强, 间接增加害虫防治难度。根据研究现状, 对重金属污染影响天敌昆虫和生物防治的未来研究方向进行了展望。

关键词: 环境污染; 重金属; 上行效应; 非生物因子; 害虫生物防治

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Transfer of heavy metals along phytophagous insects-natural enemies and their effects on pest biological control in agroecosystems

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Abstract: Heavy metal contamination in farmland is one of the important environmental problems facing global agriculture. Heavy metals are absorbed by plants, taken in, and accumulated by herbivorous insects, then affected the growth, reproduction, and behavior of natural enemies by bottom-up effects, seriously threatening the efficiency of pest biological control. In this review, the effects of heavy metal transferring along herbivorous insects on natural enemies in farmland ecosystem were systematically summarized, and the direct and indirect effects of heavy metal pollution on pest biological control were expounded. Heavy metal generally leads to negative effects such as delayed growth and development,

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reduced fecundity, and reduced predation of natural enemies, which directly affects the efficiency of pest biological control. In the meantime, heavy metal also led to the emergence of poison excitement effect and the enhancement of resistance ability of pests, indirectly increasing the difficulty of pest control. In view of the current research situation, this paper summarizes and looks forward to the deficiency of the research on the influence of heavy metal pollution on natural enemy insects and biological control, and provides reference for the study of natural enemy insects under environmental heavy metal stress and the formulation of pest biological control strategies in heavy metal polluted areas.

Key words: Environmental pollution; heavy metals; bottom-up effects; abiotic factor; pest biological control

农田重金属污染是全球农业面临的重要问题之一 (Zhao *et al.*, 2015; Tóth *et al.*, 2016)。镉 (Cd)、汞 (Hg)、砷 (As)、铜 (Cu)、铅 (Pb)、铬 (Cr)、锌 (Zn) 和镍 (Ni) 8 种重金属是我国农用地土壤污染风险筛选的基本和必测污染物 (GB 15618 - 2018)。据 2014 年《全国土壤污染状况调查公报》, Cd、Hg、As、Cu、Pb、Cr、Zn 和 Ni 的点位超标率分别为 7.0%、1.6%、2.7%、2.1%、1.5%、1.1%、0.9% 和 4.8% (环境保护部和国土资源部, 2014)。最新研究表明, 我国农田土壤的 Pb、Cd、Hg 和 Cu 的平均含量分别超标 1.04、5.73、2.22 和 1.14 倍 (Shi *et al.*, 2023)。

农田中的重金属经作物根部被吸收富集, 不仅严重影响作物的产量和品质, 而且可以通过食物链传递后在人体积累, 危害人类健康 (宋波等, 2006; Qian *et al.*, 2010; Zhao and Wang, 2020)。值得注意的是, 植食性昆虫对植物中的重金属具有生物放大作用 (Biomagnification) (Naikoo *et al.*, 2021a; Naikoo *et al.*, 2021b), 可能会破坏农业生态系统中的营养级关系、生态相互作用及功能 (Winter *et al.*, 2012; Dar *et al.*, 2015; Dar *et al.*, 2017)。重金属通过上行效应 (Bottom-up effects) 不仅直接影响植食性昆虫的生长发育、行为和逆境耐受能力 (如农药、重金属等), 还会对天敌昆虫产生间接影响, 进而影响害虫防治效果 (Burkman and Gardiner, 2014; Gardiner and Harwood, 2017; Han *et al.*, 2022)。由于人类的不当活动而导致农田重金属污染愈发严重, 农田生态系统中的植食性昆虫和天敌昆虫面临重金属胁迫概率越来越高 (Di *et al.*, 2016; 邸宁, 2017)。近年来, 国内外从多个方面综述了重金属污染对昆虫生长发育 (孙虹霞等, 2007; 陈瑾等, 2020)、昆虫行为 (Mogren and Trumble, 2010)、

生态生理 (杨世勇等, 2015)、植物抗虫性 (黄江南等, 2021) 以及植物-传粉昆虫互惠关系 (吴磊等, 2022) 等方面的影响, 也有强调了重金属沿植物 - 害虫 - 天敌昆虫传递的上行效应 (Gardiner and Harwood, 2017; Dar *et al.*, 2019; Tibbett *et al.*, 2021), 但是系统总结农田生态系统中的重金属沿植食性昆虫传递对天敌昆虫、害虫生物防治的影响未见报道。

研究重金属污染对农田生态系统中各营养级的影响及其作用机制, 可以明晰重金属胁迫对农业害虫和天敌的影响程度, 为天敌昆虫受环境重金属胁迫、重金属污染地区的害虫生物防治策略的制定提供基础数据, 促进农业的可持续健康发展。因此, 本文综述了农田重金属污染沿植食性昆虫对天敌昆虫影响的研究进展, 系统分析了农田重金属污染对害虫生物防治的影响, 以期为农田重金属污染下的害虫防治策略的制定提供基础支持。

1 重金属对植食性昆虫的影响

作为生物多样性的重要组成部分, 植食性昆虫是农田生态系统中食物链和食物网的重要环节, 并在重金属的传递与累积过程中起到重要的媒介作用 (陈瑾等, 2020; 黄江南等, 2021)。植食性昆虫取食重金属积累的植物或添加重金属的人工饲料而遭受胁迫 (孙虹霞等, 2007; 陈瑾等, 2020)。目前有关重金属对植食性昆虫影响的研究主要集中在鳞翅目和半翅目昆虫。植食性昆虫取食富集重金属的植物后, 其生长发育、繁殖力均会受到不同程度的影响 (钱媛媛等, 2017; 刘伟等, 2019; 吴梦露等, 2023)。例如, 低剂量 Cd

胁迫不会影响水稻生长,但会导致褐飞虱 *Nilaparvata lugens* (Stål) 孵化率降低、孵化期延长,降低褐飞虱田间种群数量(Chen et al., 2022)。Cd 胁迫可以导致水稻中粘虫 *Mythimna separata* (Walker) 诱导的防御化合物的含量增加,进而提高水稻对粘虫的抗性(陈雨萌等,2022)。取食 As 胁迫的辣椒后,桃蚜 *Myzus persicae* (Sulzer) 的繁殖力和产蜜露量显著降低,而存活率和发育历期无差异(Kim et al., 2019)。此外,重金属对植食性昆虫的生长发育、繁殖力的影响存在剂量效应。取食低浓度含 Cd 人工饲料后,二化螟 *Chilo suppressalis* (Walker) 的蛹重增加,而高浓度 Cd 处理后的蛹重减轻(张宇瑶等,2017)。随着食料中 Cd 浓度的增加,粘虫幼虫存活率和成虫繁殖力下降,化蛹率和蛹畸形率显著增加,低、中浓度的 Cd 处理延长了幼虫期,而高浓度则缩短了幼虫期(Wei et al., 2020)。取食含低剂量 Cd 的人工饲料后,甜菜夜蛾 *Spodoptera exigua* (Hübner) 和草地贪夜蛾 *Spodoptera frugiperda* (J. E. Smith) 的繁殖力均增加,而高剂量则导致其繁殖力下降(Su et al., 2021; 王杰等,2023)。因此,植食性昆虫的适合度受到重金属剂量的调控。

重金属胁迫还会对植食性昆虫的行为产生重要影响(Mogren and Trumble, 2010)。重金属胁迫一般会对植食性昆虫的生殖行为产生负面影响。例如,亚洲玉米螟 *Ostrinia furnacalis* (Guenée) 在 Cd 胁迫下,连续三代的雌蛾求偶行为均受到影响,求偶百分率在第一代和第二代都受到抑制,在第三代表现为促进作用,求偶持续时间随玉米螟饲养代数的增加而逐代缩短,求偶高峰出现时间在第一代和第三代均发生改变(曹红妹和魏洪义,2016);在 Ni 胁迫下,亚洲玉米螟雌蛾平均求偶持续时间逐渐减小,高浓度下雌蛾求偶高峰期出现的时间提前(曹红妹等,2015)。Cd 胁迫下,二化螟雄蛾对雌蛾的定向行为受抑制,雄蛾的兴奋、起飞和降落率分别比对照组降低 50.0%、46.7% 和 33.3% (张宇瑶等,2017);求偶率下降、求偶高峰期推迟和求偶持续时间缩短(刘玲玲,2020)。Cd 胁迫导致甜菜夜蛾的交配提前结束,并且其总求偶持续时间、每日交配率和总交配率下降(Su et al., 2021)。此外,重金属胁迫会对植食性昆虫的飞行能力和取食行为产生影响。例如,使用含有 Cd 的人工饲料饲养甜菜夜蛾,其雌雄虫飞行能力均会随处理浓度的升高而受到抑

制,且飞行抑制效果在雄虫中表现更为明显(邹金城等,2017)。麦长管蚜 *Sitobion avenae* (Fabricius) 取食 Cd 胁迫小麦时的非刺探波(np)次数增加,口针在细胞间穿刺的频率显著增高,取食行为推迟,导致其在 Cd 胁迫的小麦上取食适合度下降(武晶晶等,2012)。麦长管蚜的取食行为还会受到 Zn 的影响,并且会在高剂量 Zn 胁迫下产生积累效应,而低剂量的 Zn 则促进取食行为(张丽等,2016)。

2 重金属对天敌昆虫的影响

一般来说,植食性昆虫对植物中的重金属具有生物放大或生物富集作用(Kaminski et al., 2021; Naikoo et al., 2021a; Naikoo et al., 2021b),进而通过食物链影响天敌昆虫(Winter et al., 2012; Dar et al., 2015; Dar et al., 2017)。虽然国内外就重金属对昆虫胁迫做了许多研究,但现有研究多关注模式昆虫或植食性昆虫,对可能间接受到重金属影响的天敌昆虫类群的关注不足(Tibbett et al., 2021)。已有研究表明,重金属沿食物链传递会对天敌昆虫的生长发育和生殖能力均产生一定的影响。一般来说,重金属对寄生性天敌的影响与寄主体内的重金属含量以及转移程度有关,而捕食性天敌受重金属影响的程度则与捕食量相关(董卉,2007; Naikoo et al., 2021b)。目前有关重金属沿植食性昆虫传递对天敌昆虫影响的研究多关注于捕食性天敌。重金属 Cd 是主要的研究对象,其次是 Zn、Pb、Cu、Ni 和 As(表 1)。

2.1 生长发育

针对重金属沿食物链对捕食性天敌昆虫影响的研究主要集中在蚜虫/粉蚧-捕食性瓢虫的研究体系(表 1),如蚕豆-豌豆修尾蚜 *Megoura crassicauda* Mordvilko-异色瓢虫 *Harmonia axyridis* (Pallas)(王莎莎,2023),茄子-新菠萝灰粉蚧 *Dysmicoccus neobrevipes* Beardsley-孟氏隐唇瓢虫 *Cryptolaemus montrouzieri* (Wang et al., 2017; Sang et al., 2018; Du et al., 2019; Wang et al., 2022a),以及菜缢管蚜 *Lipaphis erysimi* (Kaltenbach) 或麦长管蚜-七星瓢虫 *Coccinella septempunctata* L. (Green et al., 2010; Dar et al., 2015; Dar et al., 2017; Butt et al., 2018)。捕食性天敌长期取食含重金属的植食性昆虫后,其生

长发育一般会受到显著抑制。如，取食含重金属 Cd 或 Ni 的新菠萝灰粉蚧后，孟氏隐唇瓢虫的幼虫期、蛹期、成虫期和产卵前期均显著延长，成虫寿命、净繁殖力和内禀增长率均显著降低 (Sang et al. , 2018)。异色瓢虫以 Cd 胁迫豌豆修尾蚜为食，其存活率降低，出现畸形表型 (王莎莎, 2023)。此外，重金属对捕食性天敌的影响存在剂量效应。取食低浓度 Cd 胁迫的甜菜夜蛾后，蠋蝽 *Arma chinensis* 的发育历期缩短，生长发育受到了促进作用；而高浓度的 Cd 胁迫下的发育历期显著延长 (陈玉青, 2020)。并且，在长期受到重金属胁迫后，捕食性天敌种群结构会受到显著影响。如取食 Cd 胁迫的食物的蠋蝽的种群出现了雌性化现象；Cd 浓度越高，雌性化程度越高；低龄蠋蝽受到低浓度 Cd 胁迫，死亡率降低，而受到高浓度 Cd 胁迫后，各龄期死亡率均显著上升 (陈玉青, 2020)。然而，七星瓢虫幼虫取食含有多种重金属的蚜虫后，发育至成虫后的体重无显著差异 (Green et al. , 2003; Dar et al. , 2015; Dar et al. , 2017)。

寄生重金属胁迫的寄主后，寄生蜂子代的羽化率和雌性比一般不受影响，如蛹寄生蜂 *Coptera occidentalis* Muesebeck (Kazimírová and Ortel, 2000)、烟蚜茧蜂 *Aphidius colemani* Viereck (Konopka et al. , 2013)、稻螟赤眼蜂 *Trichogramma japonicum* Ashmead (Wang et al. , 2024)、松毛虫赤眼蜂 *Trichogramma dendrolimi* Matsumura (王杰等, 2023) 和白蛾周氏啮小蜂 *Chouioia cunea* Yang (Yan et al. , 2023)。寄生蜂寄生重金属胁迫的寄主，其子代的个体大小和寿命普遍出现降低的现象。如，白蛾周氏啮小蜂寄生 Cd 胁迫的美国白蛾 *Hyphantria cunea* (Drury)，其个体大小和寿命显著降低 (Yan et al. , 2023)；且体重和成虫寿命显著降低，胚胎的发育历期显著延长 (Tan et al. , 2023)。稻螟赤眼蜂寄生 Cd 胁迫的米蛾 *Corcyra cephalonica* (Stainton) 卵后，其体长和后足胫节长度均显著降低，而松毛虫赤眼蜂未受到显著影响 (Wang et al. , 2024)。毒蛾绒茧蜂 *Glyptapanteles liparidis* (Bouché) 寄生低浓度 Cu 或 Zn 胁迫的舞毒蛾 *Lymantria dispar* (Linnaeus) 后，子代蛹期无差异，而高浓度下则出现蛹期延长 (Ortel et al. , 1993)。这些结果表明不同物种对重金属的耐受能力存在一定的区别。此外，研究表明，重金属对寄生蜂的影响主要是

通过降低寄主的营养成分含量或质量 (如血淋巴) (吴国星, 2005)，导致寄生蜂营养不良，降低寄生蜂的生长发育以及繁殖力 (Ortel et al. , 1993; Ye et al. , 2009)。

2.2 生殖能力

一般来说，重金属沿植食性昆虫传递会对捕食性天敌昆虫的生殖能力产生负面影响。例如，取食含 Cd 或 Ni 的新菠萝灰粉蚧后，孟氏隐唇瓢虫的繁殖力、净繁殖力和内禀增长率均显著降低 (Sang et al. , 2018)。异色瓢虫以 Cd 胁迫豌豆修尾蚜为食，其产卵前期延长，产卵周期缩短，产卵量减少，雌虫羽化第 2 天的卵巢发育较对照组迟缓，尺寸减小 (王莎莎, 2023)。Khan et al. (2024) 发现日本刀角瓢虫 *Serangium japonicum* Chapin 取食 Cd 胁迫的烟粉虱 *Bemisia tabaci* (Gennadius)，其总产卵前期显著增加，繁殖力和净繁殖力显著降低。但也有研究表明，取食 Cd 胁迫的西花蓟马 *Frankliniella occidentali* (Pergande) 后，东亚小花蝽 *Orius sauteri* (Poppius) 产卵量增加 (Liu et al. , 2023)。

重金属对寄生性天敌生殖能力影响的研究集中在寄生蜂。由于寄生蜂区别于捕食性天敌的寄生属性，重金属对寄生蜂生殖能力的影响可以分为寄生蜂对重金属胁迫植食性昆虫的寄生表现和重金属胁迫寄生蜂的寄生表现。寄生蜂对重金属胁迫寄主的寄生率或寄生量大多不受重金属影响，如毒蛾绒茧蜂 (Ortel et al. , 1993)、蛹寄生蜂 *Coptera occidentalis* (Kazimírová and Ortel, 2000)、双斑侧沟茧蜂 *Microplitis bicoloratus* Chen (夏婧等, 2006)、烟蚜茧蜂 (Konopka et al. , 2013)、粗脊蚜茧蜂 *Aphidius colemani* Viereck (Kim et al. , 2019)、稻螟赤眼蜂和松毛虫赤眼蜂 (Wang et al. , 2024)。田间试验表明，土壤 Cd 胁迫会降低褐飞虱种群数量，但不会影响稻虱缨小蜂 *Anagrus* sp. 对褐飞虱卵的寄生能力 (Chen et al. , 2022)。也有少量研究表明，寄生蜂对重金属胁迫寄主的寄生率或寄生量显著降低，如粗脊蚜茧蜂对 Pb 胁迫的夹竹桃蚜 *Aphis nerii* Boyer de Fonscolombe 的寄生量 (Ghabeish, 2014) 和白蛾周氏啮小蜂对 Cd 胁迫的美国白蛾蛹的寄生量 (Tan et al. , 2023; Yan et al. , 2023)。此外，毒蛾绒茧蜂对低浓度 Cu 或 Zn 胁迫的舞毒蛾蛹的寄生量 (Ortel et al. , 1993)、丽蝇蛹集金小蜂 *Nasonia vitripennis* (Walker) 对 Cd 或 Cu 胁迫的棕尾别麻蝇

Boettcherisca peregrine Robineau-Desvoidy 的每单位蛹重量（董卉，2007）、松毛虫赤眼蜂对 Cd 胁迫的草地贪夜蛾卵的寄生率均显著增加（王杰等，2023）。而有关重金属胁迫对寄生蜂的寄生能力影响的研究较少。Zn 胁迫的双斑侧沟茧蜂对 Zn

胁迫的斜纹夜蛾 *Spodoptera litura* Fabricius 幼虫的寄生率显著降低（夏婧等，2006）。Cd 胁迫导致稻螟赤眼蜂对米蛾卵的寄生量显著降低，而 Cd 胁迫导致松毛虫赤眼蜂对米蛾卵的寄生量显著增加（Wang et al. , 2024）。

表 1 重金属沿植食性昆虫传递对天敌昆虫的影响
Table 1 Effects of heavy metals transferred by herbivores on natural enemies

重金属 Metal	天敌昆虫 Natural enemy	植食性昆虫 Herbivore	对天敌昆虫的影响 Effect on natural enemy	参考文献 References
寄生性天敌 Parasitoid				
Cd	白蛾周氏啮小蜂 <i>Chouioia cunea</i>	美国白蛾 <i>Hyphantria cunea</i>	氧化损伤增加；F ₀ 代寄生数降低；F ₁ 代体长、体重、成虫寿命降低，胚胎发育历期延长。 Increased oxidative damage, decreased parasitic rate, number of offspring larvae, individual size and life span of offspring adults, extended duration of embryo development.	Tan et al. , 2023
	稻虱缨小蜂 <i>Anagrus nilaparvatae</i>	褐飞虱 <i>Nilaparvata lugens</i>	F ₀ 代寄生率无差异。 No effect on parasitic rate of F ₀ .	Chen et al. , 2022
	烟蚜茧蜂 <i>Aphidius colemani</i>	桃蚜 <i>Myzus persicae</i>	F ₀ 代寄生无影响；F ₁ 代羽化率、僵化时间、发育历期无差异。No effect on parasitic rate of F ₀ ，emergency rate and duration of F ₁ .	Konopka et al. , 2013
	阿维蚜茧蜂 <i>Aphidius ervi</i>	豌豆蚜 <i>Acyrtosiphon pisum</i>	F ₀ 代瞬时生长速率降低。Decreased instantaneous rates of population increase.	Kramarz and Stark, 2003
Pb	粗脊蚜茧蜂 <i>Aphidius colemani</i>	夹竹桃蚜 <i>Aphis nerii</i>	F ₀ 代繁殖力降低；F ₁ 代发育时间、死亡率增加，寿命降低。Decreased fecundity of F ₀ . Increased development times and mortality percentages, and decreased longevity of F ₁ .	Ghabeish, 2014
As	粗脊蚜茧蜂 <i>Aphidius colemani</i>	桃蚜 <i>Myzus persicae</i>	F ₀ 代对1龄和3龄若蚜寄生率无差异。寄生1龄若蚜的F ₁ 代羽化率无差异，高浓度As胁迫下寄生3龄若蚜的F ₁ 代羽化率降低。No effect on the mummification rate of F ₀ and eclosion rate of F ₁ on 1 st instar aphid. Decreased eclosion rate of F ₁ under higher concentration of As.	Kim et al. , 2019
捕食性天敌 Predator				
Cd	东亚小花蝽 <i>Oris sauteri</i>	西花蓟马 <i>Frankliniella occidentalis</i>	取食量无差异；产卵量增加；高浓度 Cd 胁迫植株驱避天敌。No effect on predation. Increased number of eggs laid. Deterred effect on the predators to plants treated at the high level of Cd.	Liu et al. , 2023
	普通草蛉 <i>Chrysoperla carnea</i>	麦长管蚜 <i>Sitobion avenae</i>	Cd 传递到草蛉蛹，生物放大。Biotransfer and biomagnification in lacewing pupae.	Green et al. , 2006
		禾谷缢管蚜 <i>Rhopalosiphum padi</i>	Cd 传递到草蛉蛹，未生物放大。Biotransfer with no-biomagnification in lacewing pupae.	Alonso et al. , 2009

续表 1 Continued table 1

重金属 Metal	天敌昆虫 Natural enemy	植食性昆虫 Herbivore	对天敌昆虫的影响 Effect on natural enemy	参考文献 References
Cd	七星瓢虫 <i>Coccinella septempunctata</i>	菜缢管蚜 <i>Lipaphis erysimi</i>	4 龄幼虫发捕食量无差异, 初羽化成虫干鲜重无差异; 雌成虫无生物放大。No effect on predation of 4 th instar larva, fresh and dry mass of newly emerged adult. No biomagnification in female.	Dar <i>et al.</i> , 2017
		菜缢管蚜 <i>Lipaphis erysimi</i>	Cd 可通过食物链传递至捕食者。Biotransfer in predator.	Dar <i>et al.</i> , 2015
	狭臀瓢虫 <i>Coccinella transversalis</i>	黑豆蚜 <i>Aphis fabae</i>	高浓度 Cd 胁迫的成虫日均捕食量降低。4 龄幼虫发育至成虫的干、鲜重无差异。Decreased predation under high level of Cd. No effect on the fresh and dry mass of newly emerged adult.	Naikoo <i>et al.</i> , 2021b
	异色瓢虫 <i>Harmonia axyridis</i>	豌豆修尾蚜 <i>Megoura crassicauda</i>	成虫捕食量降低, 存活率和生殖力降低, 畸形。雌虫羽化 2 d 卵巢发育迟缓, 尺寸减小。雌成虫 <i>Vg1</i> 和 <i>Vg2</i> 的表达水平降低。Decreased predation, survival rate and fecundity. Increased abnormality rate of adults. Retarded and decreased in size of the ovaries. Decreased expression levels of <i>Vg1</i> and <i>Vg2</i> in female.	王莎莎, 2023
	日本刀角瓢虫 <i>Serangium japonicum</i>	烟粉虱 <i>Bemisia tabaci</i>	抗氧化酶 (SOD、CAT 和 POD)、脂质 (糖原、甘油三酯和总胆固醇) 活性降低, 相关基因表达量增加。各龄期和总产卵前期均显著增加, 成虫寿命和体重、产卵期、繁殖力和净繁殖力、雌成虫捕食量降低。Decreased activity of the antioxidant enzymes (SOD, CAT, and POD) and energy-conserving lipids (glycogen, triglyceride, and total cholesterol) with increased gene expression, and longevity, fecundity, adult body weight, oviposition days, net reproductive rate and predation of female. Increased developmental period and total pre-oviposition period.	Khan <i>et al.</i> , 2024
	孟氏隐唇瓢虫 <i>Cryptolaemus montrouzieri</i>	新菠萝灰粉蚧 <i>Dysmicoccus neobrevipes</i>	己糖激酶、琥珀酰辅酶 a、胰蛋白酶类蛋白、半胱氨酸蛋白酶、细胞分裂周期蛋白的表达发生变化。Cd 传递到瓢虫, 生物最小化。发育历期增加; 寿命、繁殖力、净繁殖力和内禀增长率降低。Changes in expression of proteins like hexokinase, succinyl-CoA, trypsin like proteins, cysteine proteases, cell division cycle proteins, and yellow gene proteins of adult. Biotransfer and biomimicry in predator. Increased developmental periods. Decreased longevity, fecundity, net reproduction rate and intrinsic rate of increase.	Wang <i>et al.</i> , 2017; Sang <i>et al.</i> , 2018; Wang <i>et al.</i> , 2022a
	异色瓢虫 <i>Harmonia axyridis</i>	豌豆修尾蚜 <i>Megoura crassicauda</i>	4 龄发育至成虫体重获得量、幼虫和蛹存活率、雌虫生殖力、卵孵化率降低。雌成虫 <i>Vg1</i> 、 <i>Vg2</i> 和 <i>VgR</i> 表达水平降低。Decreased weight gain, survival rate, egg production and hatchability. Decreased expression levels of <i>Vg1</i> , <i>Vg2</i> and <i>VgR</i> in female.	Shi <i>et al.</i> , 2020

续表1 Continued table 1

重金属 Metal	天敌昆虫 Natural enemy	植食性昆虫 Herbivore	对天敌昆虫的影响 Effect on natural enemy	参考文献 References
Cd	异色瓢虫 <i>Harmonia axyridis</i>	苜蓿蚜 <i>Aphis medicaginis</i>	成虫 24 h 捕食量降低。产卵率下降不显著。 Decreased predation in 24 h. No effect on egg production.	Xie et al., 2014
Pb	狭臀瓢虫 <i>Coccinella transversalis</i>	黑豆蚜 <i>Aphis fabae</i>	高浓度 Pb 胁迫下, 成虫日均捕食量降低。高浓度 Pb 胁迫的 4 龄幼虫发育至成虫的干、鲜重降低。 Decreased biomass and predation rate of adult.	Naikoo et al., 2019
	孟氏隐唇瓢虫 <i>Cryptolaemus montrouzieri</i>	新菠萝灰粉蚧 <i>Dysmicoccus neobrevipes</i>	Pb 被生物最小化。各发育历期、产卵前期、世代时间和翻倍时间增加; 寿命、繁殖力和内禀增长率降低。 Biotransfer and bio-minimization in predator. Increased developmental periods, mean generation time and doubling time. Decreased longevity, fecundity, and intrinsic rate of increase.	Zhang et al., 2017; Sang et al., 2018
Cu	圆斑弯叶毛瓢虫 <i>Nephus ryuguus</i>	腺刺粉蚧 <i>Ferrisia virgata</i>	高浓度 Cu 胁迫的 4 龄幼虫发育至成虫的干重降低。 Decreased dry weight of adult under high level of Cu.	Wang et al., 2022b
Ni	狭臀瓢虫 <i>Coccinella transversalis</i>	黑豆蚜 <i>Aphis fabae</i>	高浓度 Ni 胁迫下日均捕食量降低。4 龄幼虫发育至成虫的干、鲜重无差异。 Decreased daily predation under high level of Ni. No effect on the fresh and dry weight of adult.	Naikoo et al., 2021a
	孟氏隐唇瓢虫 <i>Cryptolaemus montrouzieri</i>	新菠萝灰粉蚧 <i>Dysmicoccus neobrevipes</i>	各发育历期、产卵前期、世代时间和翻倍时间增加; 寿命、净繁殖力、内禀增长率及周限增长率降低。 Increased developmental periods, pre-oviposition, mean generation time, and doubling time. Decreased longevity, net reproductive rate, intrinsic rate and finite rate of increase.	Sang et al., 2018

2.3 行为影响

重金属对天敌昆虫的行为影响研究主要分为两类, 一是天敌昆虫对重金属胁迫植食性昆虫的寄生或捕食表现, 二是重金属胁迫的天敌昆虫的寄生或捕食表现。目前有关重金属对天敌昆虫行为影响的研究主要集中于捕食性天敌的生殖和捕食行为, 寄生性天敌尚未见相关研究。

捕食性天敌一般不喜好取食重金属胁迫的植食性昆虫。例如, 狹臀瓢虫 *Coccinella transversalis* Fabricius 对 Ni 或 Pb 胁迫黑豆蚜 *Aphis fabae* Scopoli (Naikoo et al., 2019; Naikoo et al., 2021a)、异色瓢虫对 Zn 胁迫的苜蓿蚜 *Aphis medicaginis* Koch (Xie et al., 2014) 和 Cd 胁迫的豌豆修尾蚜 (王莎莎, 2023) 以及日本刀角瓢虫对 Cd 胁迫的烟粉虱的捕食量均显著降低 (Khan et al., 2024)。此

外, 有研究表明重金属胁迫的植株对东亚小花蝽具有驱避作用 (Liu et al., 2023)。已有研究表明, 重金属胁迫的捕食性天敌生殖行为发生显著变化。例如, 利用红外摄像观察蠋蝽的求偶和交配行为, 陈玉青 (2020) 发现 Cd 胁迫影响了蠋蝽的求偶行为: 在低浓度 Cd 胁迫下, 雄虫前 4 d 求偶率均低于对照, 然而从第 2 天开始其求偶率持续上升, 且在第 5 天后高于对照组; 而在高浓度胁迫下, 其求偶率均显著低于对照组, 且一直呈下降趋势; 低浓度 Cd 胁迫下, 蠋蝽的交配时间短于对照组, 而高浓度 Cd 胁迫下, 蠔蝽未产生交配行为。

3 天敌昆虫对重金属的积累与排泄

重金属胁迫已成为昆虫重要的环境非生物因

子, 其驱动昆虫演化出特定的行为、生理解毒机制以降低过量重金属对机体稳态的影响, 适应性地生存下来 (Mikkola and Rantala, 2010; 杨世勇等, 2015)。昆虫取食含有重金属的食物后, 可以通过蜕皮、粪便等形式将部分重金属排泄到体外, 但体内还会存储一部分重金属, 其积累水平主要取决于昆虫受胁迫时间的长短、取食量的大小以及对重金属的排泄能力等 (胡蒙蒙等, 2012)。此外, 昆虫体内重金属含量在组织、虫态、性别以及世代间存在显著差异 (舒迎花等, 2010; 陈瑾等, 2020)。

捕食性天敌昆虫对重金属的积累与猎物重金属含量、取食时间、取食量和重金属类型相关。锥须步甲 *Bembidion lampros* Hbst 体内 Zn 含量与取食蚜虫量正相关 (Winder et al., 1999); 七星瓢虫体内 Zn 含量与取食的麦长管蚜体内 Zn 含量、取食时间和取食率正相关 (Green et al., 2010)。一般来说, 捕食性天敌对通过食物链累积到体内的重金属不具有生物放大作用 (Alonso et al., 2009; Dar et al., 2017), 例如中华草蛉 *Chrysoperla carnae* (Stephens) (Alonso et al., 2009)、七星瓢虫 (Dar et al., 2017) 和孟氏隐唇瓢虫 (Wang et al., 2017) 对 Cd, 孟氏隐唇瓢虫对 Pb (Zhang et al., 2017) 均不存在生物放大作用。这也表明, 鞘翅目和膜翅目昆虫对重金属 (如 Cd、Pb 和 Zn) 的生物富集能力有限 (Dar et al., 2015; Mukhtorova et al., 2019)。天敌昆虫对不同类型重金属累积作用存在显著差异。如取食含重金属的甜菜夜蛾后, 斑腹刺益蝽 *Podisus maculiventris* (Say) 对 Cu 和 Zn 具有生物富集作用, 而对 Ni 无显著富集 (Cheruiyot et al., 2013)。重金属的相互作用也会影响重金属在昆虫体内的积累。Green and Walmsley (2013) 研究发现, 相较于单一重金属胁迫, Cu、Ni 和 Zn 同时存在时的七星瓢虫累积重金属含量显著增加到 144%。研究表明, Cd 和 Zn 很容易通过食物链转移到天敌昆虫; Pb 虽然不易被植物吸收传递到植食性昆虫, 但捕食性昆虫体内 Pb 含量随蚜虫 Pb 含量增加而显著增加, 这也表明 Pb 可能会对天敌昆虫产生重要影响 (Dar et al., 2015)。

天敌昆虫经捕食或寄生行为积累重金属后, 可以通过蜕皮、粪便等形式将部分重金属排泄到体外。蛹寄生蜂 *Coptera occidentalis* Muesebeck 寄生 Cd 胁迫的地中海实蝇 *Ceratitis capitata*

(Wiedemann) 蛹, 寄生蜂羽化后残留的寄主蛹中仍含有重金属, 寄主蛹到寄生蜂成虫的转移系数为 0.02, 但寄生蜂的活力和繁殖力不受寄主重金属污染的影响, 表明寄生蜂可能拥有一种有效降解重金属的调节机制, 在化蛹前调节有毒金属的排泄, 并减少寄主体内高浓度重金属的潜在危害 (Kazimírová and Ortel, 2000)。捕食性瓢虫如孟氏隐唇瓢虫和七星瓢虫可以通过蛹代谢体内的重金属 (Dar et al., 2017; Naikoo et al., 2021a; Naikoo et al., 2021b)。Wang et al. (2024) 研究发现, 寄生 Cd 胁迫的米蛾卵后, 稻螟赤眼蜂可以显著积累 Cd, 而松毛虫赤眼蜂则无, 这可能是由于不同物种对重金属的积累和代谢能力存在差异。关于天敌昆虫对重金属的积累与代谢的研究多集中在捕食性天敌, 个体小而导致重金属检测困难可能是寄生性天敌相关研究较少的重要原因。

4 天敌昆虫对重金属胁迫的响应

重金属沿植食性昆虫传递会影响天敌昆虫的营养物质含量、应激酶活性的生理生化反应和基因表达水平改变的分子水平响应。

4.1 生理生化响应

多种重金属 (Cd、Ni、Zn 和 Pb) 共同胁迫下, 孟氏隐唇瓢虫雌成虫的总蛋白质、糖原、胆固醇和甘油三酯含量显著增加 (Du et al., 2019)。Cd 胁迫下, 日本刀角瓢虫雌成虫的脂质 (糖原、甘油三酯和总胆固醇) 含量显著降低 (Khan et al., 2024)。受到 Cd 胁迫后, 白蛾周氏嗜小蜂体内的过氧化氢 (H_2O_2)、谷胱甘肽过氧化物酶 (GSH) 和抗坏血酸 (ASA) 含量显著增加, 而超氧化物歧化酶 (SOD) 含量显著降低, 过氧化酶 (POD) 含量未发生改变 (Yan et al., 2023); 丙二醛 (MDA) 含量显著增加, 而总抗氧化能力 (T-AOC) 显著降低 (Tan et al., 2023); 日本刀角瓢虫雌虫的抗氧化酶 (SOD、过氧化氢酶 CAT 和 POD) 含量降低 (Khan et al., 2024)。多种重金属 (Cd、Ni、Zn 和 Pb) 共同胁迫下, 孟氏隐唇瓢虫雌成虫的内源酶 (酸性磷酸酶和碱性磷酸酶)、抗氧化酶 (SOD、POD 和 CAT) 活性均显著增加 (Du et al., 2019)。

4.2 分子水平响应

重金属胁迫 (Pb 和 Cd) 导致孟氏隐唇瓢虫雌成虫的己糖激酶、琥珀酸、胰蛋白酶样蛋白、半

胱氨酸蛋白酶、细胞分裂周期蛋白和黄色基因蛋白等蛋白的表达发生显著变化 (Wang et al., 2022a)。Cd 或 Zn 胁迫下, 异色瓢虫雌虫卵黄蛋白原基因 *VgI* 和 *Vg2* 以及卵黄原蛋白受体基因 *VgR* 的表达水平显著降低 (Shi et al., 2020; 王莎莎, 2023)。日本刀角瓢虫受 Cd 胁迫后, 雌虫的 SOD1、CAT、POD、糖原和甘油三酯合成相关基因的表达量显著增加 (Khan et al., 2024)。

5 重金属污染对害虫生物防治的影响

重金属对害虫生物防治的影响主要体现在两个方面: 一是通过影响天敌昆虫的捕食或寄生能力, 直接影响害虫生物防治; 二是通过影响害虫抗逆性等影响种群发展, 间接影响害虫防治。

5.1 直接影响

重金属通过影响天敌昆虫对害虫生物防治产生的直接影响可以归纳为短期和长期。短期影响是指天敌昆虫对重金属胁迫的植食性昆虫的控制能力, 长期影响是指重金属胁迫后的天敌昆虫控害能力及种群变化。

5.1.1 天敌昆虫对重金属胁迫害虫的控制能力

一般来说, 捕食性天敌对重金属胁迫的植食性昆虫的捕食量显著降低。狭臀瓢虫对 Ni 或 Pb 胁迫的黑豆蚜 (Naikoo et al., 2019; Naikoo et al., 2021a)、异色瓢虫对 Zn 胁迫的苜蓿蚜 (Xie et al., 2014) 和 Cd 胁迫的豌豆修尾蚜 (王莎莎, 2023)、日本刀角瓢虫对 Cd 胁迫的烟粉虱的捕食量均显著降低 (Khan et al., 2024)。而寄生性天敌对重金属胁迫植食性昆虫的寄生率或寄生量大多不受重金属影响, 如卵寄生蜂稻螟赤眼蜂和松毛虫赤眼蜂 (Wang et al., 2024)、幼虫寄生蜂双斑侧沟茧蜂 (夏婧等, 2006) 和毒蛾绒茧蜂、蚜茧蜂 (Konopka et al., 2013; Kim et al., 2019) 以及蛹寄生蜂 (Kazimírová and Ortíz, 2000), 这可能是由于寄生蜂无法识别寄主内部毒物情况, 存在无选择性的寄生。

5.1.2 重金属胁迫对天敌昆虫种群发展影响

天敌昆虫取食或寄生重金属胁迫的植食性昆虫后, 个体繁殖力或种群增长受到抑制, 会削弱其害虫生物防治效果, 对害虫防治产生长期影响。例如, 取食含重金属的害虫后, 孟氏隐唇瓢虫、异色瓢虫以及日本刀角瓢虫的繁殖力显著降低

(Sang et al., 2018; 王莎莎, 2023; Khan et al., 2024)。寄生重金属胁迫的寄主后, 寄生蜂的子代寄生能力显著降低 (夏婧等, 2006; Wang et al., 2024)。此外, 重金属胁迫会导致天敌昆虫的种群丰度或丰富度显著降低, 可能降低田间自然天敌昆虫种群的自然控害能力 (Kramarz and Stark, 2003)。Pb 污染区域的寄生蜂 (如菜蛾啮小蜂 *Oomyzus sokolowskii* (Kurdjumov)) 和捕食性天敌 (如异食蚜蝇 *Allograpta exotica* (Wiedemann)) 丰度显著降低 (Morales-Silva et al., 2022)。

5.2 间接影响

重金属胁迫会对害虫产生毒物兴奋效应 (Hormesis)、抗逆性增强等负面影响, 导致害虫抗逆性增强, 种群暴发, 间接增加害虫防治难度; 亦会通过降低害虫的免疫能力而增加害虫对病原菌的感染程度, 产生害虫防治效果增强的正面作用。

5.2.1 害虫产生的毒物兴奋效应

毒物兴奋效应是指化学物对生物体在低剂量时表现为促进其生长发育, 而高剂量时表现负面影响的现象 (Chapman, 2001)。重金属可能作为一种毒物兴奋剂, 导致害虫产生毒物兴奋效应, 引起害虫种群暴发, 降低天敌昆虫的防治效果 (Agathokleous et al., 2023)。已有研究表明, 一定浓度的 Cd 胁迫导致甜菜夜蛾 (Su et al., 2014)、二斑叶螨 *Tetranychus urticae* Koch、伊氏叶螨 *Tetranychus evansi* Baker and Pritchard (Godinho et al., 2018; Godinho et al., 2022) 和米蛾 (Wang et al., 2024) 的产卵量显著增加。

5.2.2 害虫的抗逆性增强

经重金属胁迫多代的昆虫会产生交互耐受性, 不仅对重金属具有逐渐增强的耐受能力, 还能对其他逆境 (比如高温、 H_2O_2 和农药) 等的耐受性增强。 Pb 暴露 96 h 后, 斜纹夜蛾取食氯氰菊酯后的体重增加, 死亡率降低; 胁迫 5 世代后, 斜纹夜蛾幼虫中肠和脂肪体中解毒酶基因细胞色素 P450 的表达量增加 (Zhou et al., 2012)。刘耀明等 (2013) 研究表明, 高浓度 Cd 和 Cr 可以激活中华稻蝗 *Oxya chinensis* (Thunberg) 体内羧酸酯酶 (CarE) 活性。经过 Cd 胁迫多代后, 甜菜夜蛾对 H_2O_2 耐受能力增强, 其 DNA 损伤程度降低 (Augustyniak et al., 2016); 对多杀菌素的耐受性增加, 其 *HSP70* 表达水平显著增加 (Augustyniak et al., 2017)。Cu 胁迫甜菜夜蛾幼虫通过介导

H_2O_2 来增强细胞色素 P450 基因表达水平，增强对花椒毒素 (Lu et al., 2019a) 和高效氯氰菊酯的抗性 (Lu et al., 2019b)。昆虫体内的 P450 和 CarE 活性增强与昆虫抗药性增加有关 (徐莉等, 2020)。因此，一定浓度的重金属胁迫可能会显著提高害虫的抗药性，对害虫防治产生负面影响。

5.2.3 害虫对微生物杀虫剂易感性增加

重金属胁迫可以降低害虫的免疫能力，进而增加其对病原菌的感染程度。Ni 胁迫降低了大蜡螟 *Galleria mellonella* (Linnaeus) 对球孢白僵菌 *Beauveria bassiana* 的抗性 (Dubovskiy et al., 2011)。Cd 胁迫降低美国白蛾幼虫免疫及能量代谢能力，增加了其对微生物杀虫剂枯草芽孢杆菌 (Bt)、球孢白僵菌以及甘蓝夜蛾核型多角体病毒 (MbNPV) 的易感性 (Li et al., 2023; Xu et al., 2023)。这表明微生物杀虫剂适用于重金属污染区域的害虫防治。

6 总结与展望

本文系统总结了重金属胁迫沿植食性昆虫传递对天敌昆虫的生长发育、生殖能力以及行为影响，阐明了农田重金属污染对害虫生物防治的直接与间接影响。总的来说，重金属胁迫对天敌昆虫一般会产生负面影响，如生长发育延缓、生殖力降低、捕食量减少等，直接影响害虫生物防治效果；但特定的浓度会导致害虫的毒物兴奋效应和抗性能力增强，间接增加害虫防治难度。

目前，重金属胁迫对天敌昆虫的影响受到越来越多的关注，研究对象不断扩展，研究手段也越来越丰富。基于对已有研究成果的总结，本文认为以下几点可能成为未来一段时间研究重金属胁迫对天敌昆虫影响时值得考虑及关注的方向。

(1) 重金属胁迫的长期效果。长期作用效果可能不同于短期内观察到的结果的现象已在植食性昆虫中得到证实，如豌豆蚜 *Acythosiphon pisum* Harris 在 Cd 胁迫的初期阶段死亡率较低，并与对照无显著差别，但 22 d 后其死亡率增加、显著高于对照，短期毒理测试可能过高或过低估计了重金属的生态毒性 (Laskowski, 2001)。此外，昆虫可将大量的重金属排出体外，但在卵中也常有重金属的存在；同时，虽然部分昆虫对重金属的长期胁迫可产生耐受性，但某些昆虫种类对重金属有高度敏感性 (孙虹霞等, 2007)。有研究表明，

采矿区停止采矿 75 年后仍对周围溪流水生昆虫群落产生负面影响 (Lefcort et al., 2010)。因此，开展持续多代研究重金属胁迫对天敌昆虫产生的影响具有更重要的实践意义，明确重金属胁迫后的天敌昆虫捕食或寄生表现对于评估重金属对农田生态系统的自然天敌种群维持或控害具有重要意义。

(2) 多种重金属的混合效应。田间多种重金属混合污染是重金属研究困难的重要因素之一 (Boyd, 2010; Di et al., 2016, 2020)，但毒理学研究通常侧重于单一重金属的影响，可能不是判断实际影响的现实模型。一般来说，重金属组合会产生叠加、协同或拮抗作用。例如，Cd 和 Zn 同时存在对桃蚜的毒性显著高于单种重金属，导致蚜虫种群灭亡 (Stolpe and Mueller, 2016)。重金属与农药等其他化合物也存在互作效应 (郭欣等, 2023; 徐凡舒等, 2023)。因此，应深化重金属复合污染对昆虫的影响及其机制的研究。

(3) 利用多个指标综合评价生态效应。目前关于重金属污染对害虫生物防治影响只关注于天敌控害能力是否受到影响，而作物 - 害虫 - 天敌昆虫是一个整体系统，需要综合考量重金属胁迫对害虫种群和天敌昆虫控害及种群发展等多重指标的影响程度，进而明确重金属污染对害虫生物防治的实际影响。此外，作物、害虫和天敌也仅为农业生态系统中的一部分，而重金属对整个农业生态系统的影响是无主动选择差别的，所以还应综合考虑同一生境中的非作物植物、节肢与非节肢动物。

(4) 田间大尺度研究。重金属胁迫对天敌昆虫影响的研究大部分是实验室工作，通过在人工饲料中添加重金属来研究其上行效应。但有研究表明重金属通过人工饲料的上行效应弱于经由植物吸收传递后的毒性和积累效应 (Li et al., 2018)，因而实验室小尺度的试验无法完全明确重金属的实际生态效应。此外，目前的研究多关注于物种水平，重金属污染对田间昆虫功能种群 (如野生传粉蜂) 的丰度或多样性存在负面影响 (Morón et al., 2012; Shi et al., 2023b, 2024)，但有关重金属胁迫区域的田间害虫 - 天敌昆虫种群影响的研究较为缺乏，探索重金属污染对生态单元的影响更具有应用意义 (Boyd, 2010)。因此，以农业生产的主粮或者经济作物为对象，从个体或群落角度研究重金属沿害虫 - 天敌昆虫的

上行效应更近实际情况。虽然由于群落和生态系统的复杂性造成田间大尺度研究较为困难,但更全面的解析重金属在田间的上行效应对特定农田或地区的生态衍生效应,将有助于减轻或者控制人为重金属污染物对地球生物区系的有害影响。

(5) 影响机制的研究。重金属胁迫会导致植物挥发物发生改变,进而影响植食性昆虫对寄主的识别(Winter *et al.*, 2012; Lin *et al.*, 2022)。天敌昆虫作为农业生态系统中植物-植食性昆虫-天敌三级营养级重要的组成部分,其需要利用植物挥发物作为关键的化学信息物质搜寻寄主(Turlings and Erb, 2018)。而目前尚未有人报导Cd胁迫植物挥发物对天敌昆虫的影响作用。此外,我们对重金属的一般毒性和特别是神经毒性作用的了解仍处于初期阶段,需要进行遗传学、生物化学和行为学的机理研究,以更好地了解这些重金属如何改变昆虫的记忆和学习。对参与调节昆虫行为的分子途径和神经底物,以及重金属是如何参与破坏生物过程,均需进一步研究(Oliveira *et al.*, 2022)。昆虫的神经系统较哺乳动物相对简单,因此昆虫可以作为一种模式生物,用于研究重金属的分子靶标以及介导重金属毒性效应的分子途径。

此外,重金属通常以施肥、打药等农业活动进入农田,需要综合考虑多种环境非生物因子的上行效应(Han *et al.*, 2022)。铜制剂不仅直接降低天敌昆虫的捕食或寄生率,还会因为长期喷施导致土壤Cu积累,进而影响害虫和天敌(Rehman *et al.*, 2019; Nusillard *et al.*, 2023)。一般来说,重金属胁迫的植食性昆虫对寄生性天敌寄生能力影响较小,因此可以在重金属污染区域采取以寄生性天敌释放为主的生物防治策略,从而保障害虫防治效果。重金属可诱导害虫产生毒物兴奋效应(Wang *et al.*, 2024),或可用作增效剂促进人工规模扩繁天敌昆虫的替代寄主(如米蛾卵、夜蛾幼虫)生产。

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