

PxCAD1 与 Cry1Ac 蛋白混合物对小菜蛾生长发育及体内酶活性的影响*

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摘要 【目的】 PxCAD1 肽段可显著增强 Cry1Ac 的杀虫活性, 探究其与 Cry1Ac 混合物对靶标昆虫生物学及体内酶活性的影响对明确其增效机制具有重要意义。【方法】 采用叶片浸渍法, 以 PxCAD1 肽段与 Cry1Ac 毒素的混合蛋白饲喂小菜蛾 *Plutella xylostella* 3 龄幼虫, 观察并统计小菜蛾死亡率、化蛹率和羽化率, 并测定小菜蛾幼虫体内羧酸酯酶、谷胱甘肽-S-转移酶、总蛋白酶和类胰蛋白酶的变化趋势。

【结果】 与对照相比, 处理组幼虫的死亡率显著升高, 化蛹率减少, 羽化率显著降低; 3 龄幼虫在取食 PxCAD1 肽段与 Cry1Ac 毒素混合蛋白 24 h 和 48 h 后, 羧酸酯酶活性显著升高, 72 h 显著降低, 谷胱甘肽-S-转移酶活性在 24 h 显著升高, 48 h 显著降低, 72 h 则无显著差异, 而总蛋白酶活性仅在 72 h 显著低于对照, 类胰蛋白酶活性在各时间点无显著变化。【结论】 PxCAD1 不仅对 Cry1Ac 具有显著增效作用, 同时对小菜蛾幼虫的生长发育及体内羧酸酯酶、谷胱甘肽-S-转移酶及总蛋白酶的活性产生不利影响。该结果将有助于进一步研究中肠受体蛋白对 Cry1Ac 的增效机制。

关键词 小菜蛾; Cry1Ac; 钙粘蛋白; 生长发育; 解毒酶; 消化酶

Effects of PxCAD1 and Cry1Ac protein mixture on the growth, development and *in vivo* enzyme activity of *Plutella xylostella*

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Abstract 【Objectives】 To investigate the synergistic mechanism responsible for the increased insecticidal activity of Cry1Ac when combined with the PxCAD1 peptide. 【Methods】 The leaf dip bioassay method was used to treat leaves fed to a randomly selected group of 3rd instar *Plutella xylostella* larvae with a mixture of the PxCAD1 peptide and Cry1Ac toxin, after which their larval mortality, pupation rate and emergence rate were recorded and compared to those of a control group. In addition, trends in Carboxylesterase, Glutathione-S-transferase, total protease and trypsin-like activity, were measured and compared between groups. 【Results】 The mortality rate and emergence rate of larvae fed leaves treated with the PxCAD1 peptide and Cry1Ac toxin mixture were significantly higher than that of the control group, and their pupation rate was also lower. The carboxylesterase activity of treatment group larvae was significantly higher than that of the control group after 24 h and 48 h, then significantly decreased after 72 h. Glutathione-S-transferase activity was significantly higher after 24 h, then decreased significantly after 48 h with no further change after 72 h. Total protease activity was significantly lower than that of the control group only at 72 h, and there was no significant change in trypsin activity. 【Conclusion】 PxCAD1 not only has a significant synergistic effect on Cry1Ac, but also has an adverse effect on the growth and development of *P. xylostella* larvae and the activity of Carboxylesterase, Glutathione-S-transferase and total protease *in vivo*. These results facilitate further study of the synergistic effects of midgut receptor proteins on Cry1Ac.

*资助项目 Supported projects: 国家自然科学基金项目 (31772200); 湖南省自然科学基金项目 (2019JJ50269)

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收稿日期 Received: 2020-10-12; 接受日期 Accepted: 2021-02-03

Key words *Plutella xylostella*; Cry1Ac; cadherin; growth and development; detoxification enzymes; digestive enzymes

小菜蛾 *Plutella xylostella* (鳞翅目: 夜蛾科) 作为世界范围内分布最广的寡食性害虫, 是国际上公认的抗药性最严重的蔬菜害虫之一 (Talekar and Shelton, 1993; Chen *et al.*, 2020)。根据密歇根州立大学 Arthropod Pesticide Resistance Database (APRD) 的研究数据, 小菜蛾已对 97 种不同的杀虫活性成分产生了抗药性 (<http://www.pesticideresistance.org>)。同时, 小菜蛾也是对十字花科蔬菜破坏能力最强的害虫 (Wang and Wu, 2012), 仅在中国, 其对十字花科蔬菜的为害面积从 1990 年的 100 万 hm^2 增加到 2010 年的 223 万 hm^2 , 每年导致的经济损失可达 7.7 亿美元 (Li *et al.*, 2016)。

苏云金芽孢杆菌 (*Bacillus thuringiensis*, Bt) Cry 杀虫毒素因其具有对非靶标生物安全、可生物降解的特点, 被认为是化学杀虫剂的有效替代品, 已成为最常用的生物杀虫剂 (Sanahuja *et al.*, 2011; Guo *et al.*, 2015)。然而, 随着靶标害虫抗药性的发展, 它的有效性受到挑战 (Gahan *et al.*, 2001; Tabashnik *et al.*, 2008)。1990 年首次在夏威夷的田间发现小菜蛾对 Bt 制剂产生抗性 (Tabashnik *et al.*, 1990), 2016 年针对中国华中地区湖南、湖北两省的调查发现小菜蛾田间种群对 Bt 的抗性倍数已达 250-400 倍 (李振宇等, 2016)。靶标害虫对 Bt 抗性水平的增加导致杀虫剂的作用效果减弱和作物产量的下降, 从而对农业生产造成巨大经济损失。昆虫对 Bt 形成抗性的成因主要有以下 3 类: 1) Cry 原毒素活化失败, 包括不同原因导致的 Cry 原毒素水解不完全或过度水解 (Rajagopal *et al.*, 2009; Yao *et al.*, 2014); 2) 各类 Cry 毒素受体的突变或减少, 如钙粘蛋白 (Cadherin, CAD)、碱性磷酸酶 (Alkaline-phosphatase, ALP)、氨肽酶 N (Aminopeptidase- N, APN) 和三磷酸腺苷结合盒转运蛋白 (ATP-binding cassette transporters, ABC 转运蛋白) 等 (Tiewisiri and Wang, 2011; Pardo-Lopez *et al.*, 2013); 3) 昆虫免疫系统的调节 (Rahman *et al.*, 2004; Caccia *et al.*, 2016)。

在鳞翅目、鞘翅目和双翅目等昆虫中, 位于中肠的 CAD 作为 Bt Cry 毒素的初级受体介导了毒素结构域 I 中 α 螺旋的切除和毒素的寡聚化, 在 Cry 毒素的作用机制中发挥重要作用 (Soberón *et al.*, 2007)。一些研究表明, 将靶标昆虫的 CAD 与 Bt 杀虫毒素结合使用可能是一种有效的害虫管理策略 (Chen *et al.*, 2007; Ma *et al.*, 2019)。Chen 等 (2007) 报道烟草天蛾 *Manduca sexta* MsCAD CR12-MPED 肽段可通过额外增加 BMW 上的毒素结合位点以实现 Cry1A 毒素的增效作用。而在 Cry1 类毒素对美洲棉铃虫 *Helicoverpa zea*、小地老虎 *Agrotis ipsilon* 和甜菜夜蛾 *Spodoptera exigua* 的毒杀过程中, 不同大小的 CAD 片段均可起到一定的协同增效作用 (Abdullah *et al.*, 2009)。与 CR12-MPED 不同, Pacheco 等 (2009) 发现烟草天蛾的 CR12 肽段是通过促进毒素低聚物的形成而增强 Cry1Ac 的杀虫活性。除此之外, 草地贪夜蛾 *Spodoptera frugiperda* 的 SfCad 肽段与烟草天蛾的 MsCad 肽段可通过抑制中肠蛋白酶的水解作用保护 Cry 毒素不被降解, 从而起到协同增效作用 (Rahman *et al.*, 2012)。

尽管钙粘蛋白被证明可作为 Bt Cry 毒素的增效物质, 但钙粘蛋白与 Cry 毒素混合物对靶标昆虫生长发育及体内酶活性的影响仍然未知。在这项研究中, 以常德田间小菜蛾种群为对象, 测定小菜蛾钙粘蛋白肽段 PxCAD1 对 Cry1Ac 毒素的杀虫增效活性, 同时测定该肽段与 Cry1Ac 混合物对小菜蛾幼虫生长发育及体内酶活性的影响。该结果将有助于进一步研究中肠受体蛋白对 Cry1Ac 的增效机制。

1 材料与方法

1.1 供试材料

实验所用的小菜蛾于 2019 年 6 月采自中国汉寿商业化甘蓝种植田, 参考中国农业科学院蔬菜花卉研究所室内饲养小菜蛾的方法 (郭兆将

等, 2015), 将野外采集的小菜蛾幼虫在室内进行传代培养。种植田经常施用各种杀虫剂(记为小菜蛾田间种群, DBM Field)。

PxCAD1 肽段通过本实验室已构建的原核表达系统表达并收集(龚莉君等, 2016)。Cry1Ac 毒素购于北京诺思特生物技术有限公司。

使用康为世纪 Super-Bradford Protein Assay Kit (CW0013S) 测定蛋白浓度。谷胱甘肽-S-转移酶 (Glutathione -S-transferase, GSTs) 和羧酸酯酶 (Carboxylesterase, CarE) 活性测定试剂盒 (A004-1-1; A133-1-1) 购自南京建城生物工程研究所。乙二胺四乙酸 (Ethylene diamine tetraacetic acid, EDTA)、二硫苏糖醇 (Dithiothreitol, DTT)、丙基硫氧嘧啶 (Propylthiouracil, PTU)、苯甲基磺酰氟 (Phenylmethylsulfonyl fluoride, PMSF) 均购自北京索莱宝科技有限公司。

1.2 PxCAD1 肽段对 Cry1Ac 杀虫活性的影响

Cry1Ac 毒素对小菜蛾田间种群毒力的生物测定采用叶片浸渍饲喂法(杨中侠等, 2009; Liu *et al.*, 2019), 得到对应 LC_{50} 值, 选择略低于 LC_{50} 的浓度进行试验。混合 PxCAD1 (终浓度为 $500 \mu\text{g}\cdot\text{mL}^{-1}$) 与 Cry1Ac (终浓度为 $5 \mu\text{g}\cdot\text{mL}^{-1}$) 并饲喂 3 龄幼虫, 以饲喂 Cry1Ac (终浓度为 $5 \mu\text{g}\cdot\text{mL}^{-1}$) 作为对照。每个处理均设 12 个重复, 每重复 15 头 3 龄幼虫。实验过程中记录各组取食后 72 h 的死亡率、4 龄历期、化蛹率、蛹重、蛹长、蛹期及羽化率。

1.3 PxCAD1 肽段对小菜蛾体内酶活性的影响

与上述 1.2 相同的饲喂方法, 在幼虫取食 24、48 和 72 h 时, 分别取出 5 头幼虫移入预冷的匀浆器中, 加入 1 mL 磷酸缓冲液 (Phosphate buffer saline, PBS) (含 $1 \text{ mmol}\cdot\text{L}^{-1}$ EDTA、 $1 \text{ mmol}\cdot\text{L}^{-1}$ DTT、 $1 \text{ mmol}\cdot\text{L}^{-1}$ PTU、 $1 \text{ mmol}\cdot\text{L}^{-1}$ PMSF, pH7.4) 在冰浴中匀浆, 匀浆液在 $12\ 000 \text{ r}\cdot\text{min}^{-1}$, $4\text{ }^{\circ}\text{C}$ 条件下离心 20 min。取离心后的上清液作为 CarE 和 GSTs 活性测定的酶源, 分装后置于 $-20\text{ }^{\circ}\text{C}$ 冷藏。测定蛋白浓度和酶活性, 每个处理重复 3 次。GSTs 和 CarE 活性测定参照试剂盒说明书。

在幼虫取食不同处理的杀虫剂 24、48 和 72 h 时, 分别取出 10 头幼虫, 用蘸取 75% 酒精的棉球进行消毒后, 置于冰上解剖。取出小菜蛾幼虫的完整的中肠组织及其内容物, 并置于 1.5 mL 离心管中, 立即加入 1 mL PBS 缓冲液 (含 $1 \text{ mmol}\cdot\text{L}^{-1}$ EDTA、 $1 \text{ mmol}\cdot\text{L}^{-1}$ DTT、 $1 \text{ mmol}\cdot\text{L}^{-1}$ PTU、 $1 \text{ mmol}\cdot\text{L}^{-1}$ PMSF, pH7.4), 在冰浴中匀浆, 匀浆液在 $12\ 000 \text{ r}\cdot\text{min}^{-1}$ 、 $4\text{ }^{\circ}\text{C}$ 条件下离心 20 min, 取上清液作为总蛋白酶及类胰蛋白酶活性测定的酶源, 分装后冷藏于 $-20\text{ }^{\circ}\text{C}$, 分别测定蛋白浓度和酶活性, 每个处理重复 3 次。总蛋白酶及类胰蛋白酶的活性测定分别参照赵爱平等 (2017) 及王琛柱和钦俊德 (1996) 的方法, 使用 Super-Bradford 蛋白浓度检测试剂盒进行蛋白质定量。

1.4 数据分析

所有数据使用 IBM® SPSS® Statistics 24 (IBM Co., USA) 软件进行统计分析, 并使用 GraphPad Prism 8.0 (GraphPad Software, Inc., La Jolla, CA) 软件绘图。通过配对 *t*-检验比较两处理间死亡率、各生物学参数及酶活性是否存在显著差异 ($P<0.05$)。

2 结果与分析

2.1 PxCAD1 肽段对 Cry1Ac 杀虫活性及小菜蛾生物学参数的影响

通过毒力测定实验, 获得 Cry1Ac 毒素对小菜蛾田间种群的 LC_{50} 为 $11.31 \mu\text{g}\cdot\text{mL}^{-1}$, 毒力回归方程为 $y = -0.445 + 0.897x$, $R^2 = 0.989$, 其中 x 为浓度以 10 为底的对数, y 为死亡率 (表 1)。PxCAD1 组的死亡率显著高于对照组 ($P<0.05$), 说明 PxCAD1 肽段显著增强了 Cry1Ac 对小菜蛾 3 龄幼虫的杀虫活性 (表 2)。与对照组相比, PxCAD1 组的化蛹率较低 ($P=0.089$), 羽化率显著降低 ($P<0.05$), 但 4 龄幼虫发育历期、化蛹率、雌/雄蛹重、雌/雄蛹长、雌/雄蛹期无显著差异 ($P>0.05$) (表 3)。

表 1 Cry1Ac 对小菜蛾田间种群毒力的生物测定
Table 1 Bioassay of Cry1Ac on DBM Field

回归方程 Regression equation	相关系数 R^2	致死中浓度 ($\mu\text{g}\cdot\text{mL}^{-1}$) LC_{50}	95%置信区间 ($\mu\text{g}\cdot\text{mL}^{-1}$) 95% confidence interval ($\mu\text{g}\cdot\text{mL}^{-1}$)
$y = -0.445 + 0.897x$	0.989	11.31	6.93 - 18.47

x 为浓度以 10 为底的对数, y 为死亡率。
 x is the logarithm of the concentration base 10, y is the mortality rate.

表 2 PxCAD1 对 Cry1Ac 杀虫活性的影响
Table 2 The effect of PxCAD1 to Cry1Ac insecticidal activity

处理 Treatment	小菜蛾幼虫死亡率 (%) Mortality of <i>Plutella xylostella</i> larvae (%)	t -值 t -value
PxCAD1+Cry1Ac	75.06±3.34a	3.214
Cry1Ac	56.21±3.27b	

表中数据为平均值±标准误, 数据后标有不同小写字母表示处理间差异显著 ($P<0.05$)。下表同。
Data are mean±SE, and followed by different lowercase letters indicate significant difference at the 0.05 level. The same as below.

表 3 PxCAD1 与 Cry1Ac 混合物对小菜蛾生长发育的影响
Table 3 Effects of the mixture of PxCAD1 and Cry1Ac on the growth and development of *Plutella xylostella*

生物学参数 Biological parameters		PxCAD1+Cry1Ac	Cry1Ac
4 龄幼虫发育历期 (d) Developmental duration of 4th instar larval (d)		1.66±0.19a	1.48±0.18a
化蛹率 (%) Pupation rate (%)		47.44±5.16a	61.05±5.54a
蛹重 (mg) Pupal weight (mg)	雌 Female	3.20±0.10a	3.44±0.20a
	雄 Male	3.44±0.09a	3.77±0.28a
蛹长 (mm) Pupal length (mm)	雌 Female	4.90±0.06a	4.98±0.08a
	雄 Male	5.12±0.12a	5.20±0.09a
蛹期 (d) Pupal duration (d)	雌 Female	5.25±0.14a	5.64±0.37a
	雄 Male	5.66±0.38a	5.33±0.19a
羽化率 (%) Emergence rate (%)		48.71±1.28b	77.57±1.89a

2.2 PxCAD1 肽段对小菜蛾幼虫体内酶活性的影响

取食 PxCAD1 与 Cry1Ac 的混合物后, 小菜蛾 3 龄幼虫的 CarE 活性在 24 h 和 48 h 时均显著高于对照 ($P<0.05$), 而 72 h 时则显著低于对照 ($P<0.05$) (图 1: A); 24 h 时 GSTs 活性显著高于对照 ($P<0.05$), 48 h 时则显著低于对照组 ($P<0.05$), 到 72 h 时两组间无显著差异 ($P>0.05$) (图 1: B); 总蛋白酶活性仅在 72 h 时显著低于对照 ($P<0.05$), 其他时间点则与对照无显著差异 ($P>0.05$) (图 1: C); 而类胰蛋

白酶活性在 24、48 和 72 h 时均与对照无显著差异 ($P>0.05$) (图 1: D)。

3 讨论

广泛使用 Bt 毒素及种植转 Bt 抗虫基因作物使小菜蛾面临强烈的选择压力, 并最终导致该鳞翅目害虫的 Bt 抗性发展迅速 (Shelton *et al.*, 1993; Gahan *et al.*, 2001; Tabashnik *et al.*, 2008), 因此研究各类增效物质以提高 Bt 毒素的杀虫活性逐渐成为研究热点。本研究结果发现小菜蛾钙粘蛋白肽段 PxCAD1 可显著提高田间种群小菜

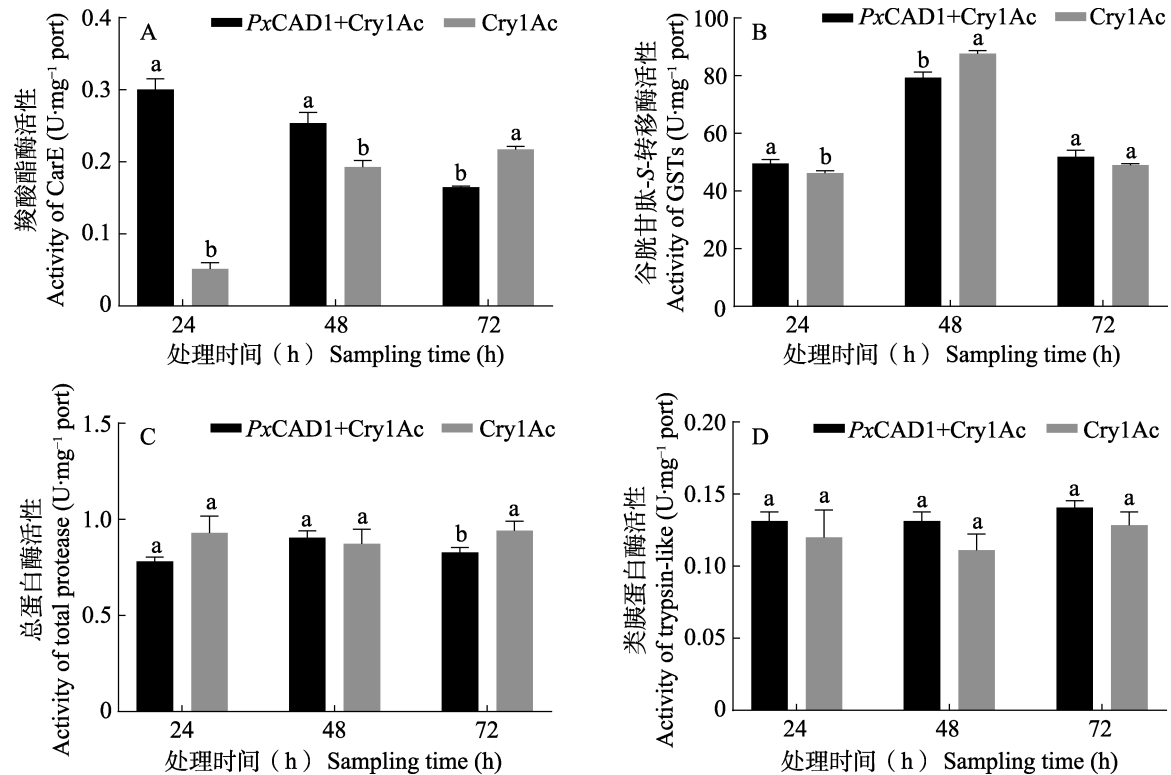


图1 PxCAD1 与 Cry1Ac 的混合物对小菜蛾 3 龄幼虫体内酶活性的影响

Fig. 1 Effects of mixture of PxCAD1 and Cry1Ac on the enzymes activities in vivo of the third instar larvae of *Plutella xylostella*

A. 羧酸酯酶; B. 谷胱甘肽-S-转移酶; C. 总蛋白酶; D. 类胰蛋白酶。

A. CarE; B. GSTs; C. Total protease; D. Trypsin-like.

图中数据为平均值±标准误。柱上标有不同小写字母表示不同处理在 0.05 水平差异显著。

Data are mean ± SE. Histograms with different letters indicate significant difference among different groups ($P < 0.05$).

蛾幼虫对 Cry1Ac 毒素的敏感性, 经 PxCAD1 与 Cry1Ac 毒素的混合物处理后, 小菜蛾幼虫的死亡率达到对照的 1.34 倍, 其杀虫效果显著优于仅使用 Cry1Ac 毒素进行处理。龚莉君等 (2016) 报道, 钙粘蛋白片段 PxCAD1 可显著提升 Cry1Ac 对敏感品系小菜蛾的毒性, 这表明 PxCAD1 在延缓小菜蛾 Bt 抗性的发展中具有一定优势。

除了对靶标昆虫的直接致死作用, 农药在实际使用过程中同样会产生强度不等的亚致死效应, 如造成昆虫的生态行为、生长发育及抗药性等方面的变化, 并可能会引起昆虫的存活率降低, 导致昆虫种群的倍增时间延长, 最终对其种群动态产生负面影响 (Desneux *et al.*, 2007; Saber *et al.*, 2013; Shen *et al.*, 2013; de França *et al.*, 2017)。其中生长发育的变化是决定靶标昆虫种

群消长的重要因素, 也是昆虫抗药性研究中不可或缺的内容。王雪丽等 (2018) 研究发现 Bt 毒素如 Cry1Ac 和 Cry2Ab 对粘虫 *Mythimna separata* 的化蛹率和羽化率均无显著影响, 而亚致死浓度的多杀菌素对小菜蛾的化蛹率和羽化率具有显著的抑制效果 (Yin *et al.*, 2009), 当使用绿僵菌 *Metarhizium anisopliae* 与 Bt 毒素的混合物对番茄潜叶蛾 *Tuta absoluta* 幼虫进行处理时, 试虫的化蛹率和羽化率均显著降低 (Mantzoukas *et al.*, 2019)。在本研究中, 与对照相比, 取食 PxCAD1 与 Cry1Ac 的混合物可导致小菜蛾幼虫的化蛹率下降, 羽化率显著降低 28.86%。这表明 PxCAD1 不仅显著提高了 Cry1Ac 对小菜蛾的毒性, 也对小菜蛾的生长发育产生了负面影响, 降低小菜蛾的存活率, 最终可能对小菜蛾的种群动态产生一定的负面作用。

面对杀虫剂的选择压力,调控升高解毒酶的活性是鳞翅目害虫抗性机制中的关键 (Ishaaya, 1993; Shono *et al.*, 2004), 其中 CarE 可通过水解羧基酯键等催化增加外源有毒物质的水溶性 (Oppenoorth, 1984; Zhang *et al.*, 2012), 而 GSTs 则通过催化谷胱甘肽与毒素结合形成毒性较低的共轭物, 最终将其排出细胞 (Enayati *et al.*, 2005; Bajda *et al.*, 2015)。Candas 等 (2003) 报道, Bt 抗性品系印度谷螟 *Plodia interpunctella* 的 CarE 活性高于敏感品系, 而小菜蛾经 Cry1Ac 毒素选育后, 抗性品系小菜蛾 GSTs 活性明显高于敏感品系 (杨柳等, 2013), 这表明高水平的 CarE 和 GSTs 在鳞翅目害虫对杀虫剂的抗性中起重要作用。在本研究中, 小菜蛾幼虫取食 PxCAD1 与 Cry1Ac 毒素的混合物后, 与对照相比, 幼虫体内 CarE 及 GSTs 活性在 24 h 处均显著升高, 表明这 2 种酶可能参与了虫体对该毒素混合物的抗性过程, 但取食 48 h 和 72 h, GSTs 与 CarE 的活性分别受到强烈抑制。结合 Cry1Ac 及亚致死浓度的茚虫威影响棉铃虫体内 GSTs 与 CarE 活性先升高后降低的报道 (张彦等, 2012; Vojoudi *et al.*, 2017), 本研究结果可能表明, 摄入具有增效作用的 PxCAD1 肽段与 Cry1Ac 蛋白混合物后, 试虫体内 CarE 及 GSTs 水平迅速升高以参与对 Cry1Ac 毒素的抗性过程, 但由于增效肽段的存在, CarE 及 GSTs 无法完全抑制该混合物的毒性, 使毒素代谢受到影响, 进而增强了 Cry1Ac 对小菜蛾幼虫的毒性。

在靶标昆虫对蛋白类杀虫物质的抗性机制中, 消化酶对蛋白质的消化分解作用也是重要一环 (Lightwood *et al.*, 2000; Celińska *et al.*, 2015)。Forcada 等 (1996) 对 Bt 抗性种群烟芽夜蛾 *Heliothis virescens* 进行研究后发现, 该种群抗性的产生是由于中肠蛋白酶对原毒素活化作用的下降及对活化毒素降解作用的上升。本研究中, Cry1Ac 毒素与 PxCAD1 混合物导致试虫体内总蛋白酶活性在 24 h 处降低, 在 72 h 处显著受到抑制, 结合小菜蛾热激蛋白 Hsp90 通过抑制肠蛋白酶的水解作用使 Cry1Ac 毒素增强与受体的结合能力的报道 (García-gómez *et al.*, 2019), 表

明 PxCAD1 对 Cry1Ac 活化毒素的增效作用可能与抑制小菜蛾幼虫体内总蛋白酶的水解活性有关。有研究表明, Bt 抗性可能也与类胰蛋白酶活化作用的降低有关 (Oppert *et al.*, 1997; Liu *et al.*, 2014)。最新报道显示, 类胰蛋白酶基因 *PxTryp_SPc1* 的低表达与田间小菜蛾种群对 Cry1Ac 的抗性有关, 但不参与钙粘蛋白基因影响的小菜蛾 Bt 抗性机制 (Gong *et al.*, 2020)。在本研究中, 小菜蛾取食 PxCAD1 与 Cry1Ac 活化毒素的混合物后, 体内的类胰蛋白酶活性与对照相比均无显著差异, 进一步说明了类胰蛋白酶可能与小菜蛾 PxCAD1 对 Bt 活化毒素的增效机制无关。

综上所述, 小菜蛾钙粘蛋白肽段 PxCAD1 与 Cry1Ac 毒素的混合物不仅显著提高了田间种群小菜蛾幼虫的死亡率, 抑制了存活试虫的化蛹率和羽化率, 而且试虫体内 CarE、GSTs 及总蛋白酶活性也产生了显著变化, 最终可能对小菜蛾的种群动态产生一定的负面影响。本研究结果将有助于中肠受体蛋白对 Cry1Ac 的增效机制的研究, 也为延缓小菜蛾 Bt 抗性的发展提供了新思路。

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