

植物次生代谢物对甜菜夜蛾生长发育及解毒酶的影响*

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摘要 【目的】明确植物次生代谢物对甜菜夜蛾 *Spodoptera exigua* 生长发育及解毒酶的影响, 探索利用植物次生物质防控甜菜夜蛾的潜在途径。【方法】本研究选用 3 种含量 (0.01%、0.1% 和 1.0%) 的槲皮素、山奈酚和香豆素, 分别与人工饲料混合均匀后饲养甜菜夜蛾 3 龄初幼虫, 观察植物次生代谢物对幼虫生长发育的影响; 并测定幼虫取食添加 0.1% 的槲皮素、山奈酚和香豆素的人工饲料 24、48 和 72 h 后, 幼虫羧酸酯酶 (Carboxylesterase, CarE)、谷胱甘肽-S-转移酶 (Glutathione S-transferase, GSTs) 和 P450 解毒酶活性。【结果】添加不同次生物质的人工饲料显著影响甜菜夜蛾幼虫生长和解毒酶活性。与对照组相比, 3 种次生代谢物均显著提高了幼虫死亡率。幼虫取食添加 1% 槲皮素的人工饲料后, 蛹重显著降低, 发育历期明显延长。而取食添加 0.1% 山奈酚的人工饲料后, 可诱导幼虫 CarE 活性显著增强, 0.1% 槲皮素和 0.1% 香豆素对幼虫 CarE 活性均有显著抑制作用。添加槲皮素对幼虫 GSTs 活性无显著性影响, 添加 0.1% 山奈酚和 0.1% 香豆素可诱导幼虫 GSTs 活性显著升高。0.1% 槲皮素和 0.1% 香豆素可促进幼虫 P450 活性增强但未达到显著水平, 但 0.1% 山奈酚处理 48 h 后, 幼虫 P450 活性显著降低。【结论】植物次生代谢物种类与含量对甜菜夜蛾生长发育及解毒酶活性存在不同程度的影响。

关键词 槲皮素; 山奈酚; 香豆素; 死亡率; 羧酸酯酶; 谷胱甘肽-S-转移酶; P450

Effects of plant secondary metabolites on the growth, development and detoxification enzyme activity, of *Spodoptera exigua*

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Abstract 【Objectives】To determine the effects of plant secondary metabolites on the growth, development and detoxification enzyme activity, of *Spodoptera exigua*, and investigate the potential of using these substances to control this pest. 【Methods】Three different concentrations (0.01%, 0.1% and 1.0%) of three different plant secondary compounds, quercetin, kaempferol or coumarin, were added to the artificial diet fed to 3rd instar *S. exigua* larvae and their growth and development were observed and compared. In addition, the activity of carboxylesterase, glutathione S-transferase and cytochrome P450, were measured 24, 48 and 72 h after larvae had been treated with 0.1% quercetin, kaempferol or coumarin. 【Results】All three secondary metabolites significantly increased larval mortality. The pupal weight of larvae treated with of 1.0% quercetin was significantly less than that of the control group, whereas their developmental duration was obviously longer. CarE activity was significantly higher in larvae treated with 0.1% kaempferol, but 0.1% quercetin and 0.1% coumarin significantly inhibited CarE activity. Although quercetin had no significant effect on GSTs, 0.1% kaempferol and 0.1% coumarin increased GSTs. The P450 activity of larvae treated with 0.1% quercetin or 0.1% coumarin was higher than that of the control group, although not significantly so, whereas the P450 activity of larvae treated with 0.1% kaempferol was significantly lower than that of the

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control group after 48 hours. **[Conclusion]** Different plant secondary metabolites have different effects on the growth and detoxification enzyme activity of *S. exigua* larvae.

Key words quercetin; kaempferol; coumarin; mortality; caboxylesterase; glutathione -S-transferase; cytochrome P450

从植物次生代谢物质的角度探究寄主植物与害虫间的关系是生态学研究的重要方向之一(万年峰等, 2020)。在受到害虫侵害时, 植物会被诱导产生大量的次生代谢化合物, 用以抵御昆虫为害(张文辉和刘光杰, 2003; Lou and Baldwin, 2006; 杨乃博等, 2014)。这种基于诱导产生次生物质的植物防御反应, 会影响昆虫的多种生理和行为特征。例如, 干扰昆虫的消化系统从而阻碍昆虫吸收营养(Howe and Jander, 2008; 郭玲等, 2018), 引发昆虫产生拒食效应导致昆虫生长发育受到抑制(Blytt *et al.*, 1988; 娄永根和程家安, 1997; Taiz and Zeiger, 2006)。Berenbaum 等(1991)研究表明, 粉纹夜蛾 *Trichoplusia ni* 取食含呋喃香豆素的食物后, 其生长显著减缓。刘伟等(2010)发现, 不同浓度单宁对甜菜夜蛾 *Spodoptera exigua* 幼虫体重、蛹重、化蛹率及羽化过程均有显著的抑制作用。

为了应对寄主植物的防御机制, 昆虫体内的代谢系统会发生一系列的反应, 如诱导并激活体内的解毒酶系, 分解植物中的有害物质(Brattsten *et al.*, 1984; Li *et al.*, 2004; Duan and Schuler, 2005; John and Graeme, 2008)。羧酸酯酶(Caboxylesterase, CarE)、谷胱甘肽-S-转移酶(Glutathione-S-transferase, GSTs)和细胞色素P450(Cytochrome P450, CYP450)是昆虫体内三大解毒酶系。研究表明, 不同次生代谢物对解毒酶活性的诱导效果不同。例如, 花椒毒素和黄酮诱导草地贪夜蛾 *Spodoptera frugiperda* GSTs 活性增强, 五羟黄酮和杨梅黄酮使其 GSTs 活性降低, 而棉酚、豆甾醇和谷甾醇对其 GSTs 活性无显著影响(Yu and Hsu, 1993)。此外, 昆虫体内三大解毒酶系含量, 因取食植物种类的不同而存在一定的差异, 如Wang 等(2021)发现取食黄豆的甜菜夜蛾幼虫 CarE 活性低于取食油菜、甘蓝和玉米的幼虫。

甜菜夜蛾 *Spodoptera exigua* 是一种多食性害虫, 主要为害蔬菜、花卉等植物(Wan *et al.*, 2019a, 2019b), 这与其灵活性的生态适应机制

密切相关(Després *et al.*, 2007; Jiang *et al.*, 2013)。研究证明寄主植物的种类、营养条件以及昆虫本身的解毒能力等都会影响昆虫的寄主适应性(Hwang *et al.*, 2008; Keathley and Potter, 2008; Saha *et al.*, 2012; Carrasco *et al.*, 2015; 王金彦等, 2018)。作者所在团队前期的研究发现, 取食黄豆的甜菜夜蛾幼虫感染核型多角体病毒后的死亡率显著高于取食油菜和甘蓝的幼虫病死率(Wan *et al.*, 2016; Wang *et al.*, 2020); 进一步对寄主进行广靶代谢组检测分析, 发现黄豆叶片中槲皮素、山奈酚和香豆素 3 种次生代谢物含量较高。为此, 本文选择这 3 种物质, 研究其对甜菜夜蛾幼虫生长发育与解毒酶活性的影响, 为探索甜菜夜蛾寄主适应性的生理机制以及为利用植物次生物质防控甜菜夜蛾提供科学依据。

1 材料与方法

1.1 供试材料

供试虫源为上海市农业科学院害虫生态防控课题组室内连续饲养多代的甜菜夜蛾 3 龄幼虫。参考 Jiang 等的(2011, 2018)饲养方法, 将幼虫置于无菌圆底玻璃养虫盒(高 10 cm, 直径 15 cm)中, 在人工气候箱[温度(28±1)℃、光周期 14 L: 10 D、相对湿度 80%±5%]中进行群体饲养, 并喂食人工饲料(成分含黄豆粉、麦胚、琼脂粉、酵母、干酪素、胆固醇、肌醇、山梨酸钾、核黄素、抗坏血酸、甲酸甲酯和氯化胆碱)。

试验前, 根据试验要求的 3 种次生代谢物(槲皮素、山奈酚和香豆素)在人工饲料中的含量, 按照次生物与人工饲料的干重比, 分别配制含 0.01%、0.1%、1%次生代谢物的人工饲料, 以不加次生物的人工饲料作为对照。

供试的次生代谢物槲皮素(HPLC≥98%)、山奈酚(HPLC≥98%)和香豆素(HPLC≥98%)均由上海源叶生物科技有限公司生产。羧酸酯酶活性测试盒和谷胱甘肽-S-转移酶活性测试盒购置于北京索莱宝科技有限公司, 细胞色素 P450

活性测试盒购自上海江莱生物科技有限公司。

1.2 试验方法

1.2.1 甜菜夜蛾幼虫生长发育指标及死亡率的测定 选取大小一致的甜菜夜蛾 3 龄初幼虫单头置于玻璃试管中, 管口塞上棉塞。待幼虫饥饿 6 h 后, 分别饲喂含有 0.01%、0.1%、1% 次生物质(槲皮素、山奈酚和香豆素)及不含次生代谢物的人工饲料; 并将幼虫置于人工气候箱中饲养观察, 人工气候箱环境条件同 1.1 所述。实验期间, 每 24 h 观察并记录幼虫发育历期及存活情况, 直至化蛹或死亡; 每处理观察 20 头幼虫, 重复 3 次。

1.2.2 甜菜夜蛾幼虫体内解毒酶活性的测定 在试验 1.2.1 的同时, 选取大小一致的甜菜夜蛾 3 龄初幼虫, 转移至玻璃试管中, 每管 1 头, 饥饿 6 h。实验前, 将饥饿后的幼虫转移至分别盛有 0.1% 槲皮素、0.1% 山奈酚和 0.1% 香豆素的人工饲料的无菌圆底玻璃养虫盒中(高 10 cm, 直径 15 cm), 每盒 10 头幼虫, 以不含次生代谢物的人工饲料作为对照; 每处理测定 50 头幼虫, 重

复 3 次。供试幼虫饲养条件同 1.1 所述。

1.3 数据处理

使用 SPSS 20.0 软件对实验数据进行单因素方差分析, 并比较取食不同次生代谢物的甜菜夜蛾幼虫解毒酶活性值的差异(Turkey's HSD 检验, $P < 0.05$); 数据分析前, 将死亡率数据进行反正弦转换, 发育历期、蛹重和酶活性数据进行以 10 为底的对数转换。运用一般线性模型(General linear model)的两因素方差分析明确次生代谢物浓度、处理后时间及其交互作用对甜菜夜蛾幼虫解毒酶活性的影响。

2 结果与分析

2.1 植物次生代谢物对甜菜夜蛾生长发育的影响

与对照组相比, 添加 0.1% 和 1% 槲皮素、3 种含量的山奈酚及香豆素的人工饲料对甜菜夜蛾均有显著的致死效应($P < 0.05$); 随着次生代谢物浓度的升高, 幼虫死亡率增加(表 1)。取

表 1 不同次生代谢物对甜菜夜蛾生长发育的影响

Table 1 Effects of different secondary metabolites on growth and development of *Spodoptera exigua*

处理 Treatment	死亡率(%) Mortality rate	发育历期(d) Developmental duration	蛹重(mg) Pupal weight
对照 CK	7.50±2.50e	6.49±0.09b	138.72±3.24a
0.01% 槲皮素+人工饲料 0.01% quercetin+ artificial diet	18.33±3.33de	6.70±0.15ab	135.93±3.56a
0.1% 槲皮素+人工饲料 0.1% quercetin+ artificial diet	21.67±4.41cd	6.52±0.10b	133.31±2.48a
1% 槲皮素+人工饲料 1% quercetin+ artificial diet	40.00±2.89b	7.24±0.15a	104.39±3.97b
0.01% 山奈酚+人工饲料 0.01% kaempferol+ artificial diet	45.00±0.00b	6.42±0.10b	145.96±3.05a
0.1% 山奈酚+人工饲料 0.1% kaempferol+ artificial diet	68.33±4.41a	6.40±0.13b	140.50±4.20a
1% 山奈酚+人工饲料 1% kaempferol+ artificial diet	68.33±6.67a	6.78±0.13ab	133.42±3.50a
0.01% 香豆素+人工饲料 0.01% coumarin+ artificial diet	36.67±1.67bc	6.74±0.18ab	140.78±3.57a
0.1% 香豆素+人工饲料 0.1% coumarin+ artificial diet	41.67±3.33b	6.48±0.11b	150.03±2.47a
1% 香豆素+人工饲料 1% coumarin+ artificial diet	55.00±2.89ab	6.75±0.11ab	139.26±4.05a

表中数据为平均值±标准误, 同列数据后标有不同小写字母表示差异显著($P < 0.05$)。

Data in the table are mean ± SE, and followed by different lowercase letters indicate significant differences at the 0.05 level.

食添加 1%槲皮素人工饲料的幼虫发育历期明显延长 ($P<0.05$), 蛹重显著降低, 但取食添加低剂量香豆素和山奈酚人工饲料的幼虫蛹重与对照无显著差异 (表 1)。

2.2 植物次生代谢物对甜菜夜蛾解毒酶活性的影响

取食添加 0.1%山奈酚的人工饲料, 甜菜夜蛾 3 龄幼虫 CarE 活性显著升高 ($P<0.05$), 且随处理后时间的增加, 这种效应增强 (图 1)。取食添加 0.1%槲皮素和 0.1%香豆素的处理后 48 h, 甜菜夜蛾幼虫 CarE 活性均显著下降 ($P<0.05$) (图 1)。0.1%山奈酚和 0.1%香豆素均能显著诱导 GSTs 活性升高, 且在幼虫取食后 48 h, 山奈酚诱导的 GSTs 活性显著高于香豆素, 而 0.1%槲皮素对 GSTs 活性无显著性影响 (图 2)。与对照组相比, 0.1%槲皮素和 0.1%香豆素处理可诱导甜菜夜蛾幼虫 P450 活性提高, 但均未达到显著性差异。而 0.1%槲皮素处理的甜菜夜蛾幼虫 P450 活性在第 48 h 显著高于 0.1%山奈酚处理组 ($P<0.05$) (图 3)。

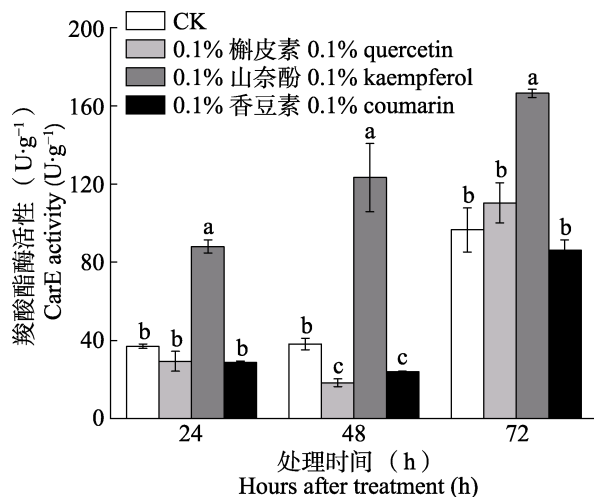


图 1 次生代谢物处理对甜菜夜蛾幼虫羧酸酯酶活性的影响

Fig. 1 Effects of secondary metabolites on carboxylesterase activity of *Spodoptera exigua*

图中数据为平均值±标准误, 柱上标有不同小写字母表示在 $P<0.05$ 水平上差异显著。下图同。

Data are mean±SE. Histograms with different lowercase letters indicate significant differences at the level 0.05 by HSD test. The same below.

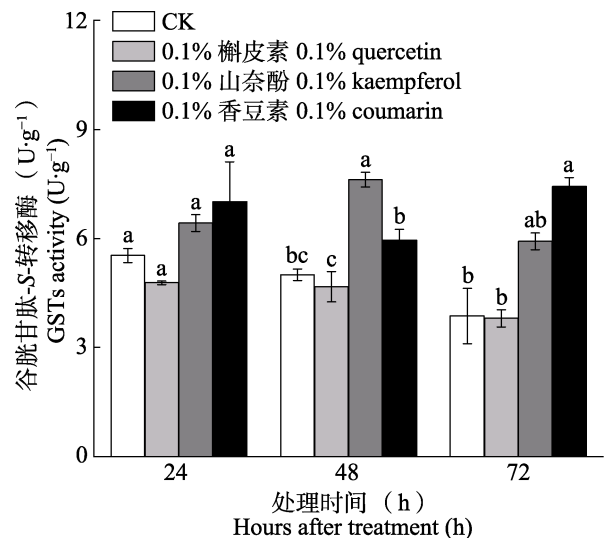


图 2 次生代谢物处理对甜菜夜蛾幼虫谷胱甘肽-S-转移酶活性的影响

Fig. 2 Effects of secondary metabolites on glutathione-S-transferase activity of *Spodoptera exigua*

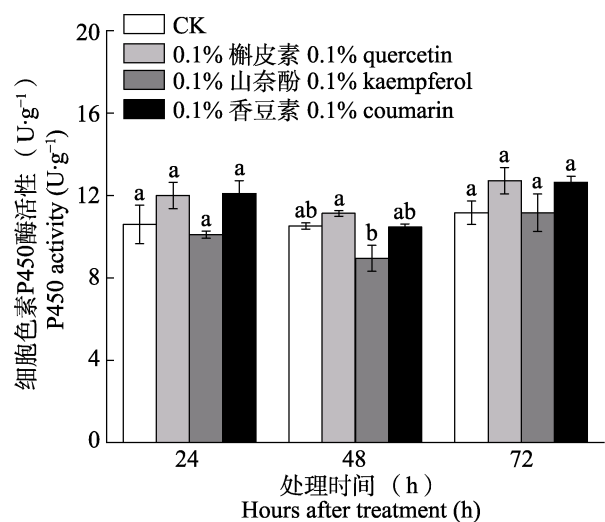


图 3 次生代谢物处理对甜菜夜蛾幼虫细胞色素 P450 活性的影响

Fig. 3 Effects of secondary metabolites on P450 activity of *Spodoptera exigua*

两因素方差分析表明, 次生代谢物显著影响幼虫 CarE、GSTs 和 P450 活性 ($P<0.05$), 处理后时间显著影响 P450 和 CarE 活性 ($P<0.05$), 而次生代谢物和处理后时间的交互作用仅对 CarE 活性有显著影响 ($P<0.05$) (表 2)。

3 讨论

植物次生代谢物质一般不直接参与植物的

表 2 次生代谢物和处理时间对甜菜夜蛾幼虫解毒酶活性影响的两因素方差分析
Table 2 Two-way analysis of variance for testing the effects of different secondary metabolites and hours after treatment on the detoxify enzyme activities of beet armyworm larvae

变量 Dependent variable	次生代谢物 Secondary metabolites			处理后时间 (h) Hours after treatment			互作效应 Interactive effect		
	F 值 F value	自由度 df	显著水平 Significant level (P)	F 值 F value	自由度 df	显著水平 Significant level (P)	F 值 F value	自由度 df	显著水平 Significant level (P)
羧酸酯酶 Carboxylesterase	80.225	3, 36	<0.001	114.521	2, 36	<0.001	3.214	6, 36	0.018
谷胱甘肽-S-转移酶 Glutathione-S-transferase	16.892	3, 36	<0.001	1.941	2, 36	0.165	2.242	6, 36	0.074
细胞色素 P450 Cytochrome P450	7.197	3, 36	0.001	8.636	2, 36	0.001	0.534	6, 36	0.777

生长发育和生殖等生命活动,也不为植食性昆虫提供营养,但却能影响昆虫的摄食、生长、发育和存活等(钦俊德,1995;刘伟等,2010;杨乃博等,2014)。Shaver 和 Lukefahr (1969)报道了槲皮素抑制棉红铃虫 *Pectinophora gossypiella* 和美洲棉铃虫 *Helioverpa zea* 的生长发育。同样,Chan 等(1978)也发现了槲皮素能抑制烟草芽叶蛾 *Heiothis virescens* 生长。本研究的结论与之类似,即 1%的槲皮素显著抑制甜菜夜蛾的生长发育。此外,值得注意的是不同含量的槲皮素、山奈酚和香豆素对甜菜夜蛾均有明显的致死效应。这与 Lindroth 和 Peterson (1988)报道的槲皮素能引起南方灰翅夜蛾 *Spodoptera eridania* 死亡,王亚军等(2018)报道的山奈酚对舞毒蛾 *Lymantria dispar* 有毒杀活性,以及贾芳翌(2008)发现的较高剂量香豆素引起棉蚜 *Aphis gossypii* 超过 80%致死率的结果类似。这种较高的致死效应,可能是因为昆虫的发育历期延长,有害物质在幼虫体内积累,毒害作用在逐步累积,对幼虫生长及生理的不良影响也在逐步累积,最终导致其死亡率增加(王晓丽等,2014)。

在长期进化过程中,昆虫通过解毒酶分解大量的次生代谢物,是其适应植物防御反应的重要方式(Piskorski and Dorn, 2011),也是其选择寄主植物的基本决定因素(Mao *et al.*, 2007)。研究表明,不同次生代谢物对解毒酶的诱导效果不同(Rani and Pratyusha, 2013;侯晓琳等,2018)。

牟少飞等(2006)发现低剂量的槲皮素可诱导烟粉虱 *Bemisia tabaci* CarE 和 GSTs 活性的增加,而高剂量的槲皮素对 2 种解毒酶有抑制作用;张月娥(2012)报道了高剂量的槲皮素可显著诱导家蚕 *Bombyx mori* P450 活性升高。本研究结果表明添加 0.1%槲皮素后显著抑制了甜菜夜蛾幼虫 CarE 和 GSTs 的活性,增加 P450 活性的效果,但与对照组相比,并未达到显著水平。这可能是 GSTs、P450 对槲皮素的响应,需要更大的浓度阈值。

王亚军等(2017)发现,0.65 mg·mL⁻¹山奈酚抑制舞毒蛾 *Lymantria dispar* CarE 和 GSTs 活性,而本研究的结果与之完全相反,这可能与山奈酚含量及昆虫的生理特性有关。目前山奈酚如何影响昆虫 P450 解毒酶系的相关研究鲜有报道,本研究发现 0.1%山奈酚能抑制甜菜夜蛾 P450 活性。王瑞龙等(2012)证实,香豆素促进斜纹夜蛾 *Spodoptera litura* GSTs 活性增加,这与本研究结果类似,而陈巨莲等(2003)报道香豆素显著抑制麦长管蚜 *Sitobion avenae* GSTs 活性。这些结果的差异可能与香豆素的含量以及与昆虫防御次生代谢物的能力有关。

植物次生代谢物对昆虫生长发育和解毒酶活性的影响,使昆虫对寄主植物表现出不同的适应性。因此,充分利用植物次生代谢物质对昆虫生长发育以及解毒酶系的破坏作用,研发基于植物次生代谢物质的新型化学农药,是实行害虫防

控的重要方向之一。本研究结果对进一步探索昆虫与寄主植物间的相互作用关系,具有重要科学意义。然而,次生代谢物质与昆虫的相互作用关系极为复杂,其分子作用机制尚需进一步探索。

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