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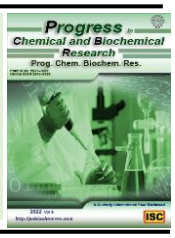

Original Research Article

Role of Detoxification Enzymes of Chlorantraniliprole Resistance in Field Strain of Cotton Leafworm, *Spodoptera littoralis* (Lepidoptera: Noctuidae)

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HIGHLIGHTS

- The moderate resistance to chlorantraniliprole was observed in field strain of *Spodoptera littoralis*.
- Resistance to chlorantraniliprole in *S. littoralis* is associated with the detoxification enzymes.
- Monooxygenase (MO) is likely the main detoxification mechanism responsible for chlorantraniliprole resistance in *S. littoralis*.

ABSTRACT

Spodoptera littoralis (Lepidoptera: Noctuidae) is a major lepidopterous pest that damages many agricultural crops in Egypt and other countries. The intensive application of chemical insecticides to *S. littoralis* led to the development of resistance against several insecticides, including chlorantraniliprole. Although resistance to the novel anthranilic diamide chlorantraniliprole is less likely. To limit the spread of the resistant populations, chlorantraniliprole resistance was investigated in field population of *S. littoralis* with elucidation of the role of the metabolic enzymes. The field strain had a medium resistance ratio, RR = 34 to chlorantraniliprole compared with the susceptible strain, according to the results of bioassays using the leaf dip method. *S. littoralis* larvae of field strain treated with triphenyl phosphate (TPP), diethyl maleate (DEM), and piperonyl butoxide (PBO), showed synergistic ratios of 1.0-, 2.0- and 4.0-fold on chlorantraniliprole, respectively. Furthermore, results showed that the activities of monooxygenase (MO), glutathione S-transferase (GST), and carboxylesterase (CarE) increased significantly in the field strain compared to the susceptible strain. However, MO is most likely the main detoxifying enzyme in charge of chlorantraniliprole resistance. These results provide information about chlorantraniliprole resistance that can help in managing populations of cotton leafworm in fields.

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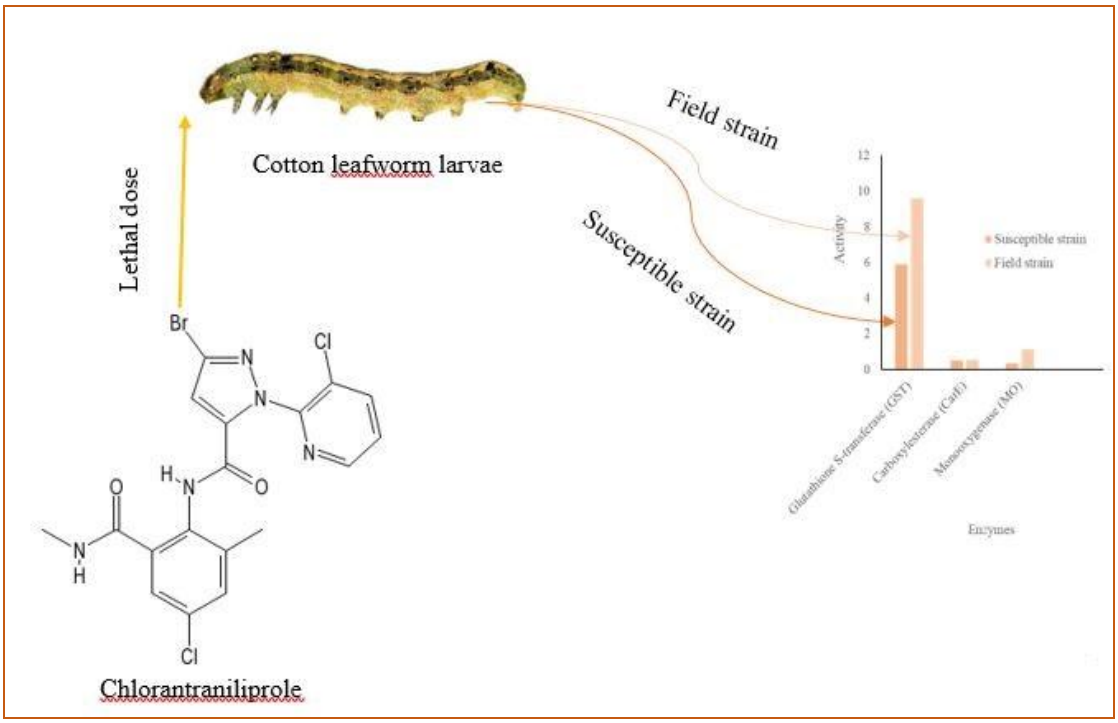
GRAPHICAL ABSTRACT



1. Introduction

The cotton leafworm, *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae), is widely distributed in Egypt and many countries. *S. littoralis* is one of the most dangerous species of lepidopterans pests and in particular its larvae can feed on more than 100 types of host plants (vegetables, cotton, and many other agricultural and horticultural crops) [1]. Due to its resistance to many different types of conventional insecticide as a result of extensive use, it has become one of the most challenging pests to control [2]. To control *S. littoralis* effectively, several new classes of insecticides, including chlorantraniliprole [3].

The novel anthranilic diamide insecticide chlorantraniliprole affects calcium homeostasis in the cell by activating the ryanodine receptor and causing the uncontrolled release of internal calcium reserves, which causes Ca^{2+} depletion, feeding cessation, lethargy, muscle paralysis, and insect death [4]. It is used for the effective control of a variety of economically important Lepidopteran pests, including *S. littoralis* [5]. However, in recent years, its effectiveness has decreased significantly [6].

Esterases (EST), glutathione S-transferases (GSTs), and cytochrome P450 monooxygenases (P450s), three key categories of detoxifying enzymes, are frequently affected or have their activity increased as a result of physiological changes in insecticide resistance [7,8,9,10]. Studies on resistance mechanisms may provide useful information for pest resistance management to overcome the observed control failures in the field. To maintain efficient control and achieve effective resistance management, it is crucial to evaluate chlorantraniliprole resistance. There is no information on the prevalence and mechanisms of chlorantraniliprole resistance in Egypt, despite the fact that lepidopterous pest resistance to the insecticide has been described in Brazil [11], China [3,6,12], India [13], and Pakistan [14]. The purpose of this study was to examine the impact of three synergists on the toxicity of

chlorantraniliprole to look at the role of the detoxification processes of CarE, GST, and MO in the assessment of chlorantraniliprole resistance in cotton leafworm. The findings of this study can be used to successfully manage *S. littoralis*'s resistance to chlorantraniliprole in fields.

2. Materials and Methods

2.1. Insects

The susceptible strain of *Spodoptera littoralis* (Boisd.) was used as the reference strain. It was provided by the Department of Insect Population Toxicology, Central Agricultural Pesticides Laboratory, Agriculture Research Center, Giza, Egypt. This strain had been reared without contact with any insecticides for more than 15 years. Another field strain of *S. littoralis* was gathered from the cotton fields of Motobas district, Kafr El-Sheikh Governorate, Egypt during July month of 2021. Egg masses samples were collected from ten different fields spread across in a Motobas district. Field egg masses were brought to the laboratory, maintained until hatching. The field-collected *S. littoralis* were mated, and the third-instar larvae were used for the bioassays. Two strains were reared on castor bean leaves (*Ricinus communis* L.) at 25 ± 1 °C, 65 ± 5% RH, and a 16-h light/8-h dark photoperiod.

2.2. Bioassay

Bioassays were conducted using commercial formulation of chlorantraniliprole (Coragen 20 SC®-DuPont Crop Protection) with third-instar larvae of *S littoralis*. LC_{50} values for chlorantraniliprole was estimated through leaf dip bioassay method. Insecticides were diluted in distilled water to the required concentrations. Bioassay for every insecticide was conducted at five concentrations to obtain LC_{50} value. Later, cleaned leaves were cut into leaf discs of 4 cm diameter. The leaf discs were submerged in insecticide dilutions for ten seconds with gentle stirring in a glass beaker (250 mL). In the control, leaf discs were dipped in distilled water. The excess insecticidal solution on the leaf disc was allowed to drain off, and the discs were then let to air dry for 20 minutes. Larvae were released into glass jars (500 mL) to feed on treated leaf discs. Each chlorantraniliprole concentration was replicated three times and every replication had ten one-day old third instar larvae (n=10). Each jar was covered by two layers of tissue paper and glass cover fixed with rubber band to prevent larvae from escaping. All jars were maintained at 25 ± 1 °C, 65 ± 5% RH and a 16-h light/8-h dark photoperiod. Larvae were allowed to feed for 48 h before mortality was recorded. If the larvae could not move after being gently prodded with a fine brush, they were deemed dead.

2.3. Synergism assays

Three synergists of piperonyl butoxide (PBO), triphenyl phosphate (TPP), and diethylmaleate (DEM) were combined with chlorantraniliprole to test the effect of inhibiting the detoxifying enzyme on its resistance. A maximum concentration of each synergist (10 mg L^{-1}) that demonstrated a death rate of less than 10% in the susceptible strain. After prior exposure to either PBO, TPP or DEM, third-instar larvae of *S littoralis* were transferred to chlorantraniliprole-treated leaf discs. The test was conducted in the same way as the aforementioned bioassay.

2.4. Estimation of the detoxification enzyme activity

Three important detoxifying enzymes' activities; carboxylesterase (CarE), glutathione S-transferase (GST), and monooxygenase (MO) were measured. In 1000 mL of 0.1 M sodium phosphate buffer (pH 7.0), 1 mM EDTA, 1 mM dithiothreitol (DTT), 1 mM phenylthiourea, 1 mM PMSF, and 20% glycerol, 50 larvae from each of the two strains were homogenized on ice. After that, the homogenates were centrifuged at 4 °C for 20 minutes at 15,000 rpm. For the spectrophotometric assessment of the enzyme activity, the resultant supernatant was used as a

crude enzyme extract. According to Bradford's method (1976) [15], protein estimation was carried out.

2.4.1. Total carboxylesterase (CarE) activity

Utilizing α-naphthyl acetate (α-NA) as a substrate, total CarE activity was determined [16]. The reaction mixture contained 50 µL of α-NA (0.2 mM) and 50 µL of enzyme solution diluted in sodium phosphate buffer (0.2 M, pH 7.2). Before adding 50 µL of Rapid Blue Stain chromatography reagent (1% fast blue salt B in ethanol [w/v]) to stop the reaction, the mixture was incubated for 15 minutes at 37 °C. The absorbance at 600 nm was used to quantify the hydrolysis of α-NA. These mean values of total esterase activity were computed using protein content and α-NA standard curves. The α-esterase-specific activities have been reported as µmole of α-NA form min^{-1} mg^{-1} protein.

2.4.2. Glutathione S-transferase (GST) activity

The Habig *et al.* (1974) [17] method was used to measure the GST activity using the substrate 1-chloro2, 4-dinitrobenzene (CDNB). 3 mL of the reaction mixture consisted of 50 µL of 50 mM CDNB substrate solution, 150 µL of 50 mM GSH, and 30 µL of enzyme solution diluted in sodium phosphate buffer (0.1 M, pH 7.5). An ultraviolet spectrophotometer (Shimadzu UV-1201) was used to measure the absorbance at 340 nm with a 5-min readout interval. The nmol min^{-1} mg^{-1} protein unit used to express the GST specific activity.

2.4.3. Monooxygenase (MO) activity

Use of 7-ethoxycoumarin (7-EC) as a substrate to assess MO activity using the method of Ullrich and Weber (1972) [18] with some modifications by Van Pottelberge *et al.* (2008) [19]. A FLUOstar® Omega multi-mode microplate reader (BMG Labtech Ltd, Aylesbury, UK) was used to read the reaction mixture, which was composed of 50 µL of the diluted enzyme solution in sodium phosphate buffer (0.1 M, pH 7.5) containing 1 mM EDTA, 0.4 mM 7-EC in methanol, and 1 mM NADPH. The plate was gently shaken and incubated for 30 minutes at 30 °C in the dark. For NADPH oxidation, 100 mM GSSG in distilled water and 0.1 units/µL of glutathione reductase were added to each well at 37 °C for 15 min. One hundred microliters of 50% (v/v) acetonitrile in 50 mM tris HCl buffer (pH 10) was used to stop the reaction. The fluorescence of 7-EC was measured at 460 nm while exciting it at 360 nm. Based on the standard 7-EC curve for converting the initial velocity into MO activity (7-EC-O-deethylation) which was expressed as nmols of 7-hydroxycoumarin formed/min/mg protein.

2.5. Statistical analysis

The Abbott formula [20] was used to corrected the mortality data. Using the statistical software SPSS (version 19.0, SPSS Inc., Chicago, IL, USA), LC_{50} values were determined by probit analysis [21]. Level of insecticide resistance was described using resistance ratio (RR) as reported by Keiding (1980) [22]. Enzyme activity measured in larvae from the field strain and those from the susceptible strain were compared on a mean (± standard error) basis.

3. Results

3.1. Toxicity and resistance

Compared with laboratory-susceptible strain, the toxicity of chlorantraniliprole was notably lower in the field-collected *S. littoralis* strain (Table 1). In this study, using the leaf-dip method, the LC_{50} value of field strain was high (71.56 ppm) compared with the susceptible strain and resistance ratio (RR) was recorded 34-fold.

Table 1. LC_{50} value and resistance ratio associated with chlorantraniliprole in field strain of *Spodoptera littoralis*

Spodoptera littoralis	N [a]	LC_{50} (95% CL) [b] (ppm)	Slope (±SE)	χ^2 (*df*) [c]	p-value	RR [d] (fold)
Susceptible strain	180	2.12 (1.31–3.46)	1.19 (±0.13)	2.29(2)	0.51	
Field strain	180	71.56 (68.00–74.87)	3.92 (±0.12)	17.02(3)	0.80	34

[a] Number of larvae tested, including control, [b] 95% confidence limits, [c] Chi-square value (χ^2), degrees of freedom (*df*), and p-value as calculated by probit analysis with SPSS.
[d] RR (Resistance Ratio) = LC_{50} (field strain)/LC_{50} (susceptible strain).

3.2. Efficacy of synergists on chlorantraniliprole resistance

While using chlorantraniliprole in combination with PBO, TPP, and DEM specific synergist for monooxygenase (MO), carboxylesterase (CarE), and glutathione S-transferase (GST), respectively, toxicity variations reflected in mortality in terms of LC_{50} value changes were observed (Figure 1). The TPP, DEM, and PBO, in field strain showed 1-, 2-, and 4-fold synergism, respectively (Table 2).

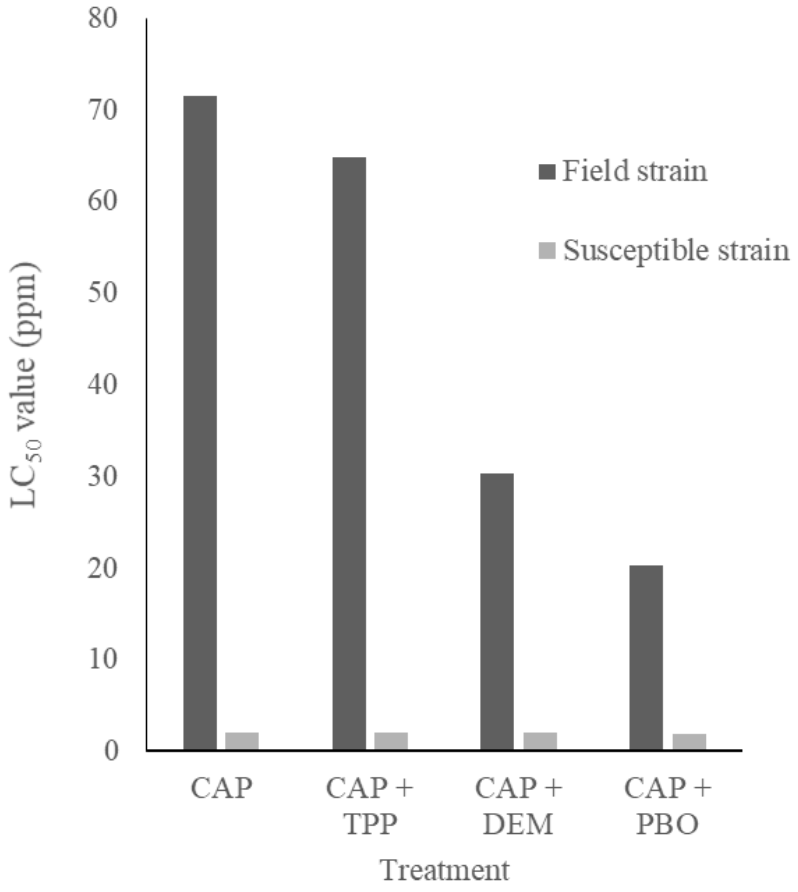


Fig. 1. Synergism of triphenyl phosphate (TPP), diethyl maleate (DEM), and piperonyl butoxide (PBO) on chlorantraniliprole (CAP) in the 3rd instar larvae of field and susceptible strains of *Spodoptera littoralis*

Table 2. Synergistic effect of PBO, TPP, and DEM on chlorantraniliprole in susceptible and field strains of *Spodoptera littoralis*

Spodoptera littoralis	Synergist	LC_{50} (95% CL) ppm	Slope (±SE)	SR [a]
Susceptible strain	Chlorantraniliprole	2.12 (1.31–3.46)	1.19 (±0.13)	
	+PBO	1.91 (1.31–3.94)	1.31 (±0.33)	1.11
	+TPP	2.11 (1.61–2.80)	1.84 (±0.28)	1.00
	+DEM	2.05 (1.51–2.94)	1.47 (±0.25)	1.03
Field strain	Chlorantraniliprole	71.56 (68.00–74.87)	3.92 (±0.12)	
	+PBO	20.30 (18.78–22.03)	2.67 (±0.36)	3.53
	+TPP	64.80 (55.79–74.17)	1.57 (±0.30)	1.10
	+DEM	30. 39 (22.53–40.93)	1.07 (±0.13)	2.32

[a] SR (Synergistic Ratio) = LC_{50} (insecticide alone)/LC_{50} (insecticide with synergist).

3.3. Activity of detoxifying enzymes

Between the cotton leafworm strain obtained in the field and the susceptible strain, there were substantial differences in the activities of carboxylesterase (CarE), glutathione S-transferase (GST), and monooxygenase (MO) (Table 3). The MO in the field strain was much higher than in the sensitive strain, where the activity ratio was 3.0-fold higher, followed by an increase in GST activity of 2.0-fold, while the detoxifying enzyme CarE had the lowest observed activity.

Table 3. Activity of detoxification enzymes in susceptible and field strains of *Spodoptera littoralis*

Enzyme	Susceptible strain	Field strain
Carboxylesterase (CarE) [µmol/min/mg protein]	0.52 ± 0.02	0.54 ± 0.07
Glutathione S-transferase (GST) [nmol/min/mg protein]	5.89 ± 0.13	9.60 ± 0.20
Monooxygenase (MO) [nmol/min/mg protein]	0.33 ± 0.01	1.13 ± 0.41

Results are shown as the mean ± standard error.

4. Discussion

In this study the results showed that the LC_{50} value of tested field strain of *Spodoptera littoralis* high compared with the susceptible strain. Likewise, moderate resistance level to chlorantraniliprole was found in field strain of *S. littoralis* (Table 1). Chlorantraniliprole resistance in Lepidoptera field populations has been found in several investigations to range from moderate to high [23,24,25]. The LC_{50} of susceptible strain did not significantly change after pre-treatment with PBO, TPP, and DEM synergists. In contrast, in the field strain, the LC_{50} value was significantly decreased after application of synergists (Table 2) and (Figure 1). From these results, synergism assays showed the detoxification enzymes might be involved in the resistance observed in field strain. Therefore, the enzyme activities of carboxylesterase (CarE), glutathione S-transferase (GST), and monooxygenase (MO) were measured to investigate metabolic resistance in the field strain. The activity of MO increased with 3.0-fold in comparison with the susceptible strain. According to the results, the correlations between the LC_{50} values of the tested field strain and the activity of detoxification enzymes are shown in Table 3. A positive correlation was observed between CarE, GST, and MO activity and LC_{50} values. This suggests that CarE, GST, and MO may be involved in chlorantraniliprole resistance in the *S. littoralis,* particularly MO. In China, a strong correlation between increased resistance of chlorantraniliprole and mixed function oxidase (MFO) level has been reported in *Spodoptera litura* populations [3]. In addition, the P450

activity, CarE, and GST are involved in chlorantraniliprole resistance, but GST might be contributing more in *Plutella xylostella* L. [26]. These results provide new evidence that insect FMOs can be recruited to provide resistance to the synthetic insecticides. A flavin-dependent monooxgenase confers resistance to chlorantraniliprole in the diamondback moth, *Plutella xylostella* [27]. High activity of MO enzyme in the field strain of *S. littoralis*, it appears to play an important role in conferring resistance to chlorantaniliprole, and thus this enzyme is key to controlling cotton leafworm.

5. Conclusion

These experiments indicated that there is a strong correlation between the activity detoxification enzymes and chlorantraniliprole resistance in *Spodoptera littoralis* and monooxygenase (MO) is likely the main detoxification mechanism responsible for resistance, although glutathione S-transferase (GST) and carboxylesterase (CarE) cannot be excluded. Therefore, further study in more detail is needed about role monooxygenase enzyme attributed resistance to diamide insecticides in insects.

Abbreviations

CarE: Carboxylesterase
DEM: Diethyl maleate
GST: Glutathione S-transferase
MO: Monooxygenase
PBO: Piperonyl butoxide
TPP: Triphenyl phosphate

Conflict of interest

None of the authors have any conflict of interest to declare.

Consent for publications

The author approved the final manuscript for publication.

Availability of data and material

Data are available on request from the author.

Authors' contributions

In this study, S.M.I. presented the design, topic selection, paper writing, data collection, data interpretation, and statistical analysis.

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Ethics approval and consent to participate

No human or animals were used in the present research.

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