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Research Article

Chlorantraniliprole selection, synergism and cross-resistance to various insecticides in tomato pinworm, *Tuta absoluta* (Meyrick)

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Abstract. *Tuta absoluta* is an invasive polyphagous pest recently reported on tomato, brinjal, and potato in India. It has acquired resistance to many chemical insecticides under field control. A toxicity test demonstrated a 31.7-fold reduction in mortality with high resistance to chlorantraniliprole selection in laboratory circumstances. The cross-resistance profile to various pesticides revealed moderate to high resistance to flubendiamide (2.3-fold) succeeded by spinosad, chlorpyrifos, cypermethrin, imidacloprid, and esfenvalerate (RR=6.0, 3.3, 3.1 and 2.8-fold). No resistance was detected to emamectin and abamectin (RR= 0.9-fold). The synergism bioassay utilizing PBO (piperonyl butoxide), DEM (diethyl-maleate) and TPP (triphenyl phosphate) revealed the potential mechanisms of esterase and P450 metabolic resistance to chlorantraniliprole in *T. absoluta*. Furthermore, six cytochrome P450 genes (CYP321A7, CYP321A9, CYP6B6, CYP6B47, CYP4M21 and CYP4C71) exhibited higher expressed level in the TN-R G7 resistant population compared to the susceptible one (SS). This work may facilitate the effective treatment of *T. absoluta* resistance to chlorantraniliprole through rotation with emamectin and abamectin.

Keywords: Chlorantraniliprole, Insecticide Synergist, Metabolic enzymes, Cross-resistance, Resistance management

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Introduction

Tuta absoluta is a polyphagous pest from the Gelechiidae family, usually referred to as the South American tomato pinworm. Due to its high reproductive potential and extensive host range, it has invaded many countries, including Europe, Africa, Western Asia, and Central America (Biondi *et al.,* 2018). Recently it has affected numerous regions of India resulting in a total decline of 80-90% in tomato production (El Aimani *et al.,* 2021; Prasannakumar *et al.,* 2021). During a *T. absoluta* outbreak, it consumed nearly all portions of the plant, ultimately resulting in bacterial and fungal proliferation (Shahini *et al.,* 2021). The management of this pest has depended on the use of chemical insecticides, resulting in a significant escalation in insecticide application. Excessive use of insecticides and pesticides can lead to soil and water contamination (Narayanan and Ma, 2024) and ultimately impact human health, resulting in various types of cancers (Mohan *et al.,* 2024; Rajinikanth *et al.,* 2024) and metabolic disorders

(Mani *et al.,* 2024). Due to the continual and recurrent use of synthetic insecticides, *T. absoluta* has developed resistance to these chemical insecticides (Ong'onge *et al.,* 2023; Narayanan & Prabhu, 2025).

Insects can acquire resistance to chemical pesticides via several mechanisms, including metabolic enzyme resistance, changed target site insensitivity due to particular mutations, and penetration and behavioral resistance. Notably, excessive protein production due to the elevated expression of one or more metabolic enzymes has been shown (Ye *et al.,* 2022). Numerous bioactive compounds obtained from plants (Parveen *et al.,* 2025b) and marine algae (Narayanan & Rajinikanth, 2025) exhibit considerable pest management and medicinal potential (Mani *et al.,* 2024; Narayanan, 2024). It is essential to address insect resistance through an integrated resistance management approach that incorporates the rotation of insecticides with varying modes of action and the application of specific enzyme synergists with insecticides (Kadry *et al.,* 2025; Yin *et al.*, 2019).

Chlorantraniliprole is a novel diamide and member of the 28th group of insecticides, functioning as a ryanodine receptor modulator (Kim *et al.,* 2025). It induces paralysis in insect muscles by triggering the uncontrolled release of internally held calcium ions (Ca^{2+}), ultimately leading to the insect's demise (Lai & Su, 2011; Radhakrishnan & Narayanan, 2025). It serves as a crucial instrument in integrated pest management (IPM) because of its minimal toxicity to mammals and beneficial creatures, and no cross-resistance has been documented with other insecticides (Campos *et al.,* 2014). In recent decades, findings indicate that lepidopteran insects have evolved resistance to chlorantraniliprole insecticide (He *et al.,* 2019). This work examined the potential mechanisms of chlorantraniliprole resistance in *T. absoluta*, both with and without synergist combinations, as well as its cross-resistance patterns to different insecticides. The expression levels of cytochrome P450 resistance genes were analyzed using qRT-PCR.

Materials and methods

Insect culture

T. absoluta susceptible populations (SS) were received from ICAR (Indian Institute of Horticulture Research), Crop Protection Division, Bangalore, Karnataka, India. This population was initially collected from a tomato field in Bangalore and preserved in insectariums for 12 generations without exposure to any chemicals. The chlorantraniliprole-resistant (TN-R G7) strain was derived from field-collected populations in Hosur, Tamil Nadu, India. First-generation (F1) larvae derived from field populations were subjected to chlorantraniliprole selection with six different concentrations (ranging from 0.1-10ppm). The LC_{50} determined for each generation was based on the probit response of the previous generation bioassay. Approximately 300 to 700 larvae were used for each generation. Both the susceptible (SS) and resistant (TN-R G7) *T. absoluta* were maintained in the insect rearing room at controlled temperature (26±1°C) with relative humidity of 70±5˚C and 12:12 light and dark photoperiod conditions.

Insecticides and chemicals

The chemical and bio-insecticides used in this study were commercially formulated. Chlorantraniliprole 18.5% SC (DuPont), indoxacarb 14.5% SC (Syngenta), flubendiamide 39.35% SC (Bayer Crop Science), fipronil 5% SC (Bayer crop Science), cypermethrin 25% EC (Syngenta), imidacloprid 30.5% SC (Syngenta), esfenvalerate 10% SC (Bayer Crop Science), chlorpyrifos 50% EC (Syngenta), methomyl 35% SC (Syngenta), chlorfluazuron 5.4% EC (Bayer Crop Science), spinosad 45% SC (Dow Agro Science), emamectin 5% SG and abamectin 5% SG (Syngenta). These chemical insecticides affect the nerve and muscular function of several insect groups classified under IRAC major groups 1, 2, 3, 5, and 6. The synergists PBO, DEM, TPP and other compounds were procured from Himedia chemicals.

Toxicity bioassay

During the 2nd instar, *T. absoluta* larvae were used for the leaf dip toxicity bioassay Chlorantraniliprole was prepared in ppm concentration with six dosages in distilled water. Uniformly sized (6×6 cm in diameter) healthy, fresh and young tomato leaves were submerged in insecticide solutions for 15 seconds and subsequently air-dried for 20 minutes at 26-28˚C. Moistened cotton pieces were placed in a bioassay container during each treatment to preserve the freshness of the leaves. Leaves immersed solely in deionized water served as controls. Larvae were

deemed deceased when they failed to respond to physical perturbation, with mortality reported at 48 hours post-treatment.

Chlorantraniliprole synergism

Synergism bioassays were conducted using 2nd instar larvae from both susceptible and resistant populations of chlorantraniliprole, employing the insecticide chlorantraniliprole in conjunction with PBO, DEM, and TPP to identify potential metabolic pathways associated with resistance. The bioassay method utilized in the synergism investigation resembled the IRAC approach; however, all larvae were topically administered 0.5µl of 15mM of each synergist one hour prior to exposure to chlorantraniliprole. All experiments were conducted in triplicate to reduce error.

Cross-resistance pattern

To detect the potential range of chlorantraniliprole cross-resistance, 2nd instar larvae were subjected to concentration mortality bioassays utilizing indoxacarb, fipronil, cypermethrin, imidacloprid, chlorpyrifos, esfenvalerate, methomyl, chlorfluazuron, spinosad, abamectin, emamectin, and flubendiamide. The bioassay approach employed was that previously delineated for leaf dip bioassay (Muthusamy *et al.*, 2024).

Detoxification inhibitory study

Enzyme preparation

Approximately, thirty early 3rd instars, both resistant and susceptible larvae, were subjected to starvation at 7 hours under cold conditions. Homogenates of larvae were prepared in 50ml of pre-chilled buffer saline (PBS, pH-7.0) with 1mM of each Ethylenediaminetetraacetic acid (EDTA), 1-4-dithiotheritol (DTT), phenyl-thiourea (PTU), and phenyl methyl-sulfonyl-fluoride (PMSF). The extract was separated by centrifugation at 15,000×g for 30 minutes at 4˚C. The finished sample was refrigerated until it was utilized for enzyme activity analysis. Protein quantification was performed with a standard substrate (Bovine Serum Albumin) in accordance with the standard Lowry method.

Detoxification enzyme assay

Esterase activity

The esterase activity was measured according to the methodology of Lokeshwari *et al.* (2016). The overall reaction volume of 6.0ml comprises 990 µl of phosphate-buffered saline (40 mM, pH 6.8), 10 µl of resistant and susceptible enzyme sample (with and without synergist), and 4000µl of 30mM α-naphthyl acetate diluted in 1ml acetone solvent. The reaction mixtures were gently agitated and incubated at 37°C for 15 minutes in the absence of light. Finally, 1.0 ml of staining solution (1% fast blue BB salt and 5% SDS) was added, and the dark color changes were measured calorimetrically at 590nm. The specific activity of esterase was calculated using standard values of α-naphthyl acetate and expressed as µmole/min/mg of protein.

Glutathione S-transferase activity

The GST activity was quantified using the conjugation of CDNB according to the method of Kao *et al.* (Kao *et al.,* 1989). The total volume of the reaction tube was 3ml, comprising 0.05ml of 2,4 dichloronitrobenzene (50mM), 0.01ml of enzyme extracts, 0.15ml of GSH (glutathione reduced form), and 2.79ml of 100mM buffer saline (PBS, pH-6.0). The reaction tubes were placed on ice for 5 minutes and the enzyme activities were measured at 340nm and expressed as µmole/min/mg of protein.

Mixed-function oxidase activity

MFO activity was measured according to Fouad *et al.* (2022) with slight modifications (Fouad *et al.*, 2022). 500 µl of 2 mM pnitroanisole with 450 µL enzyme stock solutions from resistant and susceptible populations were added to the reaction tube and mixed. After incubation for 2 min at 27°C, 50 µL of 9.6 mM NADPH was added to initiate the reaction. The activity of MFO was measured immediately at 405nm for 15 min and expressed as µmole/min/mg of protein. A standard curve of p-nitrophenol was used to calculate MFO activity.

P450s mRNA expression

The mRNA expression of nine resistant cytochrome P450 genes (CYP3, CYP4, and CYP6) was examined in laboratory-selected *T. absoluta.* Total RNA was isolated from third-instar larvae of each population utilizing the QIAwave RNA Mini Kit (Qiagen, India) in accordance with the manufacturer's instructions. M–MLV reverse transcriptase (Promega, India) was employed to synthesize the first strand of cDNA. The gene-specific primers employed in this study were derived from prior literature (Table 1). The qRT-PCR analysis was performed according to the procedure outlined in our prior study (Muthusamy & Shivakumar, 2015). Using EF-1α as a housekeeping gene, the relative gene expression levels in resistant and susceptible strains were quantified using the $2^{-\Delta\Delta CT}$ method.

Statistical analysis

The LC_{50}, together with its confidence interval and chi-square (χ^2) values, was calculated by probit analysis using SPSS statistical software package. All percentage mortality data were corrected using Abbott's formula. Resistant ratios (RR) from the larval bioassay were calculated by dividing the resistant population lethal value by the susceptible population lethal value. Synergism ratios (SR) were elucidated by dividing the insecticide lethal value alone, and the insecticide synergist combination. The data produced from enzyme activity was evaluated using the Bonferroni multiple comparison post-hoc test, whereas gene expression was assessed by column statistics. Notable discrepancies in enzyme activity and gene expression were deemed significant at $p<0.05$ using PRISM-Graph Pad (Version 5.0).

Results

Resistance selection

The chlorantraniliprole resistance assay indicated an LC_{50} value of 7.03 ppm for the field-collected F1 population. After seven generations of in-vitro selection (TN-R), a concentration of 36.54 ppm was observed, corresponding to a resistance ratio of 31.7-fold relative to the laboratory (SS) population, and a 5.19-fold resistance ratio was noted versus the unselected field population, respectively (Table 2).

Synergism of chlorantraniliprole

The synergism ratios of PBO, DEM, and TPP against resistant populations were 2.87, 1.16, and 3.19ppm (*P<0.05), while lower synergism ratios were found in susceptible populations at 1.3, 1.2, and 1.0ppm (Table 3). The synergistic effect of PBO and TPP exceeded that of the susceptible strain, indicating a potential involvement of metabolic enzymes in chlorantraniliprole resistance.

Table 1. qRT-PCR primers used in this study

Genes Accession number	Primer sequences (F/R) (5'-3')	Amplicons Length (bp)
EF-1α	GACAAACGTACCATCGAGAAG	279
(U20129)	GATACCAGCCTCGAACTCAC	
CYP321A7	AAAACAACCCCAAGACCCGT	101
(KC789750.1)	TGAGTTCGTTCCAATGCCGA	
CYP321A9	GACCCAGAAGTGTTCGACCC	125
(KC789752.1)	TGCACTTGTAGCTTGGCGTA	
CYP321B1	TACGGAGGGAAGCTGACGTA	125
(KC789754.1)	ACAGAGTCTTCCACGCACTG	
CYP6AE43	TGCCTTCGGAGTGGAGTCTA	127
(KJ671575.1)	TGGCCATGCAGCTCTACAAA	
CYP6B6 (Ortholog)	TTGAAGAAAGGCGTATGAAA	232
(KM577332)	ACACGCAAGATACACAAAGG	
CYP6B47	ACTTCACCTTGTCTCCTTATCCGA	245
(GQ465039.2)	AAAGCTGTCCATGTTTCTCCATC	
CYP4M21	TGAGCAGACGCGCGATGT	149
(EU189049)	CACCATATCCTCGGAGCTGC	
CYP4C71	CCGCCACCCATTCGCCTATG	329
(JX876506.1)	CTTCACCTTCACGCCACTCTCC	
CYP4G74	CCCGGACCTGCCATTATACC	121
(KC789745.1)	ACACTCTGACTACGTTGCCG	

Table 2. Toxicity of chlorantraniliprole against field and susceptible population of *T. absoluta*

Population	LC_{50} (95% CI ppm) *	Slope (±SE)	Df	χ^2	RR on (F1)	RR on (F7)
Field (F1)	7.03 (6.24-8.73)	2.84 (0.21)	3	1.30	-	6.1
TN-R G7	36.54 (35.93-37.48)	3.24 (0.32)	3	2.12	5.19	31.7
SS	1.15 (0.37-2.42)	1.38 (1.22)	3	1.11	-	-

LC_{50}, lethal concentration that kills 50% of the test animal; ppm, parts per million; CI, confidence interval; χ^2, chi-square; RR, Resistant ratio; df, degree of freedom done by probit analysis.

Chlorantraniliprole cross-resistance pattern

The concentration mortality test for twelve different insecticides targeting field-evolved resistant populations and susceptible populations was conducted to identify potential cross-resistance. The increased LC_{50} obtained for cypermethrin, chlorpyrifos, and esfenvalerate insecticides were 10.53, 15.44, and 13.42 ppm. Among tested insecticides, only the abamectin and emamectin showed less cross-resistance (RR-0.9), whereas higher resistance was observed for cypermethrin (3.3-fold), chlorpyrifos (6.0-fold), and spinosad (6.0-fold) Table 4.

The activity of detoxification enzymes

The activities of esterase, glutathione S-transferase, and mixed-function oxidase were assessed in the chlorantraniliprole-resistant and susceptible populations following seven generations of selection to discover the enzymes implicated in potential resistance to chlorantraniliprole. Esterase activity was elevated in the resistant field (25µmole/mg protein/min) population compared to susceptible population 11µmole/mg protein/min (Fig. 1). Similarly, GST activity in the resistant group was slightly increased (20µmole/mg protein/min) as compared to susceptible one 10µmole/mg protein/min (Fig. 2) with no significant differences in the enzyme activity (1.0 and 1.5-fold). Next, MFO activity was significantly higher in the 3rd instar larvae from the TN-R G7 population (31µmole/mg protein/min) than the (SS) susceptible population (10 µmole/mg protein/min), which is 2.5-fold increased activity P<0.001 (Fig. 3). This indicates the possible role of P450 conferring chlorantraniliprole resistance in the TN-R G7 population.

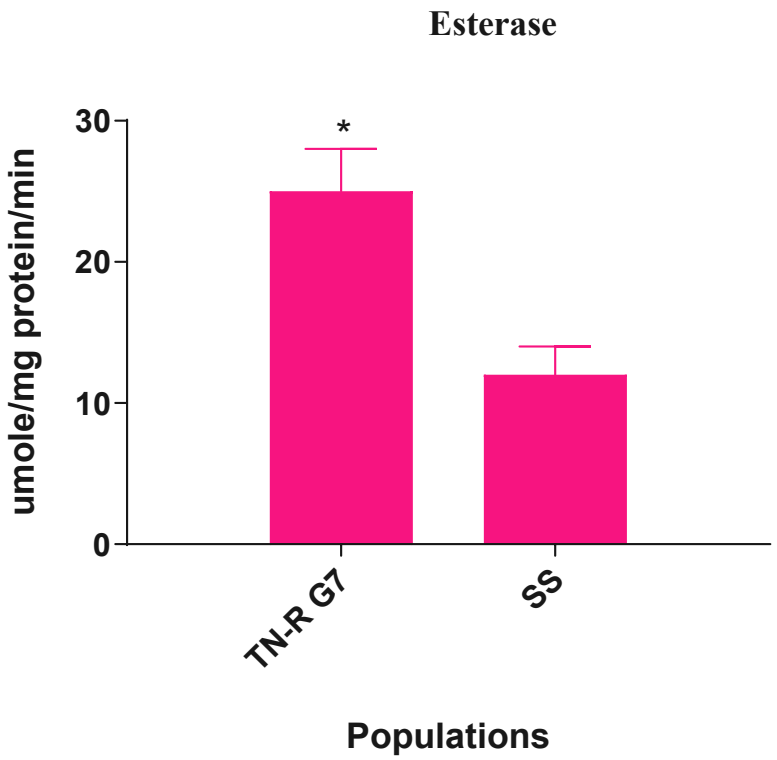

Fig. 1. Esterase activity in resistant and susceptible populations of *T. absoluta*. The bar represents the mean, standard deviation (±SD) of enzyme value. Asterisk* shows increased activity in resistant populations compared to susceptible (*P<0.05).

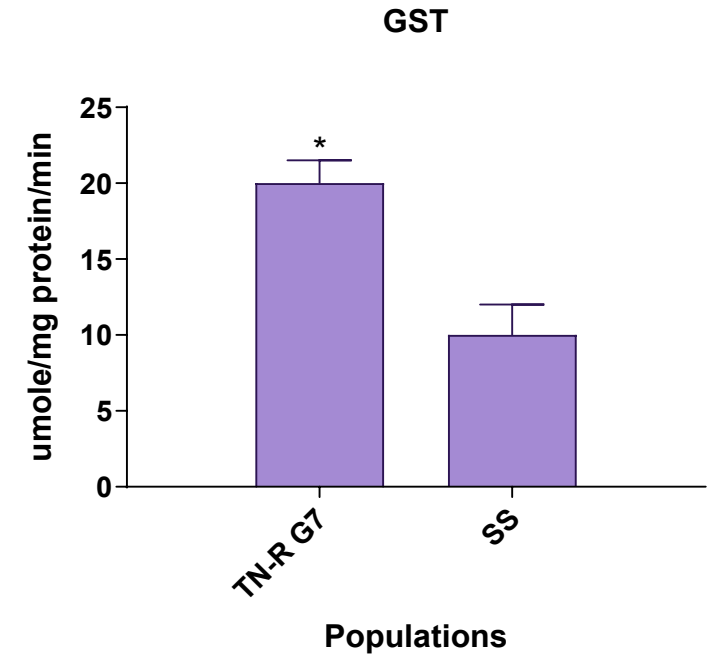

Fig. 2. Glutathione S-transferase activity in resistant and susceptible populations of *T. absoluta*. The bar represents the mean, standard deviation (±SD) of enzyme value. Asterisk* shows increased activity in resistant populations compared to susceptible ones (*P<0.05).

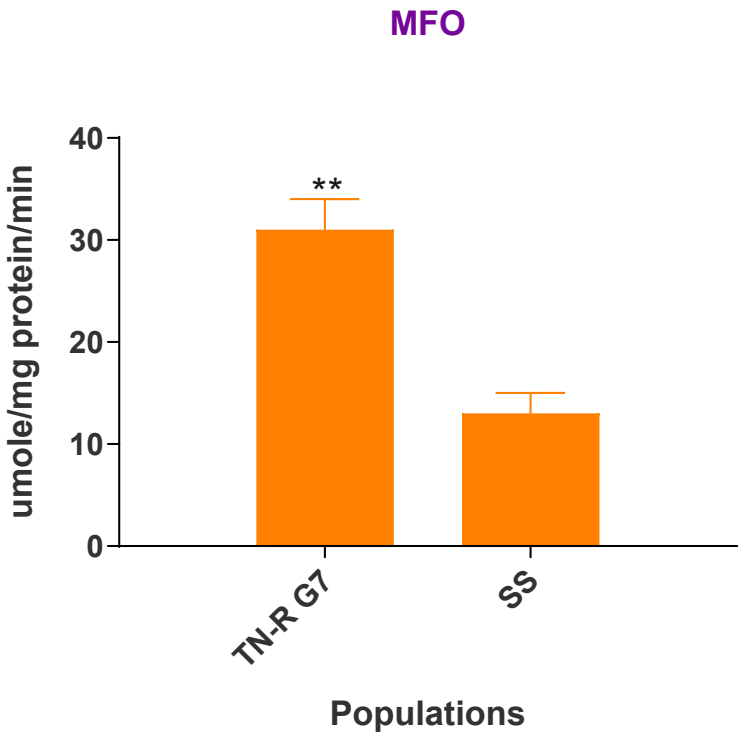

Fig. 3. Mixed function oxidase activity in resistant and susceptible populations of *T. absoluta*. The bar represents the mean, standard deviation (±SD) of enzyme value. Asterisks** show increased activity in resistant populations compared to the susceptible (*P<0.001).

Table 3. Toxicity of chlorantraniliprole in combination with different synergists against resistant and susceptible *T. absoluta*

Populations	Treatments	LC_{50} (95% CI ppm)*	Slope (±SE)	χ2	SR
TN-R G7	Chlorantraniliprole	36.54 (35.93-37.48)	1.43 (0.43)	0.31	-
	Chlorantraniliprole + PBO	12.73 (11.06-13.94)	2.42 (0.53)	1.32	2.87
	Chlorantraniliprole + DEM	31.32 (30.38-32.93)	1.43 (0.26)	2.12	1.16
	Chlorantraniliprole + TPP	11.43 (10.58-12.49)	1.33 (0.73)	0.43	3.19*
SS	Chlorantraniliprole	1.15 (0.37-2.42)	2.31(1.31)	1.64	-
	Chlorantraniliprole + PBO	0.84 (0.21-0.98)	1.42 (0.48)	1.53	1.36
	Chlorantraniliprole + DEM	0.92 (0.44-1.31)	1.31 (0.21)	0.43	1.25
	Chlorantraniliprole + TPP	0.68 (0.22-0.87)	1.11 (0.32)	1.32	1.03

LC_{50}, lethal concentration that kills 50% of the test animal; ppm, parts per million; CI, confidence interval; χ2, chi-square; SR, Synergism ratio; * Indicates significant in synergism ratio between field and susceptible population (Tukey's multiple range test at $P < 0.05$).

Expression profile of Cytochrome P450 genes

The expression levels of nine cytochrome P450 genes exhibited substantial differences between the resistant and susceptible populations (Fig.4). The expression levels of CYP321A9 and CYP6B6 were significantly elevated in TN-R (4.4 and 5.6-fold), followed by CYP321A7 (3.2-fold), CYP6B47 (5.1-fold), CYP4M21 (2.3-fold), and CYP4C71 (2.0-fold), as illustrated in Fig.4.

Discussion

Insecticide resistance poses a significant challenge in newly invasive pest species such as *T. absoluta.* The persistent and recurrent use of pesticides in agricultural management has resulted in the development of resistance and may induce cross-resistance to other classes of insecticides (Domínguez *et al.,* 2019). Consequently, meticulous assessment of insecticide resistance and its cross-resistance to other insecticides is an important tool for monitoring the resistance and integrated management program (Kadry *et al.*, 2025; Narayanan, 2025; Tarusikirwa *et al.*, 2020). This research focused on the toxicity of broad-spectrum diamide insecticide against the field-collected resistance population of *T. absoluta* under in-vitro conditions.

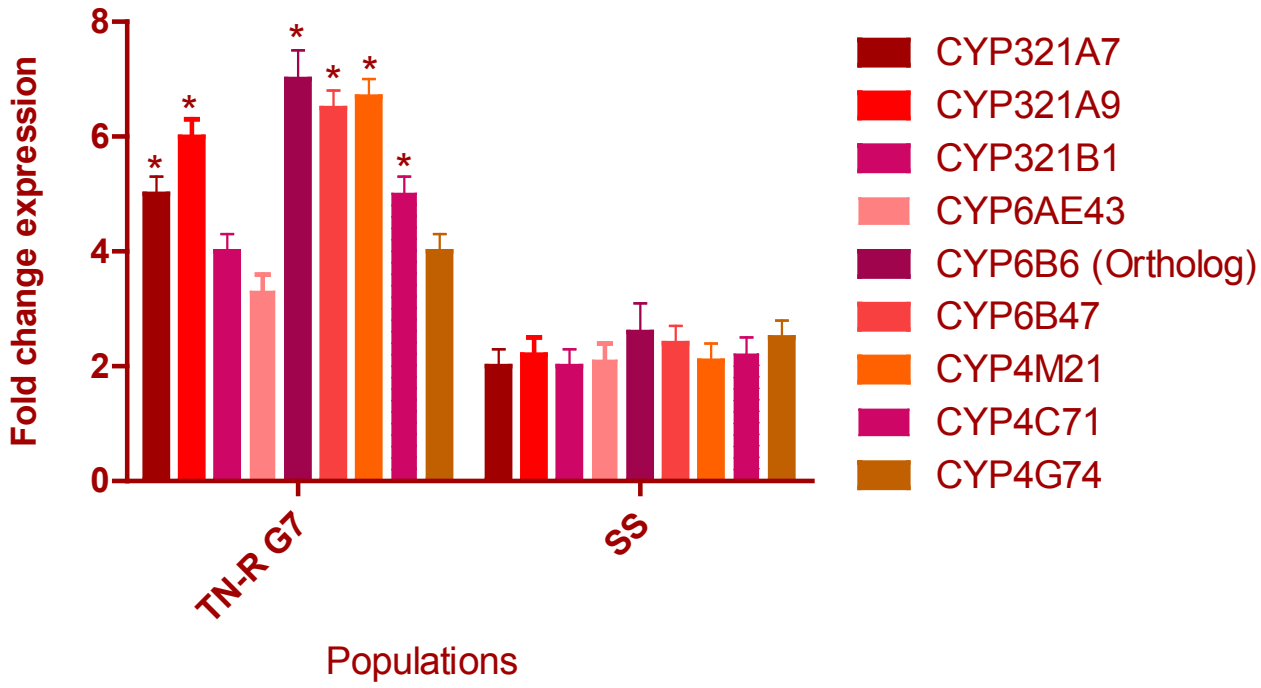

Fig. 4. Relative gene expression level of selected P450s in resistant and susceptible populations of *T. absoluta* (column statistics *P < 0.05). The error bars represent the standard deviation (n = 3).

Table 4. Cross-resistance to selective insecticides in chlorantraniliprole-resistant and susceptible strains

Strains	Insecticides	LC_{50} (95% CI ppm)*	Slope (±SE)	df	χ2	RR
TN-R G7	Indoxacarb	2.42 (1.31-3.62)	1.31 (0.32)	4	2.11	1.0
	Fipronil	4.53 (3.24-5.63)	2.42 (0.24)	3	1.31	1.5
	Cypermethrin	10.53 (8.94-11.24)	1.53 (0.66)	3	3.13	3.3
	Imidacloprid	3.53 (2.42-4.57)	0.53 (0.44)	4	2.11	3.1
	Chlorpyrifos	15.44 (14.53-13.53)	0.78 (0.14)	3	1.52	6.0
	Esfenvalerate	13.42 (12.44-14.09)	1.39 (1.40)	3	2.24	2.8
	Methomyl	4.65 (3.12-5.93)	0.94 (0.21)	3	1.56	1.8
	Chlorfluazuron	2.43 (1.31-3.45)	2.53 (1.53)	3	2.53	1.2
	Spinosad	2.54 (1.43-3.53)	1.55 (0.27)	3	3.42	6.0
	Abamectin	1.11 (0.42-1.93)	2.75 (0.64)	3	1.53	0.9
	Emamectin	1.49 (0.38-2.10)	1.77 (0.23)	3	2.42	0.9
	Flubendiamide	3.92 (2.01-4.29)	1.34 (0.13)	3	1.13	2.3
SS	Indoxacarb	2.41 (1.31-3.56)	1.66 (0.65)	4	1.64	-
	Fipronil	2.92 (1.21-3.85)	2.55 (1.01)	3	2.64	-
	Cypermethrin	3.15 (2.64-4.55)	2.74 (0.13)	3	2.53	-
	Imidacloprid	1.13 (0.25-2.40)	1.79 (0.22)	4	1.66	-
	Chlorpyrifos	2.57 (1.65-3.74)	2.99 (1.50)	3	2.75	-
	Esfenvalerate	4.64 (3.53-5.32)	1.30 (0.52)	3	1.86	-
	Methomyl	2.54 (1.31-3.23)	1.45 (0.87)	3	3.54	-
	Chlorfluazuron	1.93 (0.23-2.14)	2.09 (1.39)	3	2.66	-
	Spinosad	0.42 (0.13-1.31)	1.62 (0.66)	3	1.86	-
	Abamectin	1.13 (0.42-2.43)	0.69 (0.96)	3	3.56	-
	Emamectin	1.53 (0.8-2.24)	1.43 (0.34)	3	2.22	-
	Flubendiamide	1.64 (0.42-2.53)	2.21 (1.79)	3	1.44	-

LC_{50}, lethal concentration that kills 50% of the test animal; ppm, parts per million; CI, confidence interval; χ2, chi-square; RR, Resistant ratio; df, degree of freedom done by probit analysis.

Our findings demonstrated significant resistance to chlorantraniliprole selection in field field-evolved population (RR 31.7-fold) relative to the susceptible group. Comparable investigations indicated a resistance ratio of 14-fold for chlorantraniliprole and 11-fold for flubendiamide in several field populations of *T. absoluta* (Parveen *et al.*, 2025a; Roditakis *et al.*, 2015). Subsequently, field control failure was reported in the Italian and Greek populations of *T. absoluta,* followed by the Israeli population (> 64-fold and 22,573-fold) (Roditakis *et al.,* 2018). Zhang *et al.* (2025) also reported 24.66-fold resistance in the Chinese field population of *Tuta absoluta* upon chlorantraniliprole treatment (Vijayakumarr *et al.*, 2025; Zhang *et al.*, 2025). The emergence of elevated resistance levels in these field populations to chlorantraniliprole may result from intensified selection pressure in natural environments relative to laboratory conditions, as well as the heterogeneous composition of the population.

The possibility of cross-resistance to multiple pesticides is a significant challenge in restricting the available options for pest management. The current study indicates that the cross-resistance in chlorantraniliprole-selected *T. absoluta* seems limited to abamectin and emamectin (a GABA-gated chloride channel allosteric modulators) and moderate to high cross-resistance to flubendiamide (a ryanodine receptors activator) 2.3-fold, followed by spinosad, chlorpyrifos, cypermethrin, imidacloprid, and esfenvalerate (6.0, 3.3, 3.1, and 2.8), which primarily affect sodium channels and target nicotinic acetylcholine receptors. This result indicated that pesticides with analogous modes of action exhibit cross-resistance, while others contribute minimally. Silva *et al.* (2016) reported analogous findings in Brazilian populations with a resistance ratio ranging from 1.0 to 288,995-fold between cyantraniliprole and flubendiamide insecticides (Silva *et al.,* 2016). Campos *et al.* (2014) reported limited cross-resistance in spinosad-selected *T. absoluta* to the similar classes of insecticide (Campos *et al.,* 2014). Venkatesan *et al.,* (2022) documented minimal cross-resistance to buprofezin, pyriproxyfen, and spinosad in *Chrysoperla carnea* under acetamiprid selection study and also reported very low cross-resistance to abamectin and emamectin (0.9-fold) in *T. absoluta* under diamide selection (Venkatesan *et al.,* 2022). Ismail (2021) reported that emamectin benzoate was found to be effective against the lepidopteran pest *Agrotis ipsilon*, which can be used as an alternative to the conventional insecticide for field control (Ismail, 2021).

Esterase, P450, and, to some lesser extent, GST have been reported to be involved in the metabolic resistance to organophosphate, carbamate, pyrethroid, and newer classes of insecticides in many insect species (Bosch-Serra *et al.,* 2021; Muthusamy *et al.,* 2013; Ye *et al.,* 2022). Chlorantraniliprole is a broad-spectrum insecticide utilized for the management of several insect species, particularly in the field control of *T. absoluta;* nevertheless, the metabolic enzymes and resistance mechanisms present in the Indian field population of *T. absoluta* remain

inadequately understood (Ramkumar *et al.*, 2023). The findings of the current investigation indicated elevated activity of esterase, glutathione S-transferase, and mixed-function oxidase in the chlorantraniliprole-resistant (TN-R) group relative to the laboratory susceptible (SS) population. This finding correlated with the results of PBO and TPP synergist bioassay on chlorantraniliprole resistance *T. absoluta,* suggesting the possible mechanism of P450 and, to some lesser extent, esterase metabolic enzymes in diamide resistance. The synergism by PBO and TPP in resistance to *T. absoluta* may lead to the inhibition of P450 and esterase enzymes involved in the rendering of toxic chemicals into less toxic by phase I and II detoxification process by hydrolysis or oxidation of these enzymes (Esteves *et al.*, 2021). Ma *et al.* (2024) reported diamide resistance in the WZ field population than susceptible reference strain YN-S (Ma *et al.,* 2024). Sun *et al.* (2018) published similar findings, indicating a 38.8-fold resistance ratio in the chlorantraniliprole laboratory resistant strain (R1) of *Chilo suppressalis* (Sun *et al.,* 2018). The potential mechanism of deltamethrin resistance in *Cimex lectularius* L. (common bed bug) is linked to esterase and GST metabolic resistance, enhanced by PBO and DEM synergism (Gonzalez-Morales & Romero, 2019). Gong *et al.* (2021) reported increased activity of CarE, GST, and P450 in *M. dirhodum* aphids subjected to imidacloprid pesticide, with a 20-fold PBO synergistic effect (Gong *et al.,* 2021).

The analysis of the cytP450 resistance gene in the TN-R population revealed elevated mRNA expression relative to the susceptible group. Out of nine cytP450 genes, CYP321A9, CYP6B6, CYP321A7, and CYP6B47 showed high expression by chlorantraniliprole selection. Ullah *et al.* (2025) also reported increased expression of cytochrome P450 mRNA level of CYP321C40, followed by CYP4M116, CYP6AW1, CYP339A1, and CYP6AB327 in the SpRS *T. absoluta* (Ullah *et al.,* 2025). Earlier studies by Shi *et al.* (2018) found that members of the CYP6AE subfamily may efficiently transform fenvalerate into 4'-hydroxy fenvalerate (Shi *et al.,* 2018). Elevated expression levels of the detoxifying genes *CYP6FU1* and *CYP439A1v3* in *L. striatellus* are correlated with resistance to deltamethrin. Similarly, the overexpression of multiple P450 enzymes has been linked to pyrethroid resistance in *H. armigera*, *Ae. aegypti*, and *Ae. Albopictus* (Wan *et al.*, 2021; Xiao *et al.*, 2020; Zhao *et al.*, 2021). Hafeez *et al.* (2022) also documented the upregulation of P450 genes in indoxacarb resistance *S. frugiperda* (Hafeez *et al.,* 2022). Yang *et al.* (2021) reported a high level of permethrin resistance in *Cx. quinquefasciatus* mosquitoes (Yang *et al.,* 2021). The prior work by Matowo *et al.* (2022) indicated that CYP6M2, CYP6Z3, CYP6P3, CYP6P4, CYP6AA1, and CYP9K1 exhibited elevated expression in pyrethroid-resistant *Anopheles gambiae* (Matowo *et al.,* 2022).

Conclusion

The current study's data indicate a potential for chlorantraniliprole resistance in *T. absoluta* under laboratory selection. In vitro synergism with PBO and TPP demonstrated the role of esterase and P450-mediated metabolic resistance, while the overexpression of nine P450 genes suggested their involvement in chlorantraniliprole resistance. Moreover, there exists a moderate to low likelihood of cross-resistance to other kinds of insecticides, with no cross-resistance detected to emamectin and abamectin insecticides. This information will facilitate the efficient management of diamide resistance in *T. absoluta.*

Abbreviations

CytP450s: CytochromeP450s; BSA: Bovine serum albumin; PBO: piperonyl butoxide; DEM :diethyl maleate; TPP: triphenyl phosphate; MFO: mixed function oxidase; IRAC: insecticide resistance action committee; °C: degree Celsius; RH: Relative Humidity; GSH: reduced glutathione; DTNB: 5, 5-dithio-bis-2-nitrobenzoic acid; NADPH: Reduced nicotinamide adenine dinucleotide phosphate; CDNB-GSH: 1-Chloro-2, 4-dinitrobenzene-glutathione; ppm: parts per million; µmole: micromole; mg: milligram; SC: Suspension concentrate; U/ml: Unit per milli liter; M: Molar; mM: Milli molar; Fig: Figure; GST: Glutathione S-transferase; H_2O_2: Hydrogen peroxide; KCl: Potassium chloride; LC_{50}: Lethal concentration, 50%; P<: Probability value; pH: Potential of hydrogen; PTU: Phenylthiourea; TMBZ: Tetramethyl benzidine; UV: Ultraviolet rays.

Author's Contributions

Muthusamy R: Conceptualization, Investigation, Writing-original draft. **Ramkumar G**: Investigation, data analysis. **R.Ranjani**: Editing manuscript and data analysis. **J. Senthil Kumar:** Reviewing and editing manuscript.

Suguna Kasirajan: Reviewing and editing manuscript. **Madhi Nagendiran:** Supervision, writing, editing, and reviewing the manuscript.

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Data Availability Statement

The detailed methodology and analytical data of the present findings are available from the corresponding author on reasonable request. The methodology and result details of the current study are available from the corresponding author on reasonable request.

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Ethics Approval

Insects were used in this study. All applicable international, national, and institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Conflict of Interest

The authors declare no conflict of interest.

Generative AI statement

The authors declare that no Gen AI was used in the creation of this manuscript.

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Research Article

مقاومت مینوز گوجه‌فرنگی، *Tuta absoluta* (Meyrick) به کلرانترانیلی‌پرول و اثر آن روی هم‌افزایی و مقاومت متقاطع به حشره کش های رایج

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۲- گروه حشره‌شناسی، دانشکده علوم کشاورزی و محیط زیست، دانشگاه جورجیا، گریفین، جورجیا، ۳۰۲۲۳، ایالات متحده آمریکا

۳- بخش جانورشناسی، کالج جمال محمد (خودمختار)، تیروچیراپالی–۶۲۰ ۰۲۰، تامیل نادو، هند

۴- گروه بیوتکنولوژی، کالج هنر و علوم PSG، کویمباتور – ۶۴۱۰۴، تامیل نادو، هند

۵- مجموعه ADRC و مرکز تشخیص و تحقیقات اشوانث، تامیل نادو، هند

۶- دپارتمان علوم کشاورزی، دانشکده علوم زیستی، دانشگاه چونگ‌کینگ، چونگ‌کینگ ۴۰۰۷۱۵، چین

چکیده: *Tuta absoluta* یک آفت مهاجم پلی‌فاژ است که اخیراً روی گوجه‌فرنگی، بادمجان و سیب‌زمینی در هند گزارش شده است. این آفت در برابر بسیاری از حشره‌کش‌های شیمیایی به کار رفته در مزرعه مقاومت پیدا کرده است. در یک آزمایش سمیت، این حشره، کاهش ۳۱.۷ برابری در مرگ و میر را با مقاومت بالا در برابر انتخاب کلرانترانیلی‌پرول در شرایط آزمایشگاهی نشان داد. الگوی مقاومت متقاطع به آفت‌کش‌های مختلف، حکایت ازمقاومت متوسط بالا در برابر فلوبندیامید (۲.۳ برابر) نشان داد و آفت‌کش های اسپینوساد، کلرپیریفوس، سایپرمترین، ایمیداکلوپرید و اسفن‌والرات در رده های بعدی (RR=6.0، ۳.۳، ۳.۱ و ۲.۸ برابر) قرار گرفتند در حالی که هیچ مقاومتی در برابر امامکتین و آبامکتین (RR=0.9 برابر) مشاهده نشد. ارزیابی زیست‌سنجی روی سازوکار هم‌افزایی با استفاده از PBO (پیپرونیل بوتوکسید)، DEM (دی‌اتیل مالئات) و TPP (تری‌فنیل فسفات) نشان داد که سازوکارهای بالقوه مقاومت متابولیکی استراز و P450 به کلرانترانیلی‌پرول در *T. absoluta* وجود دارد. علاوه بر این، شش ژن سیتوکروم P450 (CYP321A7، CYP321A9، CYP6B6، CYP6B47، CYP4M21 و CYP4C71)، سطح بیان بالاتری را در جمعیت مقاوم TN-R G7 در مقایسه با جمعیت حساس (SS) نشان دادند. این پژوهش، به ما در مدیریت مؤثر مقاومت *T. absoluta* به کلرانترانیلی‌پرول از طریق کاربرد متناوب با امامکتین و آبامکتین کمک میکند.

کلمات کلیدی: کلرانترانیلیپرول، سینرژیست حشره‌کش، آنزیم‌های متابولیک، مقاومت متقاطع، مدیریت مقاومت

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