

# Risk Assessment of *Aphis gossypii* (Hemiptera: Aphididae) Development of Resistance to Afidopyropen<sup>1</sup>

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**Abstract** The cotton aphid (*Aphis gossypii* Glover) (Hemiptera: Aphididae) is a major pest of cotton (*Gossypium hirsutum* L.) grown in Xinjiang and is an agricultural pest found worldwide. With the extensive use of insecticides, *A. gossypii* in Xinjiang has developed high levels of resistance to a variety of insecticides. Afidopyropen is a new biogenic insecticide that is effective against insects with piercing-sucking mouthparts and has no cross-resistance with any commonly used insecticides in cotton fields. However, to our knowledge, the risk and stability of resistance of *A. gossypii* to afidopyropen and its detoxification enzymes under high selection pressure have not yet been elucidated. In this study, resistant *A. gossypii* specimens were selected with the cotton leaf-dipping method under laboratory conditions, and the realized heritability of *A. gossypii* resistance to afidopyropen was calculated using domain trait analysis. After 18 successive generations of selection for afidopyropen resistance, a resistant population with a median lethal dose (LC<sub>50</sub>) of 9.006 mg/L was obtained; the resistance ratios had increased 23.033 times. The realized heritability was 0.063, and a 10-fold increase in resistance required only 20–26 generations when mortality was 60–80%. The 15th generation of the resistant strain had some resistance instability, and glutathione S-transferases played an important role in the detoxification metabolism of afidopyropen. The results of this study provide a basis for application of afidopyropen and management of *A. gossypii* resistance.

**Key Words** *Aphis gossypii*, enzymes, insecticide, resistance selection, resistance risk assessment

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*Aphis gossypii* Glover (Hemiptera: Aphididae) is a worldwide pest (Cao et al. 2017, Jiang et al. 2018) and is currently the most serious pest of cotton (*Gossypium hirsutum* L.) in China (Quan et al. 2019). The overall occurrence of *A. gossypii* in Xinjiang, China was estimated to be as high as  $5.33 \times 10^5$  individuals/ha in 2022 (Li et al. 2022). Cotton fields are prone to attacks by *A. gossypii* (Liu 2021a) because of their diverse reproductive patterns, adaptability, and host plant species (Chao et al. 2019, Zhang et al. 2022a). Currently, chemical control is the dominant management strategy for *A. gossypii* outbreaks (Gao 2010, Ma et al. 2021a). However, long-term use of insecticides has led to a rapid increase in the resistance of *A. gossypii* (Patima et al. 2019, Zhang 2020, Zhao et al. 2018), especially to insecticides

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such as organophosphates, carbamates, pyrethroids, and neonicotinoids (Liang et al. 2013, Patima et al. 2019). Therefore, a new target mechanism of action for insecticides against resistant *A. gossypii* is urgently needed.

Afidopyropen, a novel biogenic insecticide (Li 2020, Shi et al. 2022), interferes with the function of insect chordotonal organs (Jiang et al. 2020), causing insects to lose their senses of gravity, balance, hearing, position, and movement (Gu and Bai 2020, Tan 2019). Afidopyropen can cause insects to immediately stop feeding (Gu and Bai 2018, Kandasamy et al. 2017, Zhang 2020), which in turn can reduce the spread of vector viruses and reduce damage to agricultural crops (Fu et al. 2022). Afidopyropen was registered in China in 2019 (Liu et al. 2022) and has been widely used with significant results in the cotton production areas of China (Shi et al. 2022). *Aphis glycines* Matsumura, *Bemisia tabaci* (Gennadius), *Diuraphis citri* Kuwayama, *A. gossypii*, and other field pests are sensitive to afidopyropen (Obiratanea et al. 2020, Shi et al. 2022, Zhang et al. 2021).

The resistance to insecticides usually develops in insects as a result of a change in the genetic structure that reduces pesticide sensitivity (Zhang 2016); this change is called realized heritability ( $h^2$ ) (Zhao et al. 2022). Resistance risk assessment is the calculation of the potential ability of pests in the field to develop resistance to pesticides (Ijaz et al. 2021, Li et al. 2013, Liu 2021b, Wang 2022). Currently, the threshold trait analysis method is widely used to calculate  $h^2$  and perform resistance risk assessments of pests (Tabashnik 1992), such as *Phenacoccus solenopsis* Tinsley, *Laodelphax striatellus* (Fallén), *Helicoverpa armigera* (Hübner), and *Plutella xylostella* (L.) (Afzal et al. 2022, Roy et al. 2023, Zhang et al. 2022b). For example, the resistance ratio of *Oxycarenus hyalinipennis* (Costa) was increased 2631.50-fold after the 19th generation of selected resistance to fipronil, with  $h^2 = 0.11$ ; a 10-fold increase in resistance ratios required six to eight generations with a greater risk of resistance when selection intensity was 60–80% (Ijaz and Shad 2022a). These studies provide an opportunity to assess the theoretical basis for predicting the occurrence of insecticide resistance in the field.

Insects gradually recover sensitivity to insecticides when their selection pressure disappears, and the rate of recovery of sensitivity is used to express resistance stability (Wen 2021). *Oxycarenus hyalinipennis* was selected for resistance to imidacloprid for 19 generations and reached a 146.5-fold resistance ratio. The resistance ratio returned to sensitive levels after eight generations without insecticide selection pressure (Ijaz and Shad 2022b). *Phenacoccus solenopsis* was selected for resistance to spirotetramat for 13 generations and reached a 328.7-fold resistance ratio, which decreased to 107.7-fold after cessation of selection pressure for four generations, with poor resistance stability (Ejaz and Ali 2017). In *L. striatellus* populations resistant to buprofezin for 10 generations and reared for 10 consecutive generations without selection pressure, resistance ratios decreased to 576.3-fold; thus, their resistance level was somewhat unstable (Muhammad et al. 2012).

However, the risk of resistance of *A. gossypii* to afidopyropen and essential enzymes required for detoxification have not yet been reported; thus, a systematic study of the resistance mechanism of *A. gossypii* to afidopyropen was needed. We selected for afidopyropen resistance for 18 consecutive generations of *A. gossypii* by using the leaf-dipping method and then assessed resistance risk and stability. The effects of detoxification enzymes and target enzymes of *A. gossypii*

resistant to afidopyropen were investigated. An attempt was made also to find the resistance mechanism of *A. gossypii* to afidopyropen at the physiological level. Our study provides a theoretical basis for the application of afidopyropen as part of a sustainable pest management program and elucidates the pesticide resistance mechanism of cotton aphids.

## Materials and Methods

**Insects and insecticide.** In 2017, *A. gossypii* strains were collected from cotton fields at the teaching experimental site of Shihezi University, Shihezi, China (where no insecticide was applied), followed by 5 yr of continuous rearing on potted cotton plants in incubators isolated by nylon nets without exposure to any chemicals. *Aphis gossypii* reproduced mainly as solitary females to form a sensitive laboratory strain ( $G_0$ ). The resistant strain was established using the sensitive strain and was propagated by successive selection for afidopyropen resistance. The sensitive and resistant strains were reared in a light incubator (light intensity = 12,000 lux, temperature =  $26 \pm 1^\circ\text{C}$ , relative humidity = 45–55%, light period:dark period = 16 h:8 h). Afidopyropen (96.1%) was obtained from BASF SE (Ludwigshafen, Germany), and acetone was produced by Shanghai Yuanye Biotechnology Co. (Shanghai, China).

**Toxicity bioassays.** Toxicity was determined using the maceration method recommended by the Food and Agriculture Organization of the United Nations with slight modifications (Shi et al. 2011). Afidopyropen (0.1 g) was dissolved in 10 ml of acetone and adjusted to 0.01, 0.1, 1, 10, and 100 mg/L by serial dilution with distilled water containing 0.05% (vol/vol) Triton X-100; distilled water containing 0.05% (vol/vol) Triton X-100 was used as the control. Six concentrations were used, and each concentration treatment was repeated three times. Cotton seedlings for the bioassay were grown hydroponically, and 18 cotton seedlings with two true leaves of uniform growth were selected. Each cotton seedling was dipped in the corresponding concentration of insecticide for 5 s and then air-dried naturally. Each cotton seedling was then inoculated with 30 wingless *A. gossypii* adults of uniform size. Each cotton seedling was covered with a nylon net, and a perforated plastic bottle was placed upside down over the seedlings. The cotton aphids were examined for mortality at 72 h. Mortality was determined by lightly touching the feet and antennae of each cotton aphid with a brush. Control mortality rate was  $\geq 90\%$ , and median lethal concentration ( $LC_{50}$ ) values were calculated and analyzed using SPSS 20.0 statistical software (IBM, Armonk, NY). The  $LC_{50}$  ratio of resistant lines to sensitive lines was calculated to obtain the resistance ratio.

**Selection for afidopyropen resistance.** Resistance screening for afidopyropen was performed with 1,000 sensitive *A. gossypii* for 18 consecutive generations, and the concentration of afidopyropen was gradually increased on the basis of the bioassay results of the previous generation. Insect-bearing cotton leaves were impregnated with the afidopyropen treatment solution for 5 s, and mortality was recorded after 72 h of exposure, with mortality maintained at 60–80%; the surviving cotton aphids were transferred to fresh untreated potted cotton plant leaves for reproduction. The resistance selection experiments were conducted under controlled laboratory conditions as described previously, and bioassays were performed for each generation for a total of 18 generations.

**Estimation of  $h^2$ .** The threshold trait analysis reported by Tabashnik (1992) and Tabashnik and McGaughey (1994) was used to assess  $h^2$  for *A. gossypii* in response to afidopyropen using the formula

$$h^2 = R/S$$

where  $R$  is the selection response and indicates the difference between the average phenotypic value of the offspring and average phenotypic value of the entire parental population.  $R$  was estimated using the following formula:

$$R = [\log(\text{final LC}_{50}) - \log(\text{initial LC}_{50})]/n$$

where  $n$  is the number of generations selected. The selection difference  $S$  is the average phenotypic difference between the parent used for screening and the whole parental generation.  $S$  was calculated as follows:

$$S = i \times \delta_p$$

where  $i$  is the intensity of selection, and  $\delta_p$  is the phenotypic standard deviation. The selection intensity ( $i$ ) was calculated as follows:

$$i \approx 1.583 - 0.0193336P + 0.0000428P^2 + 3.65194/P (10 < P < 80)$$

where  $P$  is the mean percent chance of surviving selection. The phenotypic standard deviation ( $\delta_p$ ) was estimated as follows:

$$\delta_p = 2/(\text{starting slope} + \text{final slope})$$

According to the method of Tabashnik (1992) for the evaluation of afidopyropen,  $h^2$  and  $S$  can be used to predict the number of generations required for a 10-fold increase in *A. gossypii* resistance to afidopyropen for a 50–90% *A. gossypii* lethality rate. Prediction of the rate of development of *A. gossypii* resistance to afidopyropen is based on mortality ( $S$ ) and  $h^2$  with

$$G = 1/(h^2S).$$

**Enzyme assay.** Enzyme-linked immunosorbent assay kits (Shanghai Yuanye Biological Technology Co.) were used to determine the activity of multifunctional oxidase (MFO), carboxylesterase (CES), glutathione  $S$ -transferases (GSTs), and acetylcholinesterase (AChE) in each *A. gossypii* generation. Seventy adult cotton aphids were selected from the 3rd, 6th, 9th, 12th, 15th, and 18th generations of resistant *A. gossypii* strains and the sensitive *A. gossypii* strain and were transferred to a 1.5-ml centrifuge tube with a brush. Physiological saline (100  $\mu$ l) and was added to each tube, and the cotton aphids were mashed with a grinding rod. That mixture was centrifuged at 4°C and  $3,000 \times g$  for 10 min with a high-speed refrigerated centrifuge (Shanghai Anting Scientific Instrument Factory), and the supernatant was obtained and used for three replicates.

**Statistical analysis.** SPSS 20.0 software was used to perform an analysis of variance, and the least significant difference method was used for determining the

**Table 1. Selection of resistance to afidopyropen in *A. gossypii*.**

Generation	Slope $\pm$ SE	LC <sub>50</sub> (mg/L) (95% CL)*	c <sup>2</sup>	df	P	RR**
G <sub>0</sub>	0.508 $\pm$ 0.049	0.391 (0.209–0.697)	2.788	3	0.426	1
G <sub>3</sub>	0.395 $\pm$ 0.046	1.117 (0.539–2.338)	1.172	3	0.76	2.857
G <sub>6</sub>	0.384 $\pm$ 0.046	2.771 (0.459–23.913)	6.164	3	0.104	7.087
G <sub>9</sub>	0.415 $\pm$ 0.047	2.935 (1.478–6.324)	4.199	3	0.421	7.506
G <sub>12</sub>	0.418 $\pm$ 0.048	5.237 (2.607–11.980)	2.569	3	0.66	13.394
G <sub>15</sub>	0.432 $\pm$ 0.049	9.480 (4.669–22.837)	1.714	3	0.634	24.246
G <sub>18</sub>	0.446 $\pm$ 0.049	9.006 (3.535–24.872)	2.286	3	0.515	23.033

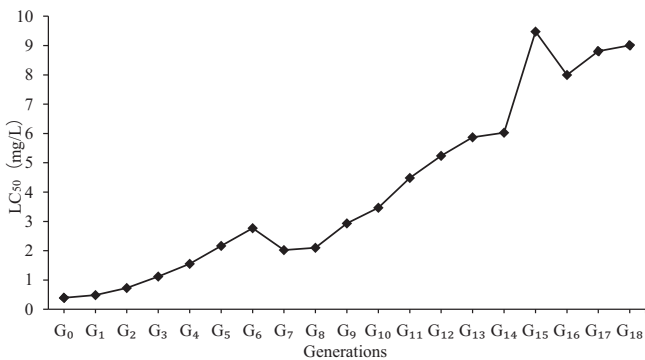
\* CL = confidence limit. For G<sub>0</sub>, the LC<sub>50</sub> data are from Wang et al. (2023). The experimental data were obtained at almost the same time.

\*\* RR = resistance ratio = LC<sub>50</sub> of the selected population/LC<sub>50</sub> of the parental population.

significance of the differences. The probability unit regression method (Probit) was used to calculate the linear equation of virulence regression and the LC<sub>50</sub> and its 95% confidence interval. Excel software was used for data processing and graphing.

## Results

**Selection for resistance to afidopyropen.** The resistance ratios and LC<sub>50</sub> values of the 18 generations of *A. gossypii* are shown in Table 1 and Fig. 1. The overall trend of the resistance ratios of G<sub>0</sub>–G<sub>15</sub> was steady growth. The most rapid growth was 10.852-fold in G<sub>12</sub>–G<sub>15</sub>, but the resistance ratios changed more slowly among other generations, and negative increases were noted for G<sub>15</sub>–G<sub>18</sub>,



**Fig. 1. Development of resistance to afidopyropen in the susceptible strain of *A. gossypii*.** For G<sub>0</sub>, the LC<sub>50</sub> data are from Wang et al. (2023). The experimental data were obtained at almost the same time.

possibly related to the production of resistant *A. gossypii* and their resulting fitness changes (Table 1). The overall LC<sub>50</sub> values of the 18 *A. gossypii* generations steadily increased (Fig. 1), with a fitted curve of  $y = 0.0212x^2 + 0.0956x + 0.3236$ ,  $R^2 = 0.953$ . From G<sub>6</sub> to G<sub>7</sub> and G<sub>15</sub> to G<sub>16</sub>, two abrupt decreases in LC<sub>50</sub> values were detected, attributed to the adaptation of *A. gossypii* to afidopyropen. During resistance selection, LC<sub>50</sub> reached a maximum of 9.480 mg/L at G<sub>15</sub>. The LC<sub>50</sub> of the resistant 18th generation was 9.006 mg/L, and the resistance level was moderate.

***h*<sup>2</sup> of *A. gossypii* to afidopyropen.** Based on the characteristics of *A. gossypii* resistance to afidopyropen, the resistance screening was divided into two stages. The resistance increased slowly in G<sub>0</sub>–G<sub>9</sub> and increased faster in G<sub>9</sub>–G<sub>18</sub> (Table 2). In the first nine generations of the selection (G<sub>0</sub>–G<sub>9</sub>),  $h^2 = 0.064$ . In the subsequent nine generations (G<sub>9</sub>–G<sub>18</sub>),  $h^2 = 0.041$ , which was not significantly different from the earlier  $h^2$  value. This result may be related to the number of generations of *A. gossypii* and its resistance stability. Some differences in  $h^2$  of resistance to insecticides have been observed at various stages of a pest resistance screening, and the higher the  $h^2$ , the faster the rate of development of resistance at that stage. In the 18 generations of resistant strains, the heritability of the resistant populations was relatively greater and the rate of development was relatively faster in the first G<sub>0</sub>–G<sub>9</sub> generations than in the subsequent generations.

**Risk assessment of *A. gossypii* resistance to afidopyropen.** The projected rate of development of resistance to afidopyropen is directly proportional to the selection intensity and  $h^2$  (Fig. 2). At 60–80% afidopyropen selection intensity, a 10-fold increase in resistance required 19.8–26.4 generations when the slope was 0.477 and  $h^2 = 0.063$ . When  $h^2 = 0.069$  and  $h^2 = 0.039$ , a 10-fold increase in resistance required 18–24 and 31.9–42.6 generations, respectively.

The projected rate of resistance evolution is inversely proportional to the slope (Fig. 3). At 60–80% afidopyropen selection intensity, a 10-fold increase in resistance required 19.8–26.4 generations when  $h^2 = 0.063$  and the slope was 0.477; when the slope was 0.577 and 0.677, a 10-fold increase in resistance required 16.4–21.8 and 13.9–18.6 generations, respectively. The results indicate that the rate of resistance development accelerated with the increase in genetic power at the same insecticide lethality, and the rate of *A. gossypii* development of afidopyropen resistance decreased with the increase in insecticide usage and application frequency under stable genetic conditions.

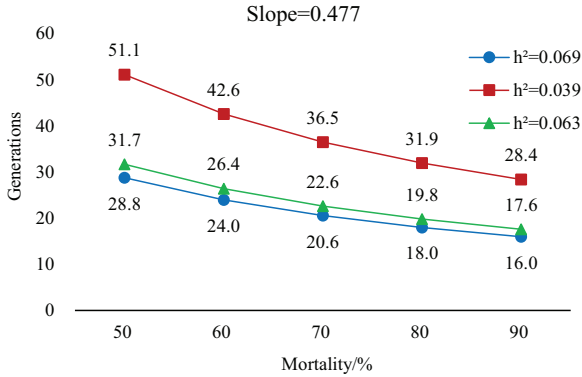
**Stability of afidopyropen resistance in resistant *A. gossypii* strains.** The resistance level of the 15th generation of the resistant cotton aphid strain had a significant decreasing trend, and the LC<sub>50</sub> values of G<sub>15</sub> for ST<sub>4</sub>-resistant strains decreased from 9.480 to 6.188 mg/L, and the resistance ratios decreased by 8.42-fold (Table 3). However, the resistance to afidopyropen was still moderate and relatively stable.

**Changes in enzyme activities of resistant and sensitive strains.** The activities of the four enzymes in the resistant (G<sub>3</sub>, G<sub>6</sub>, G<sub>9</sub>, G<sub>12</sub>, G<sub>15</sub>, and G<sub>18</sub>) and sensitive (G<sub>0</sub>) strains of *A. gossypii* were determined (Fig. 4). The CES activities of the screened resistant strains were greater than those of the sensitive strain, indicating that CES played a role in detoxification metabolism in the resistant strains; the maximum viability CES activity was 13.195 IU/L in G<sub>3</sub>. The MFO activities of most

Table 2. Realized heritability of *A. gossypii* resistance to afidopyropen.

Generation range	Estimation of response to selection*			Estimation of selection differential					$h^2$	
	Initial LC <sub>50</sub>	Final LC <sub>50</sub>	R	P**	i	Initial slope	Final slope	$\delta_p$		S
G <sub>0</sub> -G <sub>3</sub>	0.391	1.117	0.152	56.669	0.689	0.508	0.395	2.215	1.527	0.100
G <sub>3</sub> -G <sub>6</sub>	1.117	2.771	0.132	63.16	0.590	0.395	0.384	2.567	1.516	0.087
G <sub>6</sub> -G <sub>9</sub>	2.771	2.935	0.008	65.454	0.557	0.384	0.415	2.503	1.393	0.006
G <sub>9</sub> -G <sub>12</sub>	2.935	5.237	0.084	62.418	0.601	0.415	0.418	2.401	1.444	0.058
G <sub>12</sub> -G <sub>15</sub>	5.237	9.48	0.086	63.259	0.589	0.418	0.432	2.353	1.386	0.062
G <sub>15</sub> -G <sub>18</sub>	9.48	9.006	-0.007	65.682	0.553	0.432	0.446	2.278	1.261	-0.006
G <sub>0</sub> -G <sub>10</sub>	0.391	3.467	0.095	60.563	0.629	0.508	0.415	2.167	1.364	0.069
G <sub>10</sub> -G <sub>18</sub>	3.467	9.006	0.052	64.563	0.570	0.415	0.446	2.323	1.323	0.039
G <sub>0</sub> -G <sub>18</sub>	0.391	9.006	0.076	64.451	0.571	0.508	0.446	2.096	1.198	0.063

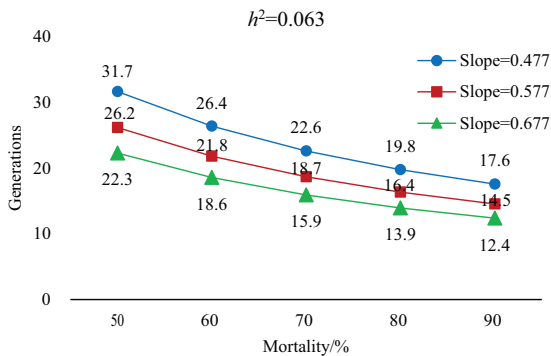
\* P = mean percent chance of surviving selection. For G<sub>0</sub>, the LC<sub>50</sub> data are from Wang et al. (2023). The experimental data were obtained at almost the same time.



**Fig. 2. Effect of realized heritability ( $h^2$ ) on the number of generations of *A. gossypii* required for a 10-fold increase in the  $LC_{50}$  of afidopyropen (slope = 0.477) at different selection intensities ( $i$ ).**

of the screened resistant strains were greater than those of the sensitive strain, indicating that MFO played a role in detoxification metabolism in the resistant strains; the maximum viability MFO activity was 136.169 IU/L in  $G_{12}$ . With the increase in the number of selected generations, the resistance of *A. gossypii* to afidopyropen increased and the viability of GSTs also increased; the role of GSTs in detoxification metabolism was the strongest in  $G_{18}$ . AChE activity did not differ significantly among the resistant and sensitive strains, and AChE did not play a substantial role in the development of resistance to afidopyropen in *A. gossypii*.

**Correlation of resistance level with enzyme activity.** The correlation of the level of resistance with detoxification enzyme activity in *A. gossypii* was analyzed, and the  $LC_{50}$  values revealed a highly significant positive correlation with the activity of GSTs, with a correlation coefficient of 0.959; a positive but not a



**Fig. 3. Effect of realized heritability ( $h^2$ ) on the number of generations of *A. gossypii* required for a 10-fold increase in the  $LC_{50}$  of afidopyropen ( $h^2 = 0.063$ ) at different selection intensities ( $i$ ).**



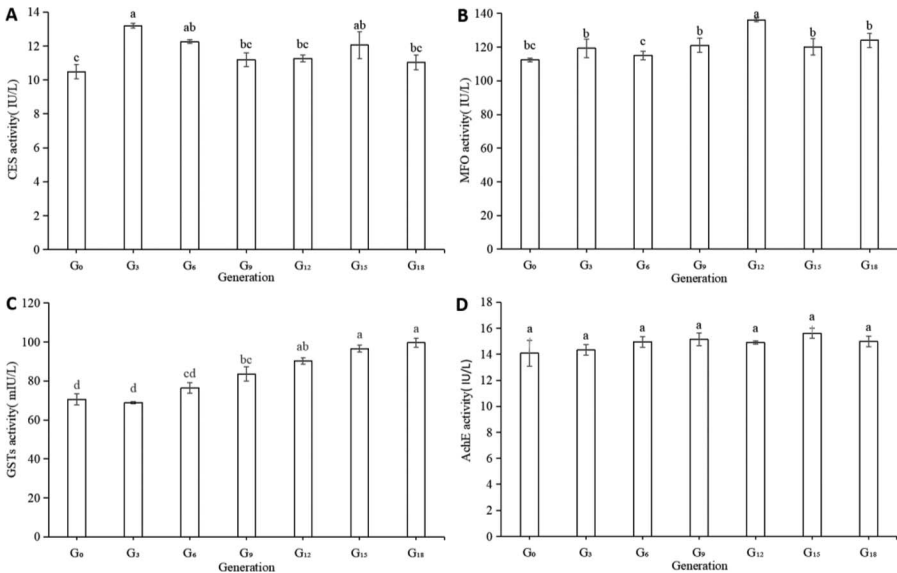
**Table 3. Resistance stability of *A. gossypii* without afidopyropen.**

Generation	Slope $\pm$ SE	LC <sub>50</sub> (mg/L) (95% CL)*	$\chi^2$	df	P	RR**
G <sub>15</sub>	0.432 $\pm$ 0.049	9.480 (4.669–22.837)	1.714	3	0.634	24.246
ST <sub>1</sub>	0.322 $\pm$ 0.045	8.815 (3.542–29.873)	1.340	3	0.720	22.545
ST <sub>2</sub>	0.384 $\pm$ 0.046	8.477 (2.892–30.116)	1.840	3	0.606	21.680
ST <sub>3</sub>	0.362 $\pm$ 0.046	8.055 (3.567–24.591)	1.880	3	0.741	20.601
ST <sub>4</sub>	0.373 $\pm$ 0.049	7.550 (3.417–20.554)	1.251	3	0.511	19.309
ST <sub>5</sub>	0.420 $\pm$ 0.048	6.188 (3.065–14.440)	0.792	3	0.851	15.826

\* CL = confidence limit.

\*\* Resistance ratio = LC<sub>50</sub> of the selected population/LC<sub>50</sub> of the parental population.

significant correlation with MFO and AChE; and a nonsignificant negative correlation with CES (Table 4). Thus, changes in the viability of GSTs were closely related to changes in the resistance of *A. gossypii* to afidopyropen, and GSTs may play an important role in the development of *A. gossypii* resistance to afidopyropen.



**Fig. 4. Detoxifying enzyme and target enzyme activity in strains of *A. gossypii*.** Bars indicate the mean  $\pm$  SE ( $P < 0.05$ ). Bars with different letters indicate significant differences between enzyme activities. For G<sub>0</sub>, the enzyme activities are from Wang et al. (2023). The experimental data were obtained at almost the same time.

**Table 4. Correlation between resistance level and enzyme activity in strains of *A. gossypii*.**

Item	LC <sub>50</sub>	CES Activity	MFO Activity	GST Activity	AChE Activity
LC <sub>50</sub>	1.000				
CES activity	-0.089	1.000			
MFO activity	0.417	-0.199	1.000		
GST activity	0.959**	-0.282	0.547	1.000	
AChE activity	0.605	0.173	-0.243	0.525	1.000

\* The LC<sub>50</sub> data and activities of each enzyme are from Wang et al. (2023). The experimental data were obtained at almost the same time.

\*\*  $P < 0.01$ .

## Discussion

Long-term use of a specific insecticide results in resistance selection pressure on pests, leading to the development of resistance. Usually, laboratory-based resistance selection is used to determine the growth rate and resistance risk of targeted pests. Our results indicate that *A. gossypii* subjected to afidopyropen resistance selection for 18 generations exhibited a 23-fold increase in resistance. In a previous study (Muhammad et al. 2017), *P. solenopsis* underwent resistance selection for afidopyropen for 23 generations and exhibited a 26,652-fold rapid increase in resistance. Wang et al. (2021) reported that when *A. gossypii* was selected for resistance to afidopyropen for 20 generations, the resistance multiplicity increased 40-fold. We observed that the resistance of *A. gossypii* to afidopyropen increased slowly at the beginning of the resistance selection process ( $G_0$ – $G_4$ ) and that the resistance ploidy increased 4.0-fold, which may be related to the low number of selection generations and low selection pressure of *A. gossypii* to afidopyropen. With the increase in the number of selections and the selection pressure, the resistance of *A. gossypii* to afidopyropen developed faster and the resistance ploidy increased from 15.4-fold to 23.0-fold from  $G_{14}$  to  $G_{18}$ , indicating the increased adaptability of *A. gossypii* to afidopyropen.

Higher  $h^2$  indicates a higher risk of resistance in the next generation, with a positive correlation of  $h^2$  with risk of resistance (Zhao et al. 2022). An  $h^2$  value of 0.1325 was obtained when 10 generations of *Spodoptera litura* (F.) was selected for indoxacarb resistance (Wang et al. 2008). When *A. gossypii* was selected for sulfoxaflor resistance for 25 generations, its resistance increased 13.44-fold. The  $h^2$  value was 0.0304 for generations  $G_0$ – $G_{15}$  of sulfoxaflor-resistant lines, which had a low risk of resistance, and was 0.1484 for  $G_{15}$ – $G_{25}$  (An et al. 2020). In our study,  $h^2$  was 0.069 in  $G_0$ – $G_{10}$ , and the risk of resistance was relatively higher and rate of resistance development in the early generations was faster; whereas,  $h^2$  was 0.039 in the  $G_{10}$ – $G_{18}$  generations and the risk of resistance was relatively low. The results of this study are consistent with the findings of Roy et al. (2023), Afzal et al. (2018), and Ijaz et al. (2016) and in contrast with the findings of

Mudassir and Ali (2022) and An et al. (2020). After 18 generations of selection for fluxametamide resistance in *P. xylostella*, a 10-fold increase in resistance required 27–40 generations when the mortality rate was 60–80% (Roy et al. 2023). A 10-generation selection for resistance to indoxacarb in *S. litura* predicted that 8–10 generations were required for a 100-fold increase in resistance at 80–90% selection intensity (Wang et al. 2008), with a very high risk of resistance. In our study, at 60–80% selection pressure, a 10-fold increase in the resistance of *A. gossypii* to afidopyropen required 19.8–26.4 generations (slope = 0.447,  $h^2 = 0.063$ ), with little risk of resistance. Therefore, we postulate that  $h^2$  of the 18th generation of afidopyropen-resistant *A. gossypii* is not high; however, under selection pressure, the multiplicity of resistant *A. gossypii* gradually accelerates, and field pest management should avoid the use of a single insecticide and mass application of insecticides.

When an insecticide ceases to act on a pest population, the proportion of resistant individuals in the population gradually decreases over time, showing an overall decreasing level of resistance. The rate of decline in population resistance is expressed in terms of resistance stability (Wang and Han 2010, Yan and Wang 2020). *Laodelphax striatellus* resistant to triflumezopyrim was screened up to the 16th generation, and 5 successive generations were then reared without exposure to the insecticide. The resistance multiplicity decreased by 2.04 times; therefore, *L. striatellus* is stable in its resistance to triflumezopyrim, which poses some difficulties for resistance management (Zhang et al. 2022b). The resistance of *O. hyalinipennis* to chlorfenapyr was screened up to the seventh generation, then rearing with the insecticide was stopped for five generations. The resistance ratios decreased by 81.98 times, and the resistance level was extremely unstable (Saif and Sarfraz 2017). The resistance of *S. litura* to spinosad was screened up to the 12th generation. Rearing with spinosad was then stopped for four generations, with a 259.5-fold decrease in resistance ratios and a highly unstable resistance level (Adeel and Shoaib 2014). In our study, after culling the resistant lines for 15 consecutive generations, the resistance ratios decreased 8.42-fold when rearing with afidopyropen was stopped for 5 generations. The level of resistance decreased rapidly, indicating that *A. gossypii* resistance to afidopyropen is somewhat unstable in the absence of selection pressure. This finding is important for afidopyropen resistance management, but the level of resistance also did not decrease from the midlevel resistance stage to the low-level resistance stage. Therefore, when *A. gossypii* develops some resistance to afidopyropen, attention must be directed to the management of *A. gossypii* in the field.

Detoxification metabolic enzymes have developed as a result of long-term adaptation of insects to the external environment (Wen 2021). Esterases (ESTs) can reduce the effective concentration of toxic substances (Coppin et al. 2012). MFO plays an important role in the oxidative metabolism of insecticides (Wei and Tang 1999). P450 is an important component of MFO and has an important function in oxidative metabolism (Zhang et al. 2002). GSTs protect insects from nucleophiles and ensure normal organismal metabolism (Enayati et al. 2005). For example, the biochemical mechanism of CES is important for the resistance detoxification of deltamethrin in *H. armigera* and of imidacloprid in *Rhopalosiphum padi* (L.) (El-Latif and Subrahmanyam 2010; Zhang 2016). CES and CYP450 belong to

an important enzyme pathway, with CES involved in the detoxification metabolism of thiamethoxam and sulfoxaflor in *A. gossypii* (Ma et al. 2019, 2021b). Many studies have shown that CES is a key detoxification enzyme for neonicotinoids and organophosphorus insecticides in *A. gossypii* (Cui et al. 2010, Guo et al. 2014, Li 2015). MFOs are important enzymes and are involved in *H. armigera* metabolism of fenvalerate, *Empoasca pirusuga* (Goethe) metabolism of thiamethoxam, and *Nilaparvata lugens* (Stål) metabolism of pymetrozine (Mu and Wang 1989, Wang et al. 2021, Zhang 2019). The results of previous studies have shown that P450s are important enzymes in *B. tabaci* resistant to afidopyropen (Wang et al. 2022b). In our study, we determined changes in the metabolic enzyme activities of moderately resistant *A. gossypii* strains and found that GSTs increased with the number of selection generations, and all resistant strains were significantly different from the control. GSTs are important for the resistance of *P. xylostella* to chlorantraniliprole, *Sitobion avenae* (F.) to pirimicarb, and *Spodoptera frugiperda* (J.E. Smith) to metabolized indoxacarb (Hu 2017, Wang et al. 2020, Wu et al. 2020). Therefore, GSTs may play an important role in the resistance of *A. gossypii* to afidopyropen.

Elevated levels of pest resistance to insecticides have been correlated with increased enzyme activity (Armstrong and Suckling 1990). A positive correlation was observed between MFO activity and fenvalerate resistance ( $r = 0.98$ ) and between EST and fenvalerate resistance ( $r = 0.97$ ) by screening fenvalerate-resistant populations of *S. litura* (Cheema et al. 2020). The resistance level of *Oedaleus asiaticus* Bey-Bienko to the highly effective beta-cypermethrin in the field was highly significantly correlated ( $r = 0.932$ ) with CES activity (Gao et al. 2022). The resistance level of *Myzus persicae* (Sulzer) to acetamiprid in the field was significantly positively correlated ( $r = 0.998$ ) with AChE activity (Cai et al. 2021). A correlation analysis of the  $LC_{50}$  with the enzyme lineage of resistant strains revealed a highly significant positive correlation between GSTs and  $LC_{50}$  ( $P < 0.01$ ), indicating the importance of GSTs in the development of resistance to afidopyropen in *A. gossypii*; however, further confirmation of this finding is needed.

Overall, our study revealed the risk of resistance and changes in the enzyme activities of *A. gossypii* resistant to afidopyropen. We screened afidopyropen-resistant *A. gossypii* strains to provide a theoretical basis for predicting the risk of *A. gossypii* becoming resistant to afidopyropen in the field. The relative stability of resistance was clarified in the  $G_{15}$  strains. Field management is necessary for rational use of afidopyropen, and it should be used for years. During the screening of *A. gossypii* for resistance to afidopyropen, a key enzyme line (GSTs) was identified, which is very different from the key enzyme lines for resistance to afidopyropen in the field previously reported by us and may be related to the different types of insecticides used in the field for long periods of time (Wang et al. 2023). Our study provides a theoretical reference for the development of resistance mechanisms and adaptations by *A. gossypii* to afidopyropen and reveals the resistance mechanism of *A. gossypii* to afidopyropen at the physiological level.

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discussion of the results. All authors read and approved the final version of the manuscript. The authors declare that they have no known competing financial interests or personal relationships that could have influenced their contributions to this study and the results reported herein.

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