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Host-Plant Switching Impacts Susceptibility and Biochemical Responses of *Cnaphalocrocis medinalis* to Abamectin and Chlorpyrifos

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Abstract: Insect tolerance to insecticides is closely related to the host plant. Migratory insects flying downwind and landing randomly may face host-plant switching after migration. However, it is not clear whether host-plant switching affects the tolerance of migratory insects to insecticides. In the present work, *Cnaphalocrocis medinalis*, a migratory pest destructive to rice, was studied to explore this issue. The results show that the host-plant switch reduced the susceptibility of rice and wheat larvae populations to abamectin but increased that of wheat larvae populations to chlorpyrifos, indicating that host switching resulted in different tolerance to different insecticides. Enzyme activity determination showed that, although abamectin and chlorpyrifos affect the activities of detoxification enzymes (carboxylesterase, multifunctional oxidase, and glutathione *S*-transferases), antioxidant enzymes (superoxide dismutase, peroxidase, and catalase), and acetylcholinesterase at sublethal dosages, the effect depends on the host plant and insecticide species. Overall, our findings show that the induction of *C. medinalis* by host switching affects its susceptibility and biochemical responses to abamectin and chlorpyrifos. Insecticides against *C. medinalis* should be used with consideration of the potential impact of host switching. Reasonable selection and usages of insecticides can help in the resistance management and control of migratory insects.

Keywords: *Cnaphalocrocis medinalis*; host-plant switching; insecticide susceptibility; detoxification enzyme; antioxidant enzyme; acetylcholinesterase

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1. Introduction

In the course of long-term synergistic evolution, plants have developed a set of resistance defense mechanisms in complex interactions with herbivorous insects [1,2]. The composition and induction of direct and indirect defenses in host plants can influence various physiological and behavioral traits in herbivorous insects to which they must adapt [3]. In particular, host plants can resist insect infestation through a range of chemical defense responses, such as the production of toxic secondary metabolites or defense proteins [4]. In response to these host-plant defense mechanisms, herbivorous insects have simultaneously developed a series of strategies to overcome them [3], including changes in the activity and structure of various detoxification enzymes [5,6]. However, adaptation to host plants

can be achieved through a variety of mechanisms, such as by increasing detoxification enzyme metabolism and altering detoxification enzyme activity, allowing insects to develop adaptive mechanisms, such as poison avoidance and detoxification, thereby making the insect more tolerant to insecticides [7,8]. Many studies have demonstrated that host plants affect the susceptibility of many arthropods to insecticides, including Lepidoptera, Coleoptera, Orthoptera, and spider mites [9–11]. For example, *Spodoptera litura* (Fabricius) larvae become more tolerant to insecticides, especially phoxim and emamectin benzoate, after feeding on tobacco or being administered nicotine [12]. *Leptinotarsa decemlineata* (Say) larvae fed on different host plants showed significantly different responses to pyrethroid insecticides [13]. Among the many mechanisms underlying these differences in susceptibility to different insecticides are changes in the induced detoxification enzymes of different host plants.

The rice leaf folder, *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae), is one of the most destructive pests in rice. Their larvae spit silk and roll up rice leaves to feed on the leaf flesh, affecting photosynthesis in rice and causing extensive yield reduction and even crop failure [14]. Various management tools are available in response to Lepidoptera pests in rice or other plants, including natural enemy insects, insecticides, and Bt rice [9–11]. As a migratory insect, *C. medinalis* flies long distances in Southeast Asia several times a year, and it usually migrates downwind and lands randomly [15,16], which means that it faces host switching after migration. *C. medinalis* larvae can infest host plants, such as rice and wheat plants [17,18]. Long-distance migration may make the host plants of *C. medinalis* switch between rice and wheat. Although rice and wheat are both cereal crops, they have different defenses against insects [19,20], which usually results in differences in the susceptibility of insects feeding on rice and wheat to insecticides. Changes in insecticide susceptibility and activities of detoxifying enzymes and target enzymes after feeding on rice and wheat have been found in *Laodelphax striatellus* (Fallén) and *Oxya chinensis* (Thunberg) [21,22]. Although migration is a key factor in the widespread outbreak of *C. medinalis*, their occurrence is also closely related to their selectivity and adaptability to host plants [23]. The survival rate of long-term wheat-feeding *C. medinalis* populations was found to be significantly reduced after selecting rice as a host, indicating that host-plant switching affects the population fitness of *C. medinalis* [24]. The effect of host-plant switching on the adaptability of larvae may change their insecticide susceptibility. However, it is unclear whether host-plant switching of *C. medinalis* larvae feeding on wheat and rice populations affects their insecticide susceptibility.

In this study, an investigation of the relationship of the toxicities of abamectin and chlorpyrifos to *C. medinalis* larvae in rice and wheat populations with host-plant switching was conducted, as well as the activities of carboxylesterase (CarE), multifunctional oxidase (MFO), glutathione *S*-transferases (GSTs), superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and acetylcholinesterase (AChE) (Figure 1). Our results contribute to deepening understanding of the relationship between the susceptibility of *C. medinalis* larvae to insecticides and their host plants, further clarifying the role of host adaptation of pests in the formation of insecticide resistance and providing a theoretical basis for the formulation of pest-control strategies.

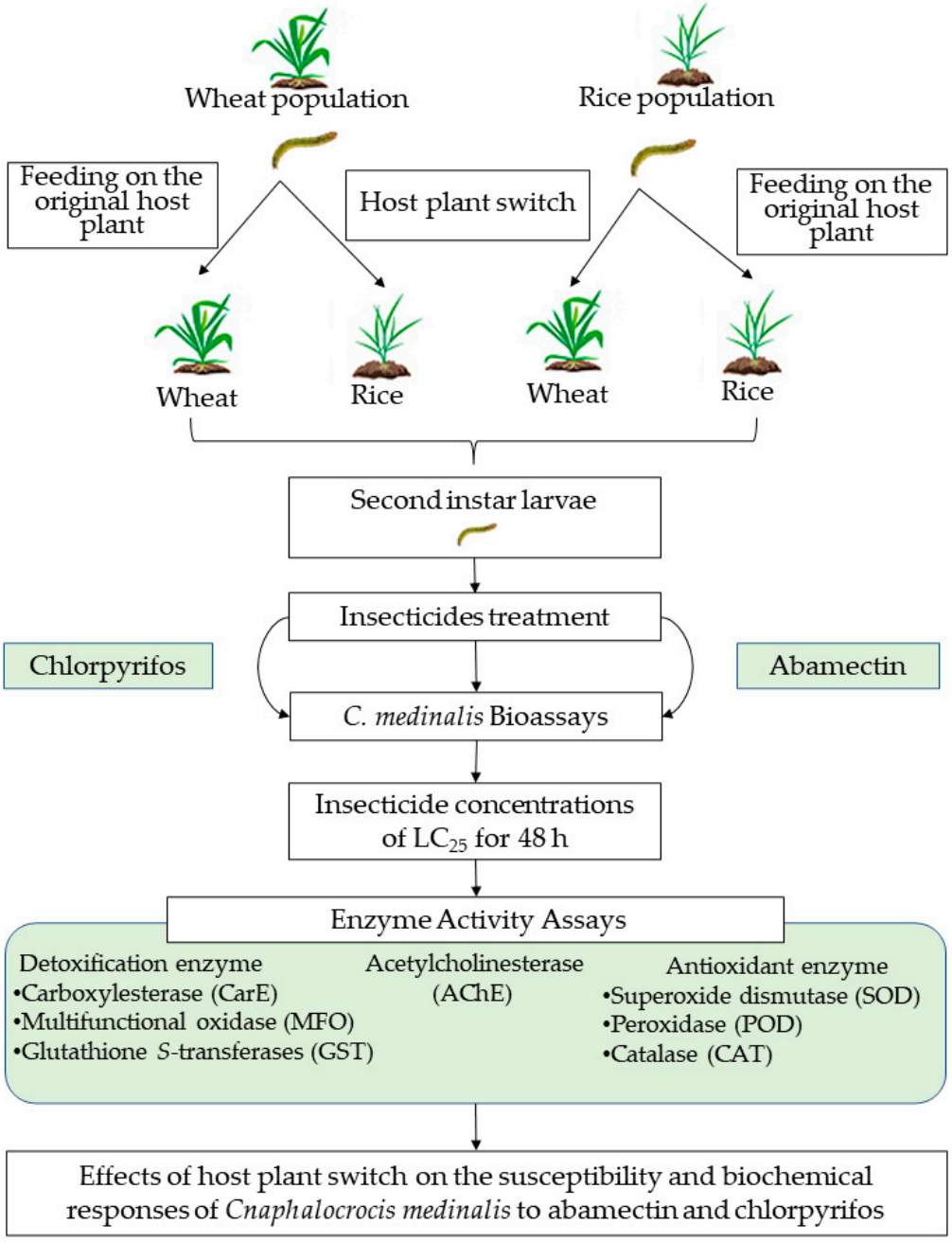

Figure 1. Graphical demonstration of the experimental setups.

2. Materials and Methods

2.1. Plant Preparation and Insect Rearing

The two host populations of *C. medinalis* used in this study were a wheat-reared population and a rice-reared population: (1) Wheat-reared population (wheat population): the larvae of this population were captured from a rice field in Nanjing, Jiangsu Province (118.78° E, 32.06° N), in 2019, and reared for more than 20 generations on wheat seedlings in an artificial climate chamber (Ningbo Jiangnan Instrument Factory, Ningbo, China) [25]. The wheat variety used for the experiment was Zhefeng 2 (Zhejiang Nongke Seed Co., Ltd., Hangzhou, China). Wheat seeds were soaked for 24 h and germinated for 24 h, then sown in 350 mL disposable plastic cups with holes punched in the bottom and incubated in an artificial climate chamber. Wheat seedlings were used to feed the larvae when they reached 10 cm in length. (2) Rice-reared population (rice population): The larvae of this population were captured from a rice field in Xiaoshan District, Hangzhou City, Zhejiang

Province (120.22° E, 30.04° N), in 2021, and reared with rice seedlings for more than 10 generations in an artificial climate chamber [26]. The rice variety used for the experiment was TN1, as it is a variety sensitive to *C. medinalis*. Rice seeds were soaked for 24 h and germinated for 48 h, then planted in a greenhouse at the Zhejiang Academy of Agricultural Sciences, Hangzhou, China (30.31° N, 120.20° E), and used to feed the larvae 45 days after germination. All host plants were free from any pests and pesticide treatments. Adult *C. medinalis* were placed in 500 mL plastic cups, the bottom of which was pre-filled with cotton moistened with 5% honey solution. The top of the cups was covered with plastic film for oviposition. All test insects and host plants were reared at 26 ± 0.5 °C, with a relative humidity of 80–90% and a photoperiod of 14 L:10 D. Unless otherwise stated, temperature, humidity, and light conditions for the following experiments were the same as for the rearing conditions.

2.2. Host-Plant Switch Treatments

Eggs from rice and wheat populations of *C. medinalis* were collected and placed on rice and wheat, respectively, for the host-plant switch treatments. Four treatments were set up: (1) R-R: rice populations feeding on rice; (2) R-W: rice populations feeding on wheat; (3) W-R: wheat populations feeding on rice; and (4) W-W: wheat populations feeding on wheat. All host plants and larvae were reared in rearing cages (50 cm × 50 cm × 50 cm). The host plants were changed regularly to maintain adequate food. The larvae were observed daily for development and were used for subsequent experiments until they reached the 2nd instar.

2.3. Insecticides and C. medinalis Bioassays

C. medinalis susceptibility to abamectin and chlorpyrifos was evaluated for different host-plant switch treatments (R-R, R-W, W-R, and W-W). The two insecticides belong to the two main chemical groups currently applied for *C. medinalis* control [26–28]. Abamectin and chlorpyrifos belong to the 16-membered macrocyclic lipid insecticides and organophosphorous insecticides, respectively [29–32]. The two formulated insecticides used in the bioassay were 98% abamectin (Hebei Weiyuan Biological Chemical Co., Ltd., Shijiazhuang, China) and 98% chlorpyrifos (Shandong Huayang Chemical Co., Ltd., Taian, China).

A stock solution of 1000 mg/L of each insecticide was created by dissolution in acetone, and working solutions were generated by dilution with distilled water. Seven concentrations of each of the two insecticides (abamectin: 0.2, 0.1, 0.05, 0.025, 0.0125, 0.006, and 0.003 mg/L; chlorpyrifos: 10, 5, 2.5, 1.25, 0.625, 0.313, and 0.156 mg/L) were then applied to determine the sublethal concentrations (LC_{25}s), in accordance with previous studies [26]. *Cnaphalocrocis medinalis* bioassays were carried out by leaf dipping, as described in a previous study [33]. The effect of the insecticide on *C. medinalis* larvae from different host-plant switch treatments was recorded. Rice or wheat leaves (about 10 cm) were soaked in the insecticide solution for 30 s. The leaves were then dried and wrapped in moistened absorbent cotton and placed in a Petri dish lined with filter paper at the bottom. Fifteen second-instar larvae from the host-plant switch treatments (starvation for 2 h) were selected at random and transferred to Petri dishes containing treated rice or wheat leaves, with three replications per concentration of each insecticide. After 48 h of treatment, the mortality of the larvae was recorded. Solvent-solution controls were used for all treatments. Each bioassay was performed with three biological replications.

2.4. Enzyme Activity Assays

The activities of seven enzymes—CarE, MFO, GSTs, SOD, POD, CAT, and AChE—were measured to analyze the biochemical responses of *C. medinalis* larvae to host-plant switching and insecticide treatment. The second-instar larvae of *C. medinalis* treated with insecticide concentrations of LC_{25} for 48 h and untreated with different host-plant switch treatment groups were taken. Twenty larvae from different treatments were used to prepare crude homogenates as an enzyme source and homogenized with 200 µL of extract in an

ice bath. The homogenate was centrifuged at 12,000 rpm for 10 min at 4 °C (Micro 17R, Thermo Fisher Scientific Inc., Karlsruhe, Germany) to separate the supernatant. A total of 3 replicates were performed for each treatment. According to the kit instructions, the absorbance was determined using a microplate reader (TU-1900, Beijing Purkinje General Instrument Co., Ltd., Beijing, China). The enzyme activity was determined according to the protein content using a kit (Jiangsu Addison Biotechnology Co., Yancheng, China) and measured with a microplate reader (SpectraMax 190, Molecular Devices, LLC., San Jose, CA, USA).

2.4.1. CarE

A volume of 10 μL of the sample to be tested was combined with 300 μL of reagent I. Then, 160 μL of reagent II was added to the assay sample, and 160 μL of distilled water was added to the control sample. Immediately after the addition of reagent II/distilled water, the timer was started, and the absorbance value was read at 450 nm after 3 min of accurate reaction at room temperature. The specific formula is as follows:

$$\text{Enzyme activity of CarE } (\Delta_{450}/\text{min/mg prot}) = (\text{absorption value of measured sample} - \text{absorption value of control sample}) \div (\text{protein concentration} \times \text{sample volume}) \div \text{reaction time} \times \text{dilution times} \quad (1)$$

2.4.2. MFO

Volumes of 10 μL of reagent I, 60 μL of reagent II, and 20 μL of reagent III were added to 50 μL of sample. The mixed solution was used to measure the absorbance value at 405 nm ($A_{405}1$), and the absorbance value was measured again after incubation at 37 °C for 30 min ($A_{405}2$). The enzyme activity of MFO was calculated using the protein concentration of the sample. The specific formula is as follows:

$$\text{Enzyme activity of MFO } (\text{nmol/min/mg prot}) = [(A_{405}2 - A_{405}1 + 0.0005) \div 1.7082 \times 10^3 \times \text{volume of extraction solution}] \div (\text{protein concentration} \times \text{sample volume}) \div \text{reaction time} \quad (2)$$

2.4.3. GSTs

A volume of 190 μL of reaction solution was added to 10 μL of sample fully mixed. The absorbance value (A1) was read at 340 nm immediately, then again five minutes later. The specific formula is as follows:

$$\text{Enzyme activity of GSTs } (\text{nmol/min/mg prot}) = [(A_{340}1 - A_{340}2) \div \text{product molar extinction coefficient} \div \text{96 well plate optical diameter} \times \text{total volume of reaction system} \times 10^9] \div (\text{protein concentration} \times \text{sample volume}) \div \text{reaction time} \quad (3)$$

2.4.4. AChE

Volumes of 10 μL of reagent I and 160 μL of reagent II were added to 20 μL of sample solution and mixed well, then incubated in a water bath at 30 °C for 15 min. Subsequently, 10 μL of reagent III was added to the solution and mixed well. Then, the absorbance value was read immediately at 412 nm. In the control group, instead of adding 10 μL of reagent I, 10 μL of reagent II was added (i.e., 170 μL of reagent II), and the other sample amounts of the added kits were the same. The specific formula is as follows:

$$\text{Enzyme activity of AChE } (\text{nmol/min/mg prot}) = [(\text{absorption value of measured sample} - \text{absorption value of control sample}) \div \text{molar extinction coefficient of 5} - \text{mercapto} - \text{nitrobenzoic acid} \div \text{96 well plate optical diameter} \times \text{total volume of reaction system} \times 10^9] \div (\text{protein concentration} \times \text{sample volume}) \div \text{reaction time} \quad (4)$$

2.4.5. SOD

Each treatment was added to a 96-well plate, as described in Table 1. The solutions were mixed well and allowed to stand for 30 min at 25 °C, protected from light, and the

absorbance values were measured at 450 nm. The percentage of inhibition was calculated based on the different absorbance values; then, the percentage of inhibition was used to calculate the enzymatic activity of SOD. The specific formulae are as follows:

$$\text{Percentage of inhibition} = \left[\left(A_{\text{blank control group 1}} - A_{\text{blank control group 2}}\right) - \left(A_{\text{Sample group}} - A_{\text{Sample control group}}\right)\right] \times 100\% \quad (5)$$

$$\text{Enzyme activity of SOD (nmol/min/mg prot)} = [\text{percentage of inhibition} \div (1 - \text{percentage of inhibition}) \times \text{total volume of reaction system}] \div (\text{protein concentration} \times \text{sample volume}) \times \text{dilution times} \quad (6)$$

Table 1. Content of each reagent during the determination of SOD activity.

Reagent Name (μL)	Sample Group	Sample Control Group	Blank Control Group 1	Blank Control Group 2
Reagent I	70	70	70	70
Reagent II	20	0	20	0
Distilled water	0	20	20	40
Sample	20	20	0	0
Reagent III	10	10	10	10
Reagent IV	80	80	80	80

2.4.6. POD

Volumes of 40 μL of reagent I, 140 μL of reagent II, and 10 μL of reagent III were added to 10 μL of sample. Immediately after mixing the solutions, the absorbance value was read at 470 nm ($A_{470}1$), then again 1 min later ($A_{470}2$). The specific formula is as follows:

$$\text{Enzyme activity of POD (nmol/min/mg prot)} = (A_{470}2 - A_{470}1) \div (\text{protein concentration} \times \text{sample volume}) \div \text{reaction time} \quad (7)$$

2.4.7. CAT

The CAT enzyme activity assay for each treatment was divided into a blank group and an assay group: (i) blank group: 80 μL of reagent I, 20 μL of reagent II, and 100 μL of reagent III were mixed; (ii) assay group: 70 μL of reagent I and 20 μL of reagent II were added to 10 μL of sample, and the reaction was carried out at 25 °C for 5 min. Subsequently, 100 μL of reagent III was added to the solution. In each treatment, 10 μL of the blank group and 10 μL of the mixed solution of the assay group were taken separately; then, 900 μL of reagent I and 290 μL of reagent IV were added. After the reaction at 25 °C for 5 min, the absorbance value was measured at 510 nm. The specific formula is as follows:

$$\text{Enzyme activity of CAT (nmol/min/mg prot)} = \left[\left(A_{\text{blank control group}} - A_{\text{assay group}} + 0.0137\right) \div 0.1412\right] \div (\text{protein concentration} \times \text{sample volume}) \div \text{reaction time} \quad (8)$$

2.5. Statistical Analysis

Data were tested for normal distribution and variance homogeneity before analysis using the Shapiro–Wilk and Levene tests. Data that did not fit a normal distribution were transformed before performing analysis of variance (ANOVA). Data that still did not conform to the normal distribution after conversion were analyzed by nonparametric tests. The chi-square test was used to analyze mortality ($p < 0.05$). Estimations of the probit parameter of the concentration mortality response of *C. medinalis* populations were calculated using the Polo Plus program (LeOra Software 2002). Regression analysis was used to fit the relationship between mortality and insecticide concentration to obtain the virulence regression equation and to calculate the LC_{25}, 95% confidence interval, and relative toxicity. LC_{50} values for a specific insecticide against *C. medinalis* larvae feeding on the same host and with host switching were considered significantly different ($p < 0.05$)

if their 95% fiducial limits did not overlap [10]. A two-way ANOVA was used to analyze enzyme activity; host-plant switch treatment (R-R, R-W, W-R, and W-W) and insecticide treatment (control, abamectin, and chlorpyrifos) plus their interactions were used as factors, and then Tukey's honestly significant difference tests or *t*-tests were used to separate the means. Statistical analyses were all performed using IBM SPSS Statistics software (v. 21, SPSS Inc.).

3. Results

3.1. Insecticide Susceptibility of Larvae from Different Host-Plant Switch Treatments

The effects of the two insecticides on the mortality of *C. medinalis* larvae differed due to the use of different host-plant switch treatments at the same concentration (Figure 2). Without insecticide treatment, the mortality of larvae of the rice population after feeding on wheat was significantly reduced (χ^2 = 5.404, df = 1, p = 0.020), and after chlorpyrifos treatment, the host-plant switch significantly reduced the larval mortality (0.003 mg/L: χ^2 = 2.045, df = 1, p = 0.153; 0.006 mg/L: χ^2 = 1.800, df = 1, p = 0.180; 0.0125 mg/L: χ^2 = 3.025, df = 1, p = 0.082; 0.025 mg/L: χ^2 = 0.401, df = 1, p = 0.527; 0.05 mg/L: χ^2 = 0.045, df = 1, p = 0.832; 0.1 mg/L: χ^2 = 0.431, df = 1, p = 0.512; 0.2 mg/L: χ^2 = 1.323, df = 1, p = 0.250), except for the concentrations of 0.313 (χ^2 = 2.493, df = 1, p = 0.114) and 10 mg/L (χ^2 = 1.746, df = 1, p = 0.186) (Figure 2). However, there was no significant difference in the mortality of the larvae of the rice population treated with abamectin, regardless of whether they changed host plants or not (0.156 mg/L: χ^2 = 5.184, df = 1, p = 0.023; 0.625 mg/L: χ^2 = 5.657, df = 1, p = 0.017; 1.25 mg/L: χ^2 = 6.480, df = 1, p = 0.011; 2.5 mg/L: χ^2 = 10.020, df = 1, p = 0.002; 5 mg/L: χ^2 = 4.464, df = 1, p = 0.035) (Figure 2). The experimental results for the wheat-population larvae were quite different. Without insecticide treatment, there was no significant difference in the mortality of larvae in the R-W treatment group (χ^2 = 2.000, df = 1, p = 0.157) (Figure 2). However, after treatment with abamectin at concentrations lower than 0.0125 mg/L (0.003 mg/L: χ^2 = 4.865, df = 1, p = 0.027; 0.006 mg/L: χ^2 = 6.480, df = 1, p = 0.011; 0.0125 mg/L: χ^2 = 4.444, df = 1, p = 0.035) and higher than 0.2 mg/L (χ^2 = 10.326, df = 1, p = 0.001), the mortality of the W-R treatment group was significantly higher than that of the W-W treatment group (Figure 2). Nonetheless, after chlorpyrifos treatment at concentrations above 1.25 mg/L, the mortality of the W-R treatment group was significantly lower than that of the W-W treatment group (1.25 mg/L: χ^2 = 5.378, df = 1, p = 0.020; 2.5 mg/L: χ^2 = 10.519, df = 1, p = 0.001; 5 mg/L: χ^2 = 4.486, df = 1, p = 0.034; 10 mg/L: χ^2 = 10.000, df = 1, p = 0.002) (Figure 2).

The LC_{50} values for abamectin and chlorpyrifos for the larvae of the R-W treatment group were higher than those of the R-R treatment group (Table 2). However, the host-plant switch had a significant effect on the susceptibility of the rice-population larvae to chlorpyrifos but no effect with respect to abamectin (Table 2). Notably, the susceptibility of the larvae of the wheat population to abamectin and chlorpyrifos differed from that of the rice population after the transformation of the host plants. The LC_{50} values for the R-W treatment group for abamectin were lower than those for the R-R treatment group (Table 2). On the contrary, the LC_{50} value for the larvae of the wheat population for chlorpyrifos after feeding on rice was 2.29 times higher than that for the original host (Table 2).

The results reported above indicate that host-plant switching affects the tolerance of *C. medinalis* larvae to abamectin and chlorpyrifos. The effect of host-plant switching on the susceptibility of *C. medinalis* larvae to insecticides is not completely consistent but changes depending on the treatment of insecticides and the host-plant switch.

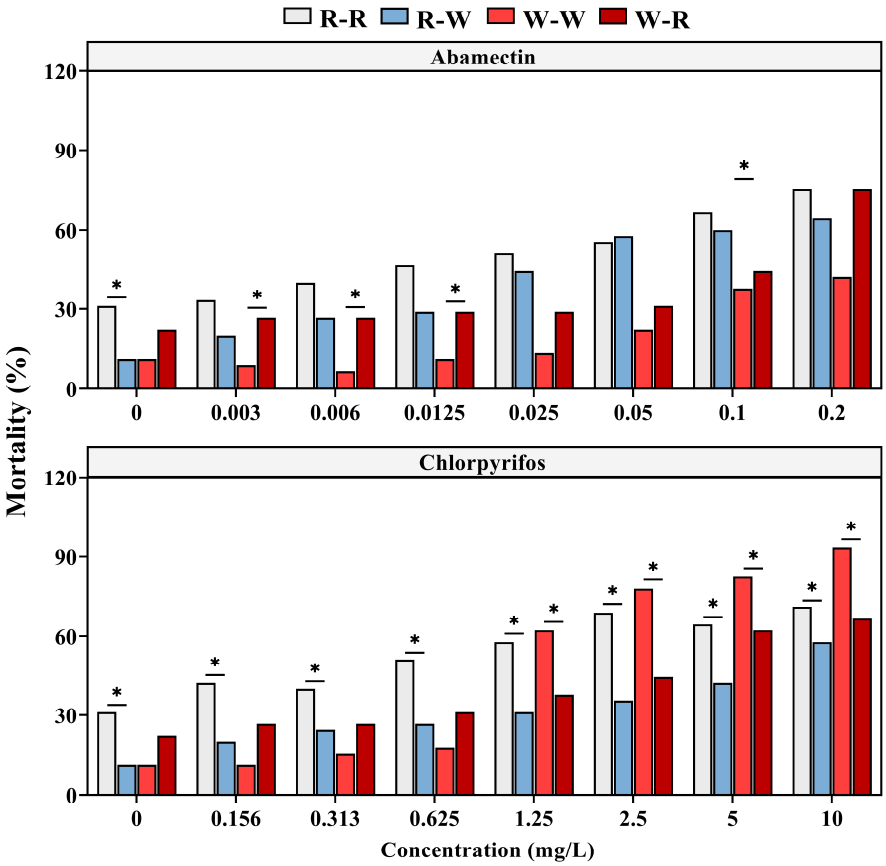

Figure 2. Effects of two insecticides on the mortality of *Cnaphalocrocis medinalis* larvae from different host-plant switch treatments. Asterisks indicate significant differences in mortality between different host-plant switch treatments at the same concentration (chi-square test; $p < 0.05$).

Table 2. Toxicity of insecticides to *Cnaphalocrocis medinalis* larvae from different host-switch treatments.

Insecticide	Treatment	LC_{25} (95% Confidence Intervals) (mg/L)	LC_{50} (95% Confidence Intervals) (mg/L)	Toxicity Regression Equation	RR
Abamectin	R-R	0.010 (0.000~0.004)	0.019 (0.009~0.033)	y = 1.337 + 0.838x	2.37
	R-W	0.005 (0.002~0.010)	0.045 (0.029~0.082)	y = 1.580 + 1.176x	
	W-W	0.054 (0.033~0.092)	0.325 (0.166~1.222)	y = 0.686 + 1.406x	0.29
	W-R	0.007 (0.000~0.012)	0.093 (0.051~0.271)	y = 0.969 + 1.002x	
Chlorpyrifos	R-R	0.021 (0.000~0.089)	0.544 (0.162~1.085)	y = 0.201 + 0.775x	15.01 *
	R-W	0.444 (0.107~0.886)	8.164 (3.808~45.448)	y = 0.792 + 0.869x	
	W-W	0.483 (0.342~0.629)	1.159 (0.863~1.551)	y = −0.185 + 2.894x	2.29 *
	W-R	0.240 (0.066~0.468)	2.657 (1.589~5.512)	y = −0.446 + 1.052x	

x and y indicate the common logarithm of dose and the probability value of the mortality conversion, respectively. RR = LC_{50} of host-switch treatment group/LC_{50} of original-host treatment group. Asterisks (*) indicate that the 95% fiducial limits of LC_{50} values for the host-switch treatment group and the original-host treatment group did not overlap and that there were significant differences between the two groups.

3.2. Effect of Insecticides on Detoxification Enzyme Activity of Larvae from Different Host-Plant Switch Treatments

Two-way ANOVA revealed that the CarE, MFO, and GST detoxification enzyme activity of *C. medinalis* larvae significantly depended on host-plant switch treatment, insecticide treatment, and their interaction (host-plant switch treatment × insecticide treatment) (Table 3). Without insecticide treatment, host-plant switching significantly reduced the CarE and MFO activities of *C. medinalis* larvae in rice (CarE: t = 4.984, df = 4, p = 0008; MFO: t = 0.130, df = 4, p = 0.009) and wheat (CarE: t = 5.629, df = 4, p = 0.005; MFO: t = 0.753, df = 4, p = 0.001) populations. When exposed to abamectin and chlorpyrifos at LC_{25}, the CarE and MFO activities of larvae of the W-R treatment group increased significantly (CarE: $F_{2,6}$ = 116.995, $p < 0.001$; MFO: $F_{2,6}$ = 52.131, $p < 0.001$) (Figure 3) and were significantly higher than those of the W-W treatment group (abamectin: CarE: t = 22.146, df = 4, $p < 0.001$; MFO: t = 10.641, df = 4, $p < 0.001$; chlorpyrifos: CarE: t = 7.465, df = 4, p = 0.002; MFO: t = 3.043, df = 4, p = 0.038) (Figure 3). However, the CarE and MFO activities of larvae of the rice population that fed on rice and wheat showed no significant difference after being treated with chlorpyrifos at the LC_{25}, whereas the CarE activities between them exhibited significant differences after being treated with abamectin at the LC_{25} (CarE: $F_{2,6}$ = 138.843, $p < 0.001$; MFO: $F_{2,6}$ = 16.406, p = 0.004) (Figure 3). Without insecticide treatment, the GST activity of the larvae of rice (t = 2.409, df = 4, p = 0.047) and wheat (t = 18.160, df = 4, $p < 0.001$) populations decreased significantly after the transformation of host plants (Figure 3). Even after abamectin and chlorpyrifos treatment at the LC_{25}, host-plant switching still significantly reduced the GST activity of rice-population larvae (abamectin: t = 9.311, df = 4, p = 0.001; chlorpyrifos: t = 8.448, df = 4, p = 0.001) (Figure 3). However, chlorpyrifos treatment at the LC_{25} significantly increased the GST activity of wheat-population larvae, and the GST activity of the W-W treatment group was significantly higher than that of the W-R treatment group (t = 5.193, df = 4, p = 0.007) (Figure 3). The results reported above indicate that host-plant switching changes the effect of insecticides on the CarE, MFO, and GST activities of *C. medinalis* larvae.

3.3. Effect of Insecticides on Acetylcholinesterase Activity of Larvae from Different Host-Plant Switch Treatments

Two-way ANOVA revealed that AChE activity of *C. medinalis* larvae was significantly affected by host-plant switch treatment and insecticide treatment and that there was interaction between them (Table 3). The AChE activity of *C. medinalis* larvae in the rice population decreased significantly after the host plant was changed to wheat (t = 4.352, df = 4, p = 0.012) but not in the wheat population (t = 1.268, df = 4, p = 0.273), suggesting that the effect of host-plant switching on the AChE activity of *C. medinalis* larvae depends on the original host (Figure 4). Abamectin and chlorpyrifos treatment at sublethal concentrations did not affect the AChE activity of rice-population larvae, regardless of host-plant switching, but affected the AChE activity of wheat-population larvae. When exposed to abamectin and chlorpyrifos at the LC_{25}, the AChE activity of wheat-population larvae fed on wheat increased significantly ($F_{2,6}$ = 9.987, p = 0.012), but the AChE activity of wheat-population larvae decreased significantly after the host plant was converted to rice ($F_{2,6}$ = 9.517, p = 0.014) (Figure 4).

Table 3. Two-way ANOVA for the effect of insecticides on the enzyme activity of *Cnaphalocrocis medinalis* larvae from different host-plant switch treatments.

Variables	Factors	df	MS	*F*	*p*
CarE	Insecticide treatment (A)	2	0.266	79.235	<0.001
	Host-plant switch treatment (B)	3	1.771	526.702	<0.001
	A × B	6	0.173	51.423	<0.001
	Error	24	0.003		
MFO	Insecticide treatment (A)	2	0.131	139.460	<0.001
	Host-plant switch treatment (B)	3	0.299	317.669	<0.001
	A × B	6	0.025	26.177	<0.001
	Error	24	0.001		
GSTs	Insecticide treatment (A)	2	10,902.800	115.115	<0.001
	Host-plant switch treatment (B)	3	7571.287	79.940	<0.001
	A × B	6	13,087.517	138.182	<0.001
	Error	24	94.712		
AChE	Insecticide treatment (A)	2	0.839	5.261	0.013
	Host-plant switch treatment (B)	3	79.910	500.902	<0.001
	A × B	6	1.646	10.315	<0.001
	Error	24	0.160		
SOD	Insecticide treatment (A)	2	96.551	17.200	<0.001
	Host-plant switch treatment (B)	3	5443.696	969.769	<0.001
	A × B	6	5.269	0.939	<0.001
	Error	24	5.613		
POD	Insecticide treatment (A)	2	1.924	5.992	0.008
	Host-plant switch treatment (B)	3	131.016	408.063	<0.001
	A × B	6	6.753	21.032	<0.001
	Error	24	0.321		
CAT	Insecticide treatment (A)	2	169,3491.089	2540.129	<0.001
	Host-plant switch treatment (B)	3	64,382.925	96.570	<0.001
	A × B	6	363,319.830	544.957	<0.001
	Error	24	666.695		

3.4. Effect of Insecticides on the Antioxidant Enzyme Activity of Larvae from Different Host-Plant Switch Treatments

Two-way ANOVA revealed that the SOD, POD, and CAT antioxidant enzyme activity of *C. medinalis* larvae significantly depended on host-plant switch treatment, insecticide treatment, and their interaction (host-plant switch treatment × insecticide treatment) (Table 3). After being treated with abamectin at the LC_{25}, the SOD activity of the R-W treatment group decreased significantly ($F_{2,6}$ = 9.053, p = 0.015), such that it was significantly lower than that of R-R treatment group (t = 6.880, df = 4, p = 0.002) (Figure 5). When exposed to chlorpyrifos at the concentration of LC_{25}, the SOD activity of R-R treatment group increased significantly to a level, such that it was significantly higher than that of the R-W treatment group (t = 3.728, df = 4, p = 0.020) (Figure 5). However, the SOD activity of wheat-population larvae did not change significantly due to host-plant switching and insecticide treatment (Figure 5). Without insecticide treatment, the host-plant switch significantly reduced the POD and CAT activities of rice-population larvae (POD: t = 82.041, df = 4, p < 0.001; CAT: t = 4.009, df = 4, p = 0.016) and significantly increased those of wheat-population larvae (POD: t = 0.334, df = 4, p = 0.755; CAT: t = 18.454, df = 4, p < 0.001) (Figure 5). After abamectin treatment at a sublethal concentration (LC_{25}), host-plant switching had no significant effect on the CAT activity of rice-population larvae or on the POD and CAT activity of wheat-population larvae (Figure 5). However, after chlorpyrifos treatment at a sublethal concentration, the POD activity of rice-population larvae fed on rice and wheat significantly increased (R-R: $F_{2,6}$ = 9.053, p = 0.015; R-W: $F_{2,6}$ = 25.165, p = 0.001), but host-plant switching still significantly affected the POD activity of rice-population larvae (t = 11.001, df = 4, p < 0.001) (Figure 5). Although chlorpyrifos treatment at a sublethal concentration significantly reduced the CAT activity of rice- and

wheat-population larvae (R-R: $F_{2,6}$ = 828.209, p < 0.001; R-W: $F_{2,6}$ = 1313.373, p < 0.001), host-plant switching still significantly affected the CAT activity of rice- (t = 4.143, df = 4, p = 0.014) and wheat- (t = 3.417, df = 4, p = 0.027) population larvae (Figure 5).

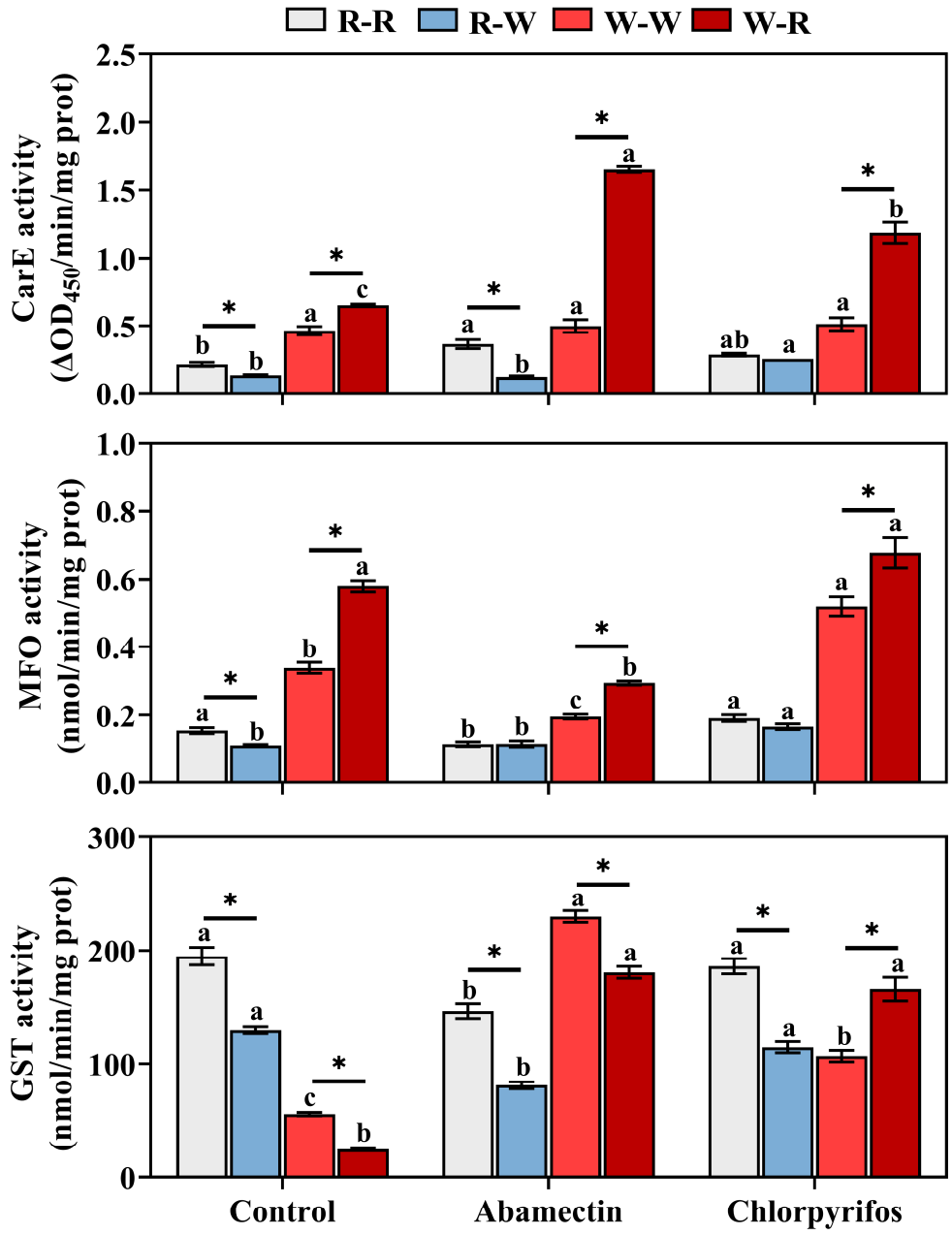

Figure 3. Effect of insecticides on the detoxification enzyme activity of *Cnaphalocrocis medinalis* larvae from different host-plant switch treatments. Asterisks indicate significant differences in detoxification enzyme activity of larvae after host-plant switch treatments. Different lowercase letters indicate significant effects of different insecticides on larval detoxification enzyme activity under the same host-plant switch treatment.

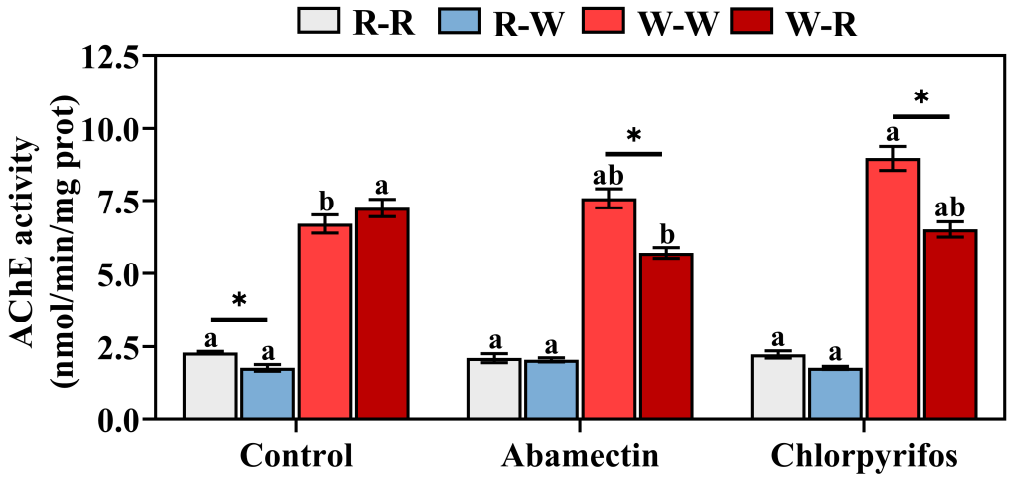

Figure 4. Effect of insecticides on the acetylcholinesterase activity of *Cnaphalocrocis medinalis* larvae from different host-plant switch treatments. Asterisks indicate significant differences in acetylcholinesterase activity of larvae after host-plant switch treatments. Different lowercase letters indicate significant effects of different insecticides on larval acetylcholinesterase activity under the same host-plant switch treatment.

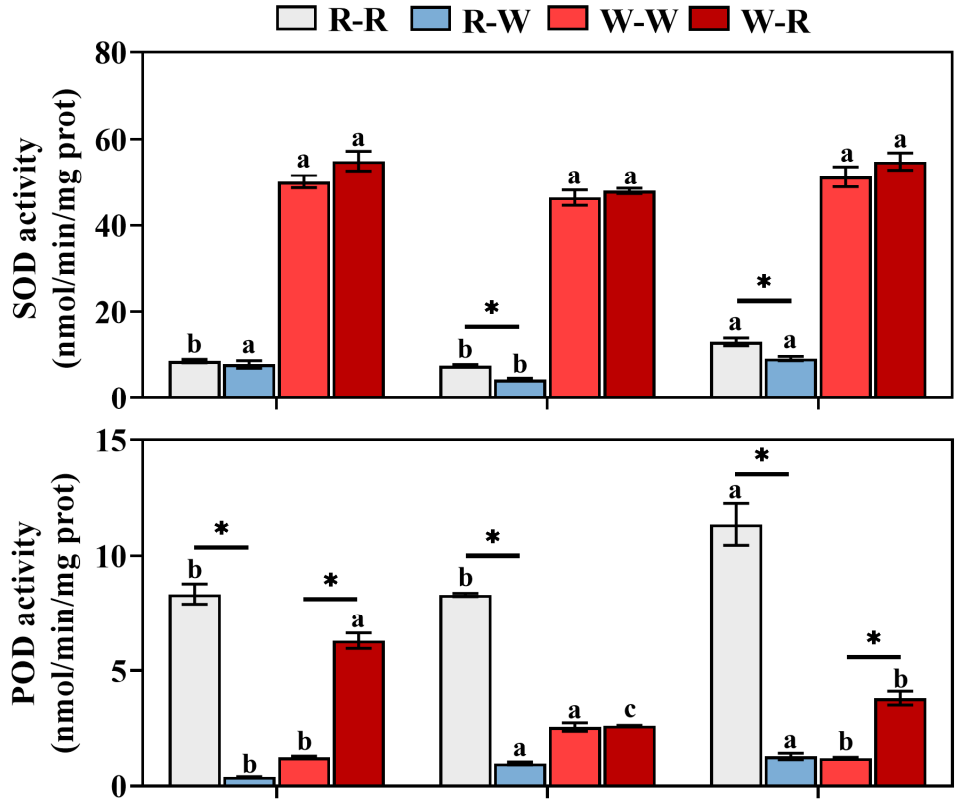

Figure 5. *Cont.*

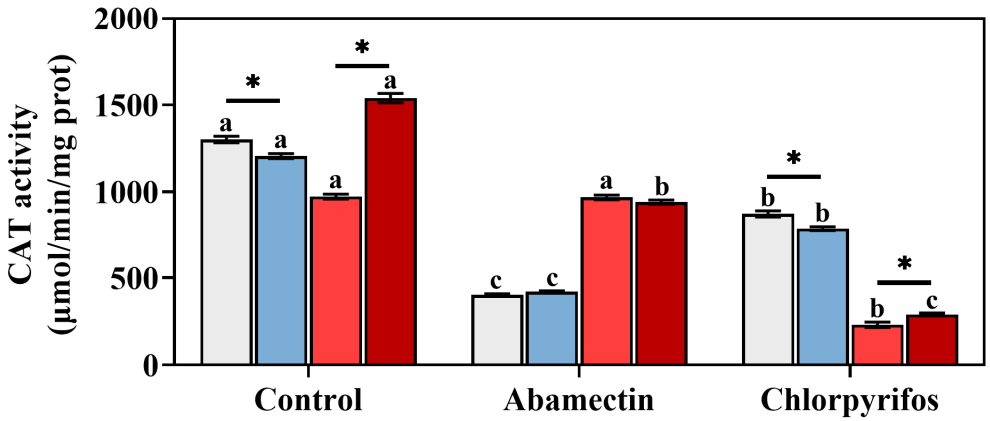

Figure 5. Effect of insecticides on the antioxidant enzyme activity of *Cnaphalocrocis medinalis* larvae from different host-plant switch treatments. Asterisks indicate significant differences in the antioxidant enzyme activity of larvae after host-plant switch treatments. Different lowercase letters indicate significant effects of different insecticides on larval antioxidant enzyme activity under the same host-plant switch treatment.

4. Discussion

For migratory insects that can only fly with the wind for a long distance, the randomness of their landing sites after migration may cause changes in their offspring host plants [15,34,35]. The evolution of mechanisms to tolerate the diversity of plant secondary metabolites encountered by some herbivorous insects has pre-adapted them to resist synthetic pesticides [7]. The difference of host plants in the offspring of migratory insects may further affect their susceptibility to insecticides. In this study, we found that host-plant switching affected the tolerance of *C. medinalis* larvae to abamectin and chlorpyrifos. The metabolic resistance of insects to insecticides usually depends on the change of one or more enzyme activities; many of these enzymes can metabolize phytochemicals and insecticides [36–38], which means that the adaptability of host plants is related to the resistance of insects to insecticides. Our findings show that the difference in susceptibility to abamectin and chlorpyrifos in *C. medinalis* with respect to host-plant switching might be related to the activities of detoxification enzymes, antioxidant enzymes, and target enzymes.

The long-term induction effect of host plants can change the susceptibility of herbivorous arthropods to pesticides, such as *Tetranychus urticae* (Koch) [39,40], *Aphis gossypii* (Glover) [41], and *Bemisia tabaci* (Gennadius) [40]. In *C. medinalis*, we found a difference in the susceptibility to insecticides of larvae populations fed on rice and wheat for a long time. However, unlike non-migratory insects, the migratory characteristics of *C. medinalis* may mean that the long-term host-plant population has to face a situation of short-term host-plant switching. Therefore, we focused on the impact of short-term host-plant switching on *C. medinalis* larvae. Our results show that the LC_{50} value of the wheat-population larvae feeding on the original host plant was 0.29 times that of the converted host plant (rice) after 48 h of exposure to the sublethal concentration (LC_{25}) of abamectin, whereas the LC_{50} value of the wheat-population larvae feeding on the original host plant was 2.29 times that for the converted host plant (rice) after 48 h of exposure to a sublethal concentration of chlorpyrifos. Interestingly, the LC_{50} value of the larvae of the rice population increased significantly after the host-plant switch, regardless of treatment with abamectin or chlorpyrifos. The diversity and induction direction of host-plant defensive compounds limit the selection pressures of special host plants on insects [42]. The different selection modes of plant-defense substances and insecticides may lead to differences in the pre-adaptation potential of insects to different insecticides [5,43], which may explain the inconsistency of the effect of host-plant switching on the insecticide susceptibility of *C. medinalis* larvae.

In the process of long-term coevolution, insects have acquired a set of detoxification metabolic systems to deal with plant secondary substances that can also effectively deal

with insecticides [5,44]. In this study, we found that host-plant switching affected the activities of MFO, CarE, and GSTs of *C. medinalis* but that changes in detoxification enzyme activity depend on the host-plant species, possibly due to the different phytochemical characteristics of rice and wheat [45] and the differing detoxication metabolic responses of *C. medinalis*. Interestingly, different insecticide treatments also have an impact on the changes in detoxification enzyme activity caused by host-plant switching. After treatment with abamectin and chlorpyrifos, the effect of host-plant switching on the enzyme activity of rice- and wheat-population larvae was significantly changed. In addition to the larvae of the rice population fed on wheat, abamectin (LC_{25}) treatment for 48 h significantly induced CarE activity in larvae treated with different host plants, although their MFO activity was significantly inhibited. However, the GST activity of rice larvae decreased significantly and that of wheat larvae increased significantly after abamectin treatment, regardless of host-plant switching. Nonetheless, after 48 h of chlorpyrifos treatment (LC_{25}), the difference in CarE activity between the larvae of rice populations that feed on rice and wheat disappeared. The GST activity of wheat larvae fed on rice was significantly higher than that of wheat-population larvae fed on wheat after 48 h of chlorpyrifos treatment. Similar to our results, in *B. tabaci*, it was also found that the activities of GSTs and CarE of *C. medinalis* responded differently after abamectin and chlorpyrifos treatments on different host plants [40]. As phase I detoxification enzymes, MFO and CarE mainly oxidize, hydrolyze, reduce, and transfer foreign compounds [46,47]. GSTs, as the main phase II detoxification enzymes, can reduce toxicity and enhance solubility by catalyzing the conjugation reaction between reduced glutathione and toxic hydrophobic and electrophilic substances, so as to achieve detoxification [48]. In order to adapt to the transformation of host plants, *C. medinalis* may induce changes in the activities of MFO, CarE, and GSTs. After treatment with different insecticides, the phase I and phase II detoxification enzymes may adjust the detoxification metabolism process according to the mechanisms of action of abamectin and chlorpyrifos, causing changes in the susceptibility of *C. medinalis* to abamectin and chlorpyrifos. We did not find that the effect of host-plant switching on AChE activity as a target enzyme of chlorpyrifos changed after abamectin and chlorpyrifos treatment. We speculated that this may be because CarE "protects" the AChE by acting as an alternative phosphorylation site for organophosphates [49]. However, in this study we did not study the correlation between detoxification enzyme and target enzyme activity changes; therefore, further research is needed.

When insects are stressed by adverse factors, a large number of reactive oxygen species accumulate in their bodies. In order to protect themselves from harm, insects coordinate the three antioxidant enzymes SOD, POD, and CAT to maintain the balance of active oxygen [50–53]. SOD first reacts to oxidative stress caused by toxic substances, converting superoxide into oxygen and hydrogen peroxide, the latter of which is decomposed by CAT and POD [54]. In many insects, such as *Frankliniella occidentalis* (Pergande), *Acanthoscelides obtectus* (Say), and *Sogatella furcifera* (Horvath), feeding on different host plants and coming into contact with pesticides change SOD, POD, and CAT activities [50,52,55]. Our results show that at the LC_{25} dose, the activities of POD and CAT in most of the host-plant switch groups decreased after abamectin and chlorpyrifos treatment, which may aggravate the accumulation of hydrogen peroxide. We also found that after abamectin treatment, the effect of host-plant switching on POD and CAT activity in wheat-population larvae disappeared and that the effect of host-plant switching on CAT activity in rice-population larvae also disappeared. However, different results were observed 48 h after exposure to chlorpyrifos (LC_{25}), partly explaining the difference in susceptibility of the larvae of rice and wheat populations of *C. medinalis* to abamectin and chlorpyrifos after host-plant switching. However, in contrast to our results, the activities of POD and CAT differed in *S. furcifera* after exposure to abamectin for varying durations, and the activities of POD and CAT were upregulated after 48 h of exposure [50]. These studies show that in insects, the activities of SOD, POD, and CAT are related to host-plant adaptability and the response

to insecticide-induced stress; however, the role of these enzymes may depend on the host plant, species, and treatment time.

In our study, *C. medinalis* larvae showed strong adaptability to host-plant switching between rice and wheat due to their enzyme system. In order to adapt to host-plant switching, *C. medinalis* larvae activate or inhibit the activities of detoxification enzymes (MFO, CarE, and GSTs), antioxidant enzymes (SOD, POD, and CAT), and AChE, affecting their tolerance to insecticides. Therefore, the adaptability of *C. medinalis* to host plants is related to insecticide tolerance, and the coordinated regulation of detoxification enzymes and antioxidant enzymes plays a key role. Host-plant switching is accompanied by the differential regulation of genes involved in transcription and transport, membrane transport, and detoxification [38,56,57], so it is necessary not only to study the related enzymes, but also to further study the role of binding proteins and transporters in host-plant switching and insecticide tolerance. Furthermore, given the need for laboratory testing, in order to facilitate feeding, an increasing number of researchers have begun to use wheat, corn, and other host plants for laboratory feeding of *C. medinalis* larvae [58,59]. If *C. medinalis* larvae feeding on other hosts are used for toxicological tests, the test results may be affected. Therefore, host plants should be reasonably selected for *C. medinalis* larvae according to experimental needs.

5. Conclusions

Our studies demonstrate the effects of host-plant switching on the susceptibility of *C. medinalis* to abamectin and chlorpyrifos. The effect of host-plant switching on insecticide susceptibility varies depending on the type of insecticide. Host-plant switching and insecticide treatment can significantly affect the activities of detoxification enzymes (MFO, CarE, and GSTs), antioxidant enzymes (SOD, POD, and CAT), and AChE. *C. medinalis* coordinates the changes of detoxification enzyme, antioxidant enzyme, and AChE activities to adapt to the induction effects of host-plant switch and insecticide treatments. This study provides some basic information about the tolerance of *C. medinalis* larvae converted from host plants to abamectin and chlorpyrifos and related enzymes, contributing to the understanding of the relationship between the adaptability of migratory insects to host plants and resistance to insecticides, as well as the development of improved management strategies.

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