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First Report of Field Resistance to Afidopyropen, the Novel Pyropene Insecticide, on *Bemisia tabaci* Mediterranean (Q Biotype) from China

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Abstract: Afidopyropen, a novel biopesticide, is derived from *Aspergillus fumigatus*, a fungus, and shows promise as a novel insecticidal agent for the management of the whitefly pest *Bemisia tabaci* in horticultural and economical crop production. In the present work, we monitored the susceptibilities of *B. tabaci* to afidopyropen in 18 field populations, sampled from 9 provinces of China, and found that, in comparison with the susceptible strain (MED-S), *B. tabaci* from most field populations were highly susceptible, except for the Haidian population (HD) which exhibited an approximately 40-fold increase in resistance. The HD population also displayed significant cross-resistance to sulfoxaflor (14.5-fold) but little cross-resistance to cyantraniliprole, flonicamid, imidacloprid, pymetrozine, and thiamethoxam. Afidopyropen resistance of the HD population was determined to be incomplete dominant and autosomal, and synergism assays demonstrated that P450 monooxygenases could contribute to the field-evolved afidopyropen resistance observed in the HD population. These results will further our understanding of the molecular underpinnings of insecticide resistance in *B. tabaci* and can inform the development of field-based pest control tactics to slow the development of afidopyropen resistance and to control whiteflies more sustainably.

Keywords: *Bemisia tabaci*; afidopyropen; sulfoxaflor; cross-resistance; inheritance; resistance management

Citation: Wang, R.; Gao, B.; Che, W.; Qu, C.; Zhou, X.; Luo, C. First Report of Field Resistance to Afidopyropen, the Novel Pyropene Insecticide, on *Bemisia tabaci* Mediterranean (Q Biotype) from China. *Agronomy* **2022**, *12*, 724. https://doi.org/10.3390/agronomy12030724

Academic Editor: Angelo Canale

Received: 16 February 2022
Accepted: 9 March 2022
Published: 17 March 2022

1. Introduction

Bemisia tabaci, the tobacco whitefly, is among the most dangerous piercing-sucking insect pests, inflicting devastating effects on economic and horticultural crop production worldwide due to its global distribution and broad host range of over 700 plant species [1,2]. Apart from directly damaging plants via feeding, *B. tabaci* can transmit over 200 species of plant viruses [3]. As management of *B. tabaci* primarily relies on chemical insecticide application, over time, *B. tabaci* populations have developed high to extremely high levels of resistance to most commercialized insecticides [2]. About 650 cases of resistance to over 60 insecticidal active ingredients were reported in whitefly populations [4]. In the past five years, the resistance of whiteflies to several popular pesticides such as spirotetramat, cyantraniliprole, cycloxaprid, and flupyradifurone were reported in various regions of China [5–9]. Therefore, widely and heavily applied insecticides are becoming an ineffective and unsustainable means of controlling *B. tabaci* in China.

Afidopyropen is one derivative of pyripyropene A, derived from the opportunistic fungal pathogen *Aspergillus fumigatus*, which is pervasive in the environment [10,11], and was found to display insecticidal activity to control leaf-sucking pests such as whiteflies, leafhoppers, and aphids [12]. Afidopyropen acts on the transient receptor potential vanilloid (TRPV) of sucking insect pests and as a modulator of the Nan-Iav vanilloid TRPV subtype, which elicits feeding cessation, starvation, dehydration, and ultimately death, thereby decreasing the transmission rate of plant viruses [13,14]. Thus far, it is suggested that afidopyropen could be utilized as an operative means for controlling destructive piercing-sucking insect pests, including *Aphis glycines*, *B. tabaci*, *Diaphorina citri*, *Carya illinoensis*, and *Stephanitis pyrioides* [15–18]. Additionally, afidopyropen shows little toxicity to natural enemies [17,19,20], and as an insecticidal agent belonging to a new insecticide group with an unknown mode of action, it could potentially be used in alternation with commonly used insecticides to improve pest control efficacy by delaying the development of resistance and improve insecticide resistance management programs.

Owing to their efficacy and convenience in the field, insecticides are heavily used in the control of *B. tabaci*; however, the overuse of insecticides gives rise to the significant development of insecticide resistance in pest populations, reducing the efficacy of currently and widely used pesticide chemistries [2]. As described previously in many other species of insect pests, gradual selection pressure resulting from continual and long-term insecticide application in the field has greatly contributed to the development of resistance in *B. tabaci*. Prior to now, few reports of resistance to afidopyropen in arthropods were recorded, and a growing number of publications indicated that a range of insect pests show high susceptibility to afidopyropen worldwide [15,18,21,22]. In the present work, we monitored the susceptibility of 18 field populations of whitefly collected from 9 provinces of China to afidopyropen and found that one field population showed moderate resistance to afidopyropen and low cross-resistance to sulfoxaflor. Subsequently, using the resistant strain and the susceptible strain (MED-S), synergism assays and inheritance tests were performed to characterize afidopyropen resistance in the HD population of *B. tabaci*.

2. Materials and Methods

2.1. Insects

The susceptible strain of *B. tabaci* (MED-S) was collected in 2009 from damaged poinsettia in the city of Beijing, China [23]. Eighteen field-collected populations of whitefly were sampled from nine provinces of China (Table 1), and identifications of cryptic species were performed on the basis of the published method [24], which confirmed that the eighteen field-collected populations were Mediterranean (MED) cryptic species. All of the populations were reared on *Gossypium hirsutum*, cotton plants, kept at 27 ± 1 °C, 60 ± 10% relative humidity, and under a 16:8 h light/dark photoperiod. For insecticide bioassays, *B. tabaci* MED adults, which emerged within seven days, were sampled at random, and the sex ratio was determined to be about 1:1 of females to males.

Table 1. Information of field-collected *B. tabaci* samples from China.

Population	Location of Collection	Site of Collection	Date of Collection	Host Plant
LY	Liaoyang, Liaoning	41.19° N, 123.11° E	August 2021	Eggplant
CY	Chaoyang, Liaoning	41.59° N, 120.50° E	August 2021	Cucumber
HD	Haidian, Beijing	39.97° N, 116.31° E	April 2021	Tomato
TZ	Tongzhou, Beijing	39.73° N, 116.69° E	June 2021	Tomato
WQ	Wuqing, Tianjin	39.35° N, 117.10° E	June 2021	Tomato
JH	Jinghai, Tianjin	38.90° N, 116.94° E	June 2021	Tomato
ZJK	Zhangjiakou, Hebei	40.58° N, 115.00° E	July 2021	Pepper
BD	Baoding, Hebei	38.82° N, 115.39° E	July 2021	Tomato
ZZ	Zhengzhou, Henan	34.91° N, 113.56° E	July 2021	Cucumber
XZ	Xinzheng, Henan	34.33° N, 113.75° E	July 2021	Pepper
JN	Jinan, Shandong	36.78° N, 117.23° E	August 2021	Tomato
TA	Taian, Shandong	36.14° N, 117.22° E	August 2021	Tomato
WH	Wuhan, Hubei	30.28° N, 114.32° E	June 2021	Pepper
XY	Xiangyang, Hubei	32.12° N, 112.03° E	June 2021	Cucumber
CS	Changsha, Hunan	28.28° N, 113.09° E	September 2021	Pepper
YY	Yueyang, Hunan	29.30° N, 113.26° E	September 2021	Pepper
HK	Haikou, Hainan	19.76° N, 110.33° E	April 2021	Melon
SY	Sanya, Hainan	18.40° N, 109.14° E	April 2021	Melon

2.2. Insecticides and Chemicals

Insecticides utilized were analytically standardized. Afidopyropen (Dr. Ehrenstorfer, Augsburg, Germany, CAS# 915972-17-7, catalog# DRE-C10047000) and sulfoxaflor (Dr. Ehrenstorfer, CAS# 946578-00-3, catalog# DRE-C17015000) were purchased from Dr. Ehrenstorfer, Germany. Flonicamid (Sigma Aldrich, Shanghai, China, CAS# 158062-67-0, catalog# 32509-25MG), pymetrozine (Sigma Aldrich, CAS# 123312-89-0, catalog# 46119-250MG-R), imidacloprid (Sigma Aldrich, CAS# 138261-41-3, 37894-100MG), thiamethoxam (Sigma Aldrich, CAS# 153719-23-4, catalog# 37924-100MG-R), cyantraniliprole (Sigma Aldrich, CAS# 736994-63-1, catalog# 32372-25MG), piperonyl butoxide (Sigma Aldrich, CAS# 51-03-6, catalog# 45626-100MG), diethyl maleate (Sigma Aldrich, CAS# 141-05-9, catalog# D97703-100G), triphenyl phosphate (Sigma Aldrich, CAS# 115-86-6, catalog# 241288-50G), dimethyl sulfoxide (Sigma Aldrich, CAS# 67-68-5, catalog# D8418-500ML), and Triton X-100 (Sigma Aldrich, CAS# 9002-93-1, catalog# 93443-100ML) were purchased from Sigma Aldrich, Shanghai, China.

2.3. Bioassays and Tests of Synergism

All bioassays of whiteflies were conducted using methods as described [8]. In brief, stock solutions of each tested chemical agent were made in dimethyl sulfoxide, from which working solutions of different concentrations were developed by diluting the stock solution in distilled water with 0.1% Triton X-100. Six working concentrations were used for the bioassays of each chemical agent. Twenty-millimeter diameter discs of cotton leaf were cut and dipped, the adaxial surface facing downwards for each insecticide and working concentration for 20 seconds. The discs were air-dried then placed into 2 mL of agar (15 g L^{-1}) in one 76 mm long glass tube; four replicates were used for each working concentration of tested insecticide. In each tube, 45–55 whitefly adults were introduced, then the tube was sealed and placed in the rearing chamber kept at 27 ± 1 °C, 60 ± 10% relative humidity and under a 16:8 h light/dark photoperiod. The mortality rate of *B. tabaci* for each bioassay was determined after 48 h, and motionless adults were regarded as dead. Statistical analysis of insecticide bioassays to determine significant differences in death rate was conducted using PoloPlus [25]. For the analysis of the synergistic effect of afidopyropen with 100 mg/L of triphenyl phosphate (TPP), piperonyl butoxide (PBO), and diethyl maleate (DEM), synergism tests with whiteflies were conducted as formerly reported [26].

2.4. Afidopyropen Resistance Heritability Tests

To demonstrate the heritability of insecticide resistance from the HD population, each strain was reciprocally crossed with the susceptible MED-S strain following a published method [26]. From each of the strains, about 150 pseudopupae were collected at random and placed individually in 96-well microplates and covered with parafilm. From 24 to 48 h, newly emerged males and females from each of the strains were collected for us in reciprocal cross experiments. Selected adults were kept on cotton plants in insect rearing cages for 6 days to allow for egg-laying. MED-S ♂ × HD ♀and HD ♂ × MED-S ♀produced offspring labeled F_{1A} and F_{1B}, respectively. According to the published method [27], the values of dominance were calculated, and the degree of dominance (*D*) was analyzed for each treatment based on lethal concentrations 50 (LC_{50}) of the test insecticides to HD and MED-S, and F_1 offspring populations.

3. Results

3.1. Monitoring and Cross-Resistance Tests

Susceptibility to afidopyropen was assessed in 18 populations sampled from 9 provinces in China in 2021 (Table 1). In comparison with the susceptible MED-S strain, 17 of the 18 populations were similarly susceptible to afidopyropen with resistance ratios ranging from 0.9 to 2.9-fold (LC_{50}: from 6.24 to 19.05 mg L^{-1}); however, one population, HD from Haidian, Beijing, showed ~43.5-fold resistance (LC_{50}: 287.76 mg L^{-1}) (Table 2). The afidopyropen resistant HD population indicated low-levels of cross-resistance to sulfoxaflor (14.5-fold) and little cross-resistance to flonicamid (1.2-fold), cyantraniliprole (1.1-fold), imidacloprid (1.3-fold), pymetrozine (1.3-fold), and thiamethoxam (0.8-fold) (Table 3).

Table 2. Afidopyropen susceptibility of field-collected *B. tabaci* populations from China.

Population	N [a]	Slope ± SE	LC_{50} (95% FL) (mg/L)	X^2 (df)	RR [b]
MED-S	957	1.01 ± 0.10	6.61 (5.48–8.12)	1.61 (3)	
LY	957	1.81 ± 0.12	14.70 (12.93–16.53)	1.46 (3)	2.2
CY	970	1.79 ± 0.11	17.98 (15.95–20.13)	2.14 (3)	2.7
HD	933	1.18 ± 0.10	287.76 (244.03–341.11)	1.24 (3)	43.5
TZ	946	2.21 ± 0.13	14.27 (12.79–15.80)	2.51 (3)	2.2
WQ	959	1.86 ± 0.12	9.61 (8.57–10.73)	1.56 (3)	1.5
JH	939	1.70 ± 0.12	10.37 (8.80–11.93)	1.17 (3)	1.6
ZJK	951	1.98 ± 0.11	11.58 (10.41–12.86)	1.99 (3)	1.8
BD	975	2.02 ± 0.12	16.96 (15.21–18.81)	2.84 (3)	2.6
ZZ	948	1.74 ± 0.15	7.48 (6.55–8.45)	2.44 (3)	1.1
XZ	961	1.75 ± 0.13	10.16 (8.66–11.65)	2.04 (3)	1.5
JN	937	1.59 ± 0.13	6.24 (5.39–7.12)	2.63 (3)	0.9
TA	964	1.93 ± 0.12	19.05 (17.06–21.20)	1.53 (3)	2.9
WH	948	1.89 ± 0.13	12.62 (11.04–14.21)	1.90 (3)	1.9
XY	963	1.62 ± 0.13	6.72 (5.53–7.89)	1.47 (3)	1.0
CS	940	1.39 ± 0.11	13.83 (11.62–16.10)	1.12 (3)	2.1
YY	961	2.03 ± 0.14	7.72 (6.70–8.72)	2.72 (3)	1.2
HK	936	1.51 ± 0.11	16.69 (14.42–19.09)	1.81 (3)	2.5
SY	944	1.79 ± 0.12	18.91 (16.89–21.08)	2.20 (3)	2.9

[a] Number of insects used. [b] RR (resistance ratio) = LC_{50} (field-collected population)/LC_{50} (MED-S).

Table 3. Resistance spectrum of the susceptible MED-S and afidopyropen-resistant HD strains of *B. tabaci*.

Insecticide	Strain	N [a]	LC_{50} (mg L^{-1}) (95% CL) [b]	Slope ± SE	X^2 (df)	RR [c]
Afidopyropen	MED-S	952	7.21 (4.83–12.04)	1.12 ± 0.10	1.76 (3)	
	HD	940	268.64 (213.55–344.87)	1.01 ± 0.12	2.54 (3)	37.3
Flonicamid	MED-S	931	1.79 (1.48–2.07)	1.32 ± 0.10	2.54 (3)	
	HD	966	2.14 (1.89–2.36)	1.01 ± 0.11	2.15 (3)	1.2
Cyantraniliprole	MED-S	948	1.38 (1.18–1.62)	1.32 ± 0.10	2.81 (3)	
	HD	925	1.58 (1.40–1.71)	0.89 ± 0.10	1.99 (3)	1.1
Imidacloprid	MED-S	950	11.84 (10.78–13.56)	1.39 ± 0.11	2.87 (3)	
	HD	917	15.63 (13.16–18.19)	1.03 ± 0.11	3.10 (3)	1.3
Pymetrozine	MED-S	933	1.24 (1.02–1.50)	1.19 ± 0.10	1.58 (3)	
	HD	928	1.63 (1.29–1.97)	1.33 ± 0.11	2.83 (3)	1.3
Sulfoxaflor	MED-S	940	9.05 (6.89–12.04)	1.39 ± 0.11	2.69 (3)	
	HD	922	131.57 (105.27–157.80)	1.03 ± 0.11	2.27 (3)	14.5
Thiamethoxam	MED-S	914	12.18 (9.97–15.14)	1.21 ± 0.11	2.35 (3)	
	HD	936	10.08 (8.29–13.00)	1.01 ± 0.11	1.69 (3)	0.8

[a] Number of insects used. [b] CL = confidence limits. [c] RR = Resistance Ratio.

3.2. Synergism Assays

The effects of synergism from piperonyl butoxide (PBO), triphenyl phosphate (TPP), and diethyl maleate (DEM) with afidopyropen in the HD and the susceptible strains are displayed in Table 4. We detected a significant synergistic effect between PBO and afidopyropen in the HD population with a synergistic ratio (SR) of 4.72, while TPP and DEM exhibited little synergism (SR = 1.20 and 1.14, respectively). The above data suggest that P450 monooxygenases are potentially associated with the afidopyropen resistance of the HD strain.

Table 4. Synergistic effects on afidopyropen toxicity in the susceptible MED-S and afidopyropen-resistant HD strains of *B. tabaci*.

Strain	Insecticide/Synergist	LC_{50} (mg L^{-1}) (95% CL) [a]	Slope ± SE	X^2 (df)	SR [b]
MED-S	Afidopyropen	7.78 (6.76–8.82)	1.76 ± 0.12	1.90 (3)	
	Afidopyropen + PBO	6.42 (5.55–7.33)	1.52 ± 0.11	1.08 (3)	1.21
	Afidopyropen + DEM	7.63 (6.38–8.87)	1.62 ± 0.12	2.67 (3)	1.02
	Afidopyropen + TPP	6.34 (5.49–7.23)	1.55 ± 0.11	2.21 (3)	1.23
HD	Afidopyropen	281.68 (241.85–324.19)	1.40 ± 0.11	1.86 (3)	
	Afidopyropen + PBO	59.62 (51.68–67.85)	1.59 ± 0.11	1.90 (3)	4.72
	Afidopyropen + DEM	247.99 (198.95–297.42)	1.17 ± 0.11	1.03 (3)	1.14
	Afidopyropen + TPP	234.41 (189.19–279.85)	1.22 ± 0.11	2.19 (3)	1.20

[a] CL = confidence limits. [b] SR (synergistic ratio) = LC_{50} (afidopyropen only)/LC_{50} (afidopyropen + synergist).

3.3. Heritability of Afidopyropen Resistance in The HD B. tabaci Strain

The concentration–response results of insecticide treatment of HD and MED-S *B. tabaci* strains and their F_1 offspring from reciprocal crosses are described (Table 5). In HD strain, no significant difference in the LC_{50} values among F_{1A} offspring (LC_{50}: 161.85 mg L^{-1}), F_{1B} offspring (LC_{50}: 175.05 mg L^{-1}), and F_1 pooled offspring (LC_{50}: 171.62 mg L^{-1}) were observed, implying that the HD resistance mechanism is autosomally inherited. Furthermore, the degrees of dominance of F_{1A}, F_{1B}, and F_1 pooled were 0.71, 0.75, and 0.74, respectively, indicating the heritability of HD resistance is incompletely dominant.

Table 5. Efficacy of afidopyropen in susceptible (MED-S) and resistant (HD) strains of *B. tabaci* and their F_1 progeny from reciprocal crosses.

Strain or Cross	LC_{50} (mg L^{-1}) (95% FL) [a]	Slope ± SE	X^2 (df)	RR [b]	*D*[c]
MED-S	7.07 (6.05–8.12)	1.51 ± 0.11	2.45 (3)	1	
HD	276.77 (232.75–321.76)	1.39 ± 0.11	1.41 (3)	39.1	
F_{1A} (MED-S ♂ × HD ♀)	161.85 (142.75–181.83)	1.79 ± 0.12	2.26 (3)	22.9	0.71
F_{1B} (HD ♂ × MED-S ♀)	175.05 (153.61–198.66)	1.56 ± 0.11	1.45 (3)	24.8	0.75
F_1 (pooled)	171.62 (148.61–197.27)	1.40 ± 0.11	2.03 (3)	24.3	0.74

[a] CL = confidence limits. [b] RR (resistance ratio) = LC_{50} (HD or F_1)/LC_{50} (MED-S). [c] The degree of dominance (*D*) ranges from −1 (completely recessive) to +1 (completely dominant).

4. Discussion

In 2019, the insecticidal compound afidopyropen was registered for the management of aphids and whiteflies on horticultural crops in China and has since exhibited excellent efficacy in killing adult *B. tabaci* field populations throughout China [18]. In this study, we sampled 18 field populations of whitefly from 9 provinces across China and found most of these exhibited high susceptibilities to afidopyropen. However, one field-collected HD population showed about 40-fold increased resistance (LC_{50}: 287.76 mg L^{-1}) in comparison with the susceptible MED-S strain. In the management of aphids, afidopyropen was highly toxic to *Aphis gossypii* from 25 field populations in China, indicating that afidopyropen is also effective for controlling *A. gossypi* [22]. Moreover, in the United States, regarding the baseline susceptibility of field-collected populations of *Aphis glycines* to afidopyropen, afidopyropen was reported to be effective against immature and adult stages of *A. glycines* [21]. To our knowledge, our work is the first report of afidopyropen resistance in sucking insect pests and could prove useful for resistance monitoring and management.

Afidopyropen, flonicamid, and pymetrozine belong to IRAC Group 9, in which the insecticides target arthropod TRPV channels indispensable to the arthropod mechanosensory system [28,29]. These insecticidal toxins result in similar symptoms, namely feeding cessation, and then gives rise to starvation and mortality of the insect [30]. In the present work, little cross-resistance to pymetrozine and flonicamid was detected in the field-collected afidopyropen-resistant strain of whitefly, and similarly, little cross-resistance between pymetrozine and afidopyropen was observed in whiteflies in a recent study [18]. However, moderate cross-resistance to sulfoxaflor was detected. So far, in addition to two multi-resistant strains exhibiting varying levels of cross-resistance to sulfoxaflor [26], most resistant strains of whitefly exhibiting moderate to high resistance to spiromesifen, cyclaniliprole, cyantraniliprole, and flupyradifurone were found to exhibit little resistance to sulfoxaflor [31–34]. Cross-resistance patterns in whitefly provide important clues in management strategies of insecticide resistance. The high risk of cross-resistance between chemical agents means these agents are expected to be considered as one individual set while implementing one pesticide rotation program for the management of whitefly.

Understanding the heritability of pesticide resistance can inform the selection of which particular chemical agents to use for controlling a specific arthropod [35]. It is well established that the degree of dominance (*D*) has an important role in the evolution of pesticide resistance, and reciprocal crosses between susceptible and resistant strains assessing the *D* value and demonstrating inheritance are pivotal for studying the mechanism of resistance. If insecticide resistance results from dominant genes, both homozygotes (RR) and heterozygotes (RS) will exhibit resistance, making management more difficult [36]. Conversely, recessive genes conferring resistance might develop more slowly than dominant gene resistance because resistant genotypes (RR and RS) are more abundant than susceptible genotypes (only SS) [36,37]. In our research, one field-collected resistant population (HD) was utilized to assess the heritability of afidopyropen resistance in *B. tabaci*. Afidopyropen resistance in the HD strain was determined to be inherited in an autosomal and incompletely dominant manner. Similarly, cases of incomplete dominance were reported in field-evolved cyantraniliprole- and pyriproxyfen-resistant strains of whitefly as well [26,38]. This pattern of resistance inheritance was also found in field-evolved resistant populations of other pests [39–41]. Since afidopyropen is one new insecticidal toxin, there is little research on resistance to afidopyropen in pests, and to date, no inheritance of afidopyropen resistance is reported. Therefore, our research results reveal the potential to see rapidly increasing afidopyropen resistance in the future and that rational use of afidopyropen will be needed to maintain its efficacy for as long as possible.

Author Contributions: Conceptualization, R.W., B.G. and C.L.; methodology, R.W. and B.G.; software, W.C.; validation, X.Z.; formal analysis, R.W., B.G. and W.C.; investigation, R.W., B.G. and W.C.; resources, C.Q.; data curation, C.Q.; writing—original draft preparation, R.W.; writing—review and editing, R.W. and C.L.; visualization, R.W.; supervision, R.W. and C.L.; project administration, C.L.; funding acquisition, R.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded bythe Scientific and Technological Innovation Capacity Construction Special Funds of the Beijing Academy of Agriculture and Forestry Sciences, China (KJCX20210437).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Most of the recorded data are available in all Tables in the manuscript.

Acknowledgments: We acknowledge excellent technical assistance from Yiyun Wei, Chongqing Normal University for the collection of the HD resistant population, which is very important for our work.

Conflicts of Interest: The authors declare no conflict of interest.

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