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Research Article

Insecticide Susceptibility Dynamics and Control Failure Risk of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) to Insecticides in Taiwan

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Abstract

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Fall armyworm (FAW), *Spodoptera frugiperda*, invaded Taiwan in 2019 and rapidly became a major pest of maize and sorghum. This study evaluated the susceptibility of field populations from different regions and years to various chemical insecticides- including organophosphates, pyrethroids, neonicotinoids, spinosyns, diamides, and insect growth regulators- and two *Bacillus thuringiensis* (Bt) formulations. At the time of invasion, the FAW population exhibited significant differences in susceptibility to the tested insecticides. Based on control failure likelihood (CFL) values at recommended concentrations, spinetoram, flubendiamide, novaluron, and chlorantraniliprole posed a negligible risk of control failure, whereas Bt subsp. *aizawai* (Bta) NB-200 and flucythrinate presented a high risk. Comparisons of FAW populations collected from mainland Taiwan in 2019 and 2023 showed significantly lower LC_{50} values for chlorantraniliprole and novaluron, but a significantly higher LC_{50} for Bta ABTS-1857, in the 2023 populations. In contrast, susceptibility to etofenprox, spinetoram, and Bta NB-200 did not change significantly. After 38 laboratory generations without insecticide exposure, the laboratory-maintained YY progeny showed a marked recovery of susceptibility to flubendiamide and chlorantraniliprole, with LC_{50} values decreasing by 9.76- and 201.91-fold, respectively. These findings highlight the importance of insecticide selection pressure in FAW resistance dynamics and are consistent with integrated pest management approaches that involve insecticide rotation and the temporary withdrawal of compounds showing elevated resistance.

Key words: Fall armyworm, Insecticide resistance, Diamide insecticides, Control failure likelihood, Integrated pest management.

INTRODUCTION

The fall armyworm (FAW), *Spodoptera frugiperda* (Smith, 1797), is a globally significant agricultural pest in the family Noctuidae (Lepidoptera), which is native to the southern regions of North America. Since its first invasion of Africa in 2016, FAW has rapidly spread across Asia and Oceania, posing a serious threat to global food security due to its preference for staple crops such as maize (*Zea mays*), rice (*Oryza sativa*), and sorghum (*Sorghum bicolor*) (Goergen

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et al. 2016; Montezano *et al*. 2018). Without effective control measures, FAW can reduce maize yields by up to 45% or cause total crop loss (Hruska & Gladstone 1988; Blanco *et al*. 2016). Its rapid invasion is facilitated by strong migratory ability, short life cycle, polyphagy, and high environmental adaptability.

FAW has also damaged maize expressing toxins of *Bacillus thuringiensis* Berliner, 1915 (Bt) in Latin America, where some populations have developed resistance, reducing the effectiveness of transgenic crop-based control strategies (Blanco *et al*. 2016). Chemical insecticides remain the primary control method. However, resistance has been widely reported in both native and invaded regions, affecting organophosphates, synthetic pyrethroids, benzoylureas, Bt toxins, and diamides (Yu 1991; Omoto *et al*. 2016; Gutiérrez-Moreno *et al*. 2019; Boaventura *et al*. 2020). According to the Arthropod Pesticide Resistance Database, FAW has resistance reports involving 47 active ingredients, with a total of 244 resistance cases documented worldwide (MSU 2025). Migration has been suggested as a potential factor influencing the distribution of resistance-related genes (Samanta *et al*. 2023). Therefore, comprehensive resistance monitoring and a deeper understanding of the underlying molecular and biochemical mechanisms are essential for sustainable management.

FAW is highly invasive, with rapid development, high survival, and extreme fecundity. At 25℃, the egg, larval, and pupal stages last approximately 3.0, 16.2, and 8.6 d, respectively, and a single female can lay over 1,600 eggs during a 7.4-d oviposition period (Huang *et al*. 2021). Since it invaded Taiwan in 2019, FAW has become a major threat to agricultural production. Infestations have been reported primarily on maize and sorghum, which together account for over 90% of reported cases. Maize damage is especially severe because larvae shelter within the whorl during vegetative growth and later bore into ears via the silks, reducing insecticide exposure and directly damaging kernels. Following the 2013 "reactivation of fallow land" policy, maize cultivation in Taiwan increased by 1.26-fold relative to the previous year and expanded to 2.22 times the 2012 level by 2023. For this study, Yunlin County, representing about 43.6% of Taiwan's sweet corn area in 2019, was selected as the primary FAW sampling region (Query of crops by cultivation scale, https://agr.afa.gov.tw/afa/afa_frame.jsp).

This study originated from the first author's participation in the early emergency response to FAW invasion into Taiwan, when information on insecticide efficacy and regional susceptibility was limited. The objectives were to evaluate the efficacy of commonly used insecticides against FAW larvae and to compare susceptibility among regional populations. This information provides a scientific basis for insecticide selection, and future resistance monitoring and management.

MATERIALS AND METHODS

Insect populations

FAW populations were collected from four locations on Taiwan's main island and one offshore island (Kinmen) for insecticide susceptibility assays (Fig. 1). The YY population was established in 2019 by pooling approximately 30–50 larvae collected from maize fields in Dongshi Township, Yunlin County (Western Taiwan), together with 5–10 larvae collected from maize fields in Toucheng Township, Yilan County (eastern Taiwan), serving as a representative FAW population for Taiwan. In 2023, the YL population was established by pooling 50–100 larvae from maize fields in Baozhong and Yuanchang Townships, Yunlin County. The KM population was collected from sorghum fields in Jinsha Township, Kinmen County. Sampling locations were plotted in MapInfo Professional 8.5 with base map data obtained from the Ministry of the Interior, Taiwan.

Collected larvae were individually reared under controlled laboratory conditions (25 ± 1℃, 12 h photoperiod, 60 ± 5% relative humidity (RH)). The YY population was maintained on fresh maize leaves for four mon

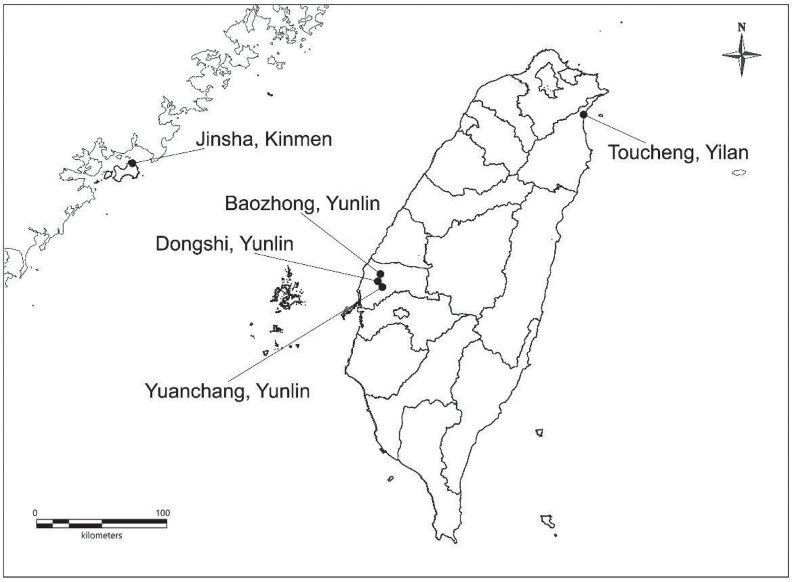

Fig. 1. Collecting locations of *Spodoptera frugiperda* populations in Taiwan and its outlying islands. Map generated with MapInfo Professional 8.5 using administrative boundary data from the Ministry of the Interior, Taiwan.

before switching to an artificial diet modified from Kao (1995), whereas the YL and KM populations were reared on the artificial diet immediately after field collection. Pupae were surface-sterilized in 1.5% sodium hypochlorite solution (Clorox bleach, 5.5–6.0% active ingredient; Clorox Company, Oakland, CA, USA) for 10 min and sexed based on the terminal abdominal segments (Luginbill 1928).

Ten female and ten male pupae were placed in an oviposition cage (diameter 14 cm × height 20 cm) for adult emergence, mating, and egg laying. Adults were supplied with 20% honey solution. At 25℃, the oviposition period of FAW is 7.4 d (Huang *et al*. 2021). To synchronize larval age and maximize egg yield, only egg masses laid 5–7 d after the onset of oviposition were collected. Larvae were initially reared in groups and then individually from the third instar until pupation. Successive generations were maintained using the same procedures.

Insecticides

The insecticides used in this study are listed in Table 1. Selection was based on commercial availability and government-recommended emergency control insecticides for FAW on maize and sorghum in Taiwan (https://faw.aphia.gov.tw/). Malathion, chlorfenapyr, and thiamethoxam were additionally included: malathion and chlorfenapyr are recommended for FAW on other host crops, while thiamethoxam, a systemic insecticide recommended for aphid control on sorghum, may be suitable for controlling FAW larvae concealed within the whorl or near the growing point of maize and sorghum (https://pesticide.aphia.gov.tw/information/).

For bioassays, each insecticide was prepared in distilled water containing 0.03% Triton X-100 (Merck KGaA, Darmstadt, Germany) as a surfactant.

Insecticide toxicity during the early invasion of FAW

1. Leaf-dip bioassay

F_1 and F_2 larvae of the YY population collected in 2019 were used. Due to the limited number of offspring, each insecticide was tested sequentially at three concentrations to rapidly identify effective compounds against

Table 1. Pesticides used in this study.

Insecticides	Active ingredient (a.i.)	Formulations[z]	IRAC MoA group[y]	Dilution fold (Target pest)[x]	Manufacturer
Malathion	50.0%	EC	1B	500× (Noctuid pests on vegetable)	Harvest Chemical
Etofenprox	20.0%	WP	3A	1,500× (FAW on maize and sorghum)	Mitsui Chemicals
Flucythrinate	5.0%	SL	3A	800× (FAW on maize and sorghum)	Chia Tai
Thiamethoxam	25.0%	SG	4A	5,000× (Aphid on sorghum)	Syngenta
Spinetoram	11.7%	SC	5	1,200× (FAW on maize and sorghum)	DOW AgroSciences
Bta NB-200	54.0%	WG	11	1,000× (FAW on maize and sorghum)	Sumitomo Chemical
Bta ABTS-1857[w]	48.1%	WG	11	1,000× (FAW on maize and sorghum)	Sumitomo Chemical
Chlorfenapyr	10.0%	SC	13	1,000× (Noctuid pests on peanut and vegetables)	BASF
Novaluron[x]	10.0%	DC	15	1,500× (FAW on maize and sorghum)	Lanlix Crop Science
Chlorantraniliprole	18.4%	SC	28	2,500× (FAW on maize and sorghum)	FMC Taiwan
Flubendiamide	20.0%	WG	28	3,000× (FAW on maize and sorghum)	Taiwan Nihon Nohyaku

[z] EC: emulsifiable concentrate; WP: wettable powder; SL: soluble liquid; SG: water-soluble granules; SC: suspension concentrate; WG: water-dispersible granules; DC: dustable powder.
[y] IRAC MoA groups are based on the Insecticide Resistance Action Committee mode of action classification.
[x] Dilution fold (target pest): based on the field application rate recommended by the Animal and Plant Health Inspection Agency (APHIA) for each target pest in Taiwan.
[w] *Bacillus thuringiensis* subsp. *aizawai* fermentation products: solids, spores, and insecticidal toxins.

the invasive population, rather than performing a conventional LC_{50} bioassay, which typically requires 5–6 concentrations. Tested insecticides (Table 1) were prepared at 0.5-, 1-, and 2-fold of their respective recommended field application rates for maize pest control in Taiwan, following the simplified resistance monitoring protocol of Cheng *et al*. (1992). Maize leaves (5–9 wk old) grown in netted greenhouses were cut into 5 × 5 cm^2 pieces, dipped in insecticide solutions containing 0.03% Triton X-100 for 15 s, and air-dried on 20 × 20 cm^2 filter paper. Control leaves were dipped only in 0.03% Triton X-100.

Petri dishes (9 cm in diameter) were lined with 7 cm filter paper moistened with 0.8 mL of distilled water. Two treated leaf pieces were placed in each dish with partial overlap, and a total of ten late second-instar larvae were transferred onto the leaves using a soft brush. Larvae were maintained at 25 ± 1℃, with a 12 h photoperiod and 75 ± 5% relative humidity. Mortality was recorded every 24 h for three consecutive days, with four replicates per treatment. Larvae unable to right themselves or showing no normal movement when gently probed were considered dead.

2. Control failure likelihood (CFL)

To assess the risk of control failure due to insecticide resistance, CFL was calculated following Guedes (2017). The CFL was calculated using the following equation:

$$CFL = 100 - [\text{observed mortality (\%)} \times 100] / \text{expected mortality (\%)}$$

The expected mortality for *S. frugiperda* was set at 70% (Pudasaini *et al*. 2022; Ahissou *et al*. 2024). CFL values were determined based on mortality recorded 72 h after treatment at the respective recommended field concentrations. CFL values were classified as low (0–10%), moderate (10–20%), high (20–30%), or extremely high (> 30%) to indicate increasing risk of control failure, and values < 0% were considered to indicate negligible risk.

Spatiotemporal variation in insecticide susceptibility

Susceptibility to seven insecticides, including etofenprox, spinetoram, Bta ABTS-1857, Bta NB-200, novaluron, flubendiamide, and chlorantraniliprole, was evaluated using laboratory-reared progeny of three FAW populations. Flucythrinate was included as a representative pyrethroid insecticide from the emergency control program for FAW in the previous CFL analysis. However, because etofenprox, another pyrethroid, is registered for use on a broader range of crops and has been applied more frequently in agricultural practice in Taiwan, it was selected for the present study to evaluate FAW susceptibility.

The populations tested included YY, collected from Yunlin and Yilan Counties during the initial invasion in 2019. Field populations, YL and KM, were collected in 2023 from Yunlin County and Kinmen County, respectively. YY F_5 was tested in 2019, whereas YY F_{43} and F_{45} were evaluated in 2023 to examine differences among laboratory generations and populations collected in different years.

After collection, all populations were reared under laboratory conditions without further exposure to insecticides. The progeny of YL and KM populations from F_1 to F_8 were evaluated. All bioassays were conducted using the leaf-dip method described above. Each insecticide was tested at six concentrations to generate dose–response curves, and median lethal concentrations (LC_{50}) were estimated using Probit Analysis using MSChart software (Finney 1971; Chi 2024).

Statistical analysis

Susceptibility among FAW populations was compared based on 95% confidence intervals (CIs) of LC_{50} values. Non-overlapping CIs were considered indicative of significant differences between populations (Deshmukh *et al*. 2020; Lira *et al*. 2020).

RESULTS

Insecticide toxicity during the early invasion of FAW

The insecticide susceptibility of the F_1 and F_2 progeny of the YY population collected during the initial FAW invasion in Taiwan in 2019 is summarized in Table 2. The tested insecticides showed marked differences in both speed of action and overall effectiveness against FAW. Spinetoram and chlorfenapyr were the fastest-acting, causing 100% mortality within 24 h at all tested concentrations (0.5-, 1-, and 2-fold recommended field rates for maize). Flubendiamide and chlorantraniliprole were comparatively slower-acting, with 48 h mortality ranging from 70.00–91.67%, reaching near-complete mortality only after 72 h. Novaluron required 72 h to achieve 83.82–100.00% mortality.

Table 2. Toxicity of insecticides to *Spodoptera frugiperda* during the initial invasion in Taiwan 2019.

Insecticide (active ingredient)	Dilution fold[z]	Active ingredient ($\mu g\ mL^{-1}$)	Mortality (mean ± *SD*) (%)		
			24 h	48 h	72 h
Control	-		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Spinetoram (11.7%)	2,400×	48.8	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
	1,200×	97.5	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
	600×	195.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
Chlorfenapyr (10.0%)	2,000×	50.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
	1,000×	100.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
	500×	200.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
Flubendiamide (20.0%)	6,000×	33.3	35.97 ± 9.99	91.67 ± 16.67	94.44 ± 6.42
	3,000×	66.7	34.19 ± 14.06	80.00 ± 16.33	100.00 ± 0.00
	1,500×	133.3	35.00 ± 17.32	82.50 ± 9.57	100.00 ± 0.00
Chlorantraniliprole (18.4%)	5,000×	36.8	5.33 ± 6.05	75.56 ± 14.17	94.44 ± 6.42
	2,500×	73.6	2.80 ± 5.54	82.22 ± 17.08	97.50 ± 10.00
	1,250×	147.2	6.73 ± 5.66	70.00 ± 11.55	97.50 ± 5.00
Novaluron (10.0%)	3,000×	33.3	0.00 ± 0.00	18.06 ± 23.73	83.82 ± 12.95
	1,500×	66.7	7.50 ± 5.00	15.70 ± 12.52	100.00 ± 0.00
	750×	133.3	7.50 ± 9.57	17.50 ± 9.57	97.50 ± 5.00
Malathion (50.0%)	1,000×	500.0	17.50 ± 9.57	30.00 ± 8.16	30.00 ± 8.16
	500×	1,000.0	44.44 ± 22.19	53.89 ± 20.58	53.61 ± 18.06
	250×	2,000.0	72.22 ± 27.31	85.00 ± 17.32	85.00 ± 17.32
Thiamethoxam (25.0%)	10,000×	25.0	7.50 ± 9.57	17.50 ± 28.72	22.50 ± 33.04
	5,000×	50.0	7.04 ± 6.12	10.00 ± 8.16	23.06 ± 4.75
	2,500×	100.0	75.00 ± 23.80	82.50 ± 17.08	82.50 ± 17.08
Bta NB-200[y] (54.0%)	2,000×	270.0	24.32 ± 17.11	29.32 ± 14.21	29.09 ± 13.38
	1,000×	540.0	31.25 ± 10.31	43.75 ± 14.93	51.25 ± 23.94
	500×	1,080.0	53.89 ± 12.53	74.17 ± 17.72	76.67 ± 17.64
Flucythrinate (5.0%)	1,600×	31.3	0.00 ± 0.00	3.13 ± 6.25	13.75 ± 16.01
	800×	62.5	40.65 ± 3.52	43.89 ± 11.28	50.14 ± 19.63
	400×	125.0	35.28 ± 20.62	41.84 ± 21.21	46.94 ± 22.89

[z] Dilution fold: Concentrations represent 0.5-, 1-, and 2-fold of the respective field application rates recommended by Animal and Plant Health Inspection Agency (APHIA).

[y] *Bacillus thuringensis* subsp. *aizawai* NB-200.

In contrast, malathion, thiamethoxam, and Bta NB-200 exhibited lower overall efficacy, with mortality varying depending on dose and exposure time. Malathion and thiamethoxam exhibited relatively rapid initial toxicity, with 72.22 and 75.00% mortality, respectively, at the highest concentration after 24 h, but mortality increased only slightly by 48 h and remained below 85%. Flucythrinate exhibited the lowest efficacy, with a maximum mortality of 50.14% after 72 h across all concentrations. These results highlight clear differences in both the speed of action and overall effectiveness among the tested insecticides.

Based on CFL values at the recommended concentrations, the risk of control failure was negligible for spinetoram, flubendiamide, novaluron, and chlorantraniliprole, whereas Bta NB-200 and flucythrinate presented a high risk of control failure. Malathion, chlorfenapyr, and thiamethoxam were excluded from this analysis, as they are not recommended for FAW control on maize or sorghum (Fig. 2).

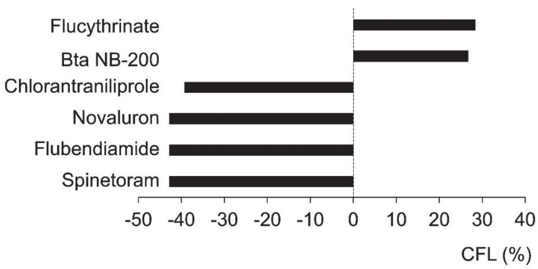

Fig. 2. Control failure likelihood (CFL) for *Spodoptera frugiperda*, evaluated at the recommended field concentrations at 72 h post-treatment during the initial invasion in Taiwan in 2019.

Spatiotemporal variation in insecticide susceptibility

FAW populations collected from different regions and years were compared across successive laboratory generations in the absence of insecticide exposure to examine regional heterogeneity and differences in susceptibility patterns among populations collected in different years. Based on this initial assessment, three FAW populations were selected for bioassays using seven insecticides (Tables 3–9).

No significant differences in LC_{50} values were observed among populations for etofenprox or spinetoram, indicating similar susceptibility to these insecticides (Tables 3–4). For Bta ABTS-1857, the YL population exhibited significantly reduced susceptibility compared with the YY population, whereas no significant differences were detected between YL and KM or between the YY F_5 and F_{45} generations (Table 5). In contrast, Bta NB-200 showed the opposite pattern, with the YL population being significantly more susceptible than YY F_{45} and KM (Table 6). Novaluron also displayed population-specific responses, with YL remaining more susceptible than YY (Table 7).

Clear generational trends were observed for flubendiamide and chlorantraniliprole. Within the YY population collected from the field in 2019, the F_{43} generation exhibited 9.8- and 201.9-fold lower LC_{50} values than the F_5 generation, respectively, indicating substantial recovery of susceptibility after prolonged laboratory rearing without insecticide exposure. For both insecticides, the YL population

Table 3. The susceptibility of different populations of *Spodoptera frugiperda* to etofenprox.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (*df*)	Resistance ratio[w]
YY	2019	F_{43}	36.06 a	19.85–64.86	2.70 ± 0.57	2.32 (2)	
YL	2023	F_7	74.25 a	29.07–42.47	1.25 ± 0.19	2.58 (3)	2.06
KM	2023	F_3	41.64 a	33.66–51.46	2.93 ± 0.40	3.45 (4)	1.15

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY population as the reference susceptible population.

Table 4. The susceptibility of different populations of *Spodoptera frugiperda* to spinetoram.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (*df*)	Resistance ratio[w]
YY	2019	F_{43}	0.070 a	0.055–0.089	3.81 ± 0.62	1.35 (2)	
YL	2023	F_1	0.042 a	0.010–0.182	1.40 ± 0.15	4.04 (2)	0.60
KM	2023	F_6	0.021 a	0.005–0.090	1.64 ± 0.20	5.26 (2)	0.30

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY population as the reference susceptible population.

Table 5. The susceptibility of different populations of *Spodoptera frugiperda* to *Bacillus thuringensis* subsp. *aizawai* ABTS-1857.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (df)	Resistance ratio[w]
YY	2019	F_{45}	238.12 a	191.15–296.72	2.18 ± 0.24	2.34 (4)	
		F_5	341.84 a	229.43–507.86	1.46 ± 0.26	2.38 (4)	1.44
YL	2023	F_8	957.51 b	554.16–1,657.84	2.79 ± 0.40	3.23 (2)	4.02
KM	2023	F_1	451.87 ab	270.08–753.84	1.97 ± 0.24	3.95 (3)	1.90

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY population as the reference susceptible population.

Table 6. The susceptibility of different populations of *Spodoptera frugiperda* to *Bacillus thuringensis* subsp. *aizawai* NB-200.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (*df*)	Resistance ratio[w]
YY	2019	F_{45}	308.76 a	218.31–437.05	2.02 ± 0.29	2.66 (3)	
		F_5	246.35 ab	102.17–585.91	0.93 ± 0.28	1.60 (3)	0.80
YL	2023	F_7	157.02 b	120.21–205.15	2.01 ± 0.23	1.12 (3)	0.51
KM	2023	F_1	476.28 a	280.82–809.16	1.70 ± 0.26	1.09 (2)	1.54

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY population as the reference susceptible population.

Table 7. The susceptibility of different populations of *Spodoptera frugiperda* to novaluron.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (*df*)	Resistance ratio[w]
YY	2019	F_{43}	1.00 a	0.65–1.42	1.50 ± 0.25	0.36 (2)	
YL	2023	F_7	0.22 b	0.12–0.41	1.54 ± 0.19	3.29 (3)	0.22
KM	2023	F_6	0.74 ab	0.37–1.34	1.47 ± 0.17	2.57 (3)	0.74

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY population as the reference susceptible population.

generally exhibited the highest LC_{50} values, while KM showed intermediate susceptibility (Tables 8 and 9).

All χ^2 tests were non-significant ($P > 0.05$), confirming an adequate fit of the Probit model and reliability of the LC_{50} estimates. Susceptibility patterns differed among populations depending on insecticide and population origin, and partial recovery was observed over successive laboratory generations.

DISCUSSION

The insecticides evaluated in this study exhibited distinct lethal dynamics against FAW, reflecting their differing modes of action. Malathion, thiamethoxam, and flucythrinate caused rapid mortality, with slight variation among mortality recorded at 24, 48, and 72 h post-treatment, indicating that most of their lethal effects occurred within the first 24 h (Table 2). Malathion inhibits acetylcholinesterase, preventing the degradation of acetylcholine and causing persistent synaptic excitation (Casida & Durkin 2013). Thiamethoxam acts as a nicotinic acetylcholine receptor (nAChR) modulator, leading to overstimulation of neural receptors (Tomizawa & Casida 2005), while flucythrinate functions as a sodium channel modulator, disrupting neuronal depolarization (Soderlund 2012). Despite acting on different neural targets, all three compounds rapidly incapacitate FAW through neurotoxic action (Casida & Durkin 2013; Sparks & Nauen 2015). However, it is important to note that although these compounds exhibit rapid initial toxicity, their overall mortality rates failed to reach the threshold for reliable field control, and some, such as thiamethoxam, are not currently registered for FAW management on maize in Taiwan.

In contrast, flubendiamide, chlorantraniliprole, and Bta NB-200 caused progressively increasing mortality, whereas novaluron required up to 72 h to exceed 80% mortality, reflecting its slower mode of action (Table 2). These mortality patterns correspond to the physiological targets

Table 8. The susceptibility of different populations of *Spodoptera frugiperda* to flubendiamide.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (*df*)	Resistance ratio[w]
YY	2019	F_{43}	0.79 b	0.53–1.17	1.38 ± 0.16	1.32 (3)	
		F_5	7.71 a	3.22–17.76	1.73 ± 0.46	0.71 (2)	9.76
YL	2023	F_2	2.85 ab	2.05–3.91	1.65 ± 0.18	2.15 (4)	3.61
KM	2023	F3	1.61 b	0.48–2.79	0.96 ± 0.18	2.33 (3)	2.04

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY population as the reference susceptible population.

Table 9. The susceptibility of different populations of *Spodoptera frugiperda* to chlorantraniliprole.

Populations[z]	Year	Generation	LC_{50} (μg mL^{-1})[y]	95% CL of LC_{50} (μg mL^{-1})[x]	Slope ± *SE*	χ^2 (*df*)	Resistance ratio[w]
YY	2019	F_{43}	0.035 b	0.031–0.039	2.01 ± 0.21	0.20 (3)	
		F_5	7.067 a	4.589–10.808	2.87 ± 0.64	1.34 (3)	201.91
YL	2023	F_6	0.585 c	0.407–0.833	4.50 ± 0.58	2.18 (2)	16.71
KM	2023	F_6	0.098 b	0.034–0.321	0.85 ± 0.12	3.87 (3)	2.80

[z] YY: initial invasion population, 2019, maize, Dongshi (Yunlin) & Toucheng (Yilan); YL: 2023, maize, Baozhong & Yuanchang (Yunlin); KM: 2023, sorghum, Jinsha (Kinmen).
[y] LC_{50} values followed by the same letter do not show significant differences based upon non-overlapping confidence limits 95%.
[x] CL: confidence limit.
[w] Resistance ratio: calculated using the YY F_{43} population as the reference susceptible population.

of the compounds. Flubendiamide and chlorantraniliprole disrupt calcium signaling by modulating ryanodine receptors (Sattelle *et al*. 2008). Bt kills FAW through the synergistic action of its Cry and Vip toxins, disrupting the midgut and causing death from septicemia (Gonzalez *et al*. 2008; Sanchis & Bourguet 2008; Pacheco *et al*. 2021; Lazo *et al*. 2025; Chang *et al*. 2026). Novaluron, a chitin synthesis inhibitor, interferes with molting and cuticle formation (Cutler & Scott-Dupree 2007).

Thus, while neurotoxic insecticides provide rapid control, compounds such as diamides, Bt, and novaluron act more slowly. This slower action may permit continued crop feeding during the lag phase. Moreover, evaluation across three concentrations indicated that spinetoram, flubendiamide, chlorantraniliprole, and novaluron maintained good efficacy even at 0.5-fold of the recommended field rate. These findings provide clearer guidance for insecticide rotation decisions and highlight the importance of including these compounds in rotation strategies to support long-term resistance management.

To facilitate rapid resistance detection in invasive FAW populations, this study adopted the simplified resistance monitoring protocol of Cheng *et al*. (1992), in which bioassays were conducted at 0.5-, 1-, and 2-fold of the respective recommended field application rates.

Based on CFL analysis at the recommended field rates, spinetoram, flubendiamide, novaluron, and chlorantraniliprole showed a negligible risk of control failure (CFL < 0%), supporting their expected efficacy under field conditions. In contrast, Bta NB-200 and flucythrinate were associated with a high risk of control failure (CFL 20–30%) at their respective recommended field rates, indicating the need for restricted use (Fig. 2).

From a resistance management perspective, insecticide rotation incorporating compounds with distinct modes of action may help reduce selection pressure on FAW populations. In addition, temporary withdrawal of insecticides a higher risk of control failure could potentially facilitate partial recovery of susceptibility, as observed in laboratory-maintained populations. Continuous susceptibility monitoring is therefore essential for monitoring the diversity of resistance profiles and for informing timely adjustments to FAW management strategies.

Collectively, the present results indicate that spinetoram, flubendiamide, novaluron, and chlorantraniliprole remain suitable candidates for inclusion in rotational programs, whereas flucythrinate and Bta NB-200 warrant careful reassessment of their use in the field. Notably, the recommended application strategies derived from these findings were communicated to the Animal and Plant Health Inspection Agency (APHIA) in 2019 and implemented immediately thereafter.

Susceptibility assays revealed clear temporal and spatial variation among FAW populations in Taiwan. The efficacies of etofenprox and spinetoram remained stable across regions and collection periods, supporting their continued use as reliable control options (Tables 3 and 4).

Regarding the two Bta products, the YL population (collected in 2023) exhibited different susceptibility profiles compared to the 2019 YY population: it showed lower susceptibility to Bta ABTS-1857 but higher susceptibility to Bta NB-200. No significant differences were observed between the YY and KM populations or among different laboratory generations of the YY population (Tables 5 and 6). These results indicate that even products within the same Bt subspecies can differ in field performance, underscoring the need for product- and population-specific susceptibility monitoring to guide effective Bt application strategies.

Both the YL and KM populations, collected in 2023, were directly compared in this analysis. The YL population exhibited significantly higher susceptibility to Bta NB-200 than the KM population (Table 6). Given that the recommended field concentration of Bta NB-200 is 540 μg/mL, the LC_{50} values of both populations were below this concentration. Probit back-calculation estimated the LC_{70} values of NB-200 to be 286.71 μg/mL for the YL population and 970.47 μg/mL for the KM population (data not shown).

These results indicate that, in 2023, Bta NB-200 is expected to achieve greater than 70% mortality in the YL population (CFL < 0%), suggesting that it remains suitable for field use against this population. In contrast, its efficacy against the KM population appears insufficient, and the application of Bta NB-200 against the KM population should therefore be temporarily suspended.

Marked population- and generation-dependent differences were also observed for the chemical insecticides novaluron, flubendiamide, and chlorantraniliprole (Tables 7–9). In particular, substantially lower LC_{50} values were detected in the F_{43} progeny of YY population compared with the F_5 progeny for both diamide insecticides. Using the F_{43} progeny of YY as a susceptible reference under laboratory conditions, resistance ratios in the F_5 progeny of YY were estimated to be 9.76-fold for flubendiamide and 201.91-fold for chlorantraniliprole, indicating pronounced resistance in earlier generations.

After 40 generations of laboratory rearing of the YY population without insecticide exposure, no substantial change in susceptibility was observed for the two Bt-based insecticides, Bta NB-200 and ABTS-1857 (Tables 5 and 6). In contrast, marked reductions in resistance were detected for flubendiamide and chlorantraniliprole (Tables 8 and 9). These results suggest that resistance to diamide insecticides, particularly chlorantraniliprole, may be at least partially reversible in the absence of selection pressure. This observation is consistent with the concept that certain resistance traits impose fitness costs and may decline when selection pressure is relaxed.

From a resistance management perspective, these results highlight the potential value of temporary withdrawal or reduced use of diamide insecticides as part of an integrated resistance management strategy, provided that resistance dynamics are continuously monitored. However, it should be noted that comparisons among populations collected from different locations or years do not necessarily reflect temporal changes within a single genetic population. Without direct population genetic evidence or long-term field-based monitoring, the observed differences in susceptibility cannot be conclusively attributed to changes in field management practices or to recovery processes occurring under field conditions.

Nevertheless, the strong recovery of susceptibility observed under controlled laboratory conditions underscores the importance of minimizing sustained selection pressure and supports the strategic use of insecticide rotation to help prolong the field efficacy of diamide insecticides.

Our findings are consistent with international reports. In Nepal, chlorantraniliprole was the most effective insecticide for FAW control, followed by spinetoram and emamectin benzoate (Karki *et al.* 2023). In India, chlorantraniliprole, spinetoram, etofenprox, flubendiamide, and novaluron effectively suppressed FAW populations, with chlorantraniliprole-treated fields yielding 1.29 times that of untreated controls. (Shahi *et al.* 2024). Similarly, our results confirm that chlorantraniliprole and spinetoram remain highly effective in Taiwan. In contrast, FAW populations in Puerto Rico have evolved extreme resistance to chlorantraniliprole and flubendiamide, with resistance ratios of approximately 160- and 500-fold, respectively (Gutiérrez-Moreno *et al.* 2019).

Since the introduction of Cry1Ab-expressing maize in Brazil in 2008, continuous monitoring has shown a progressive decline in FAW susceptibility to Bt maize, accompanied by reduced field efficacy between 2010 and 2015 (Omoto *et al.* 2016). A similar trend was observed for Bta ABTS-1857 in Taiwan, where susceptibility was lower in the 2023 YL population, as indicated by a 2.8-fold higher LC_{50} compared with the 2019 YY population. In contrast, the initially invasive field population of FAW collected from mainland Taiwan in 2019 (YY) exhibited a 1.57-fold higher LC_{50} for Bta NB-200 than the

2023 YL population, although the difference was not significant (Tables 5 and 6). These differences coincide with the higher field usage of Bta ABTS-1857 relative to Bta NB-200 (as reflected by cumulative procurement volumes in Table 10); other factors, such as genetic background or historical exposure, cannot be excluded.

Similar trends have been reported in diamondback moth, in which resistant populations showed higher resistance to commercial Bt formulations than to wild-type strains (Raymond *et al*. 2013). Different Bt formulations have also been reported to vary in their efficacy against diamondback moth (Kao & Cheng 2001). These results underscore the need for careful monitoring of Bt formulation usage and rotation to maintain field efficacy and delay resistance development in FAW populations. Resistance reversal was clearly observed when FAW populations were reared without insecticide exposure. The LC_{50} values for chlorantraniliprole and flubendiamide in the YY population decreased by 201.91-fold and 9.76-fold, respectively, over 38 generations (Tables 8 and 9). Similar declines have been observed in *Plutella xylostella* (Linnaeus, 1767) and *Spodoptera exigua* (Hübner, 1808) (Pudasaini *et al*. 2022; Rabelo *et al*. 2022), reflecting fitness costs associated with resistance (Gong *et al*. 2021). These results underscore the high value of diamides in FAW control but also the urgency of implementing rotation strategies.

The YY F_5 progeny, derived from the FAW population that invaded Taiwan in 2019, exhibited higher LC_{50} values for flubendiamide compared to the YL F_2 and KM F_3 progeny collected from the field in 2023, approximately 2.71- and 4.78-fold higher, respectively (Table 8). Similarly, for chlorantraniliprole, YY F_5 showed LC_{50} values about 12.07- and 72.11-fold higher than those of the YL and KM F_6 progeny from 2023, respectively (Table 9).

The lower LC_{50} values observed in the 2023 populations relative to the initial 2019 population may partially reflect differences in susceptibility patterns influenced by coordinated FAW management in Taiwan, including centralized insecticide procurement and extension programs that encourage rotation rather than tank-mixing, although other ecological or population factors cannot be excluded.

Pesticide application history and management strategies strongly influence the frequency and distribution of resistance alleles (Yainna *et al*. 2021). Integrated pest management (IPM) programs should therefore avoid overreliance on single active ingredients and carefully manage application frequency and dosage (Paredes-Sánchez *et al*. 2021).

Maize is most vulnerable to FAW damage during the seedling stage, early whorl development, and before tasseling (Gross *et al*. 1982). Because FAW larvae feed heavily and can damage or kill the growing points, young maize plants are highly susceptible. Moreover, as larvae grow, they move deeper into the whorl, hide at the leaf base, or bore into ears, thereby reducing insecticide contact and making control

Table 10. Official procurement and field application records of selected insecticides used for the control of *Spodoptera frugiperda* in Taiwan in 2020.

Insecticide	Active ingredient	Quantity (package)	Price per package (NTD)	Application quantity (package)[z]
Spinetoram	11.7%	100 mL	750	3,282
Bta ABTS-1857	48.1%	100 g	171	44,100
Bta NB-200	54.0%	200 g	420	1,810
Novaluron	10.0%	200 mL	435	81,108
Flubendiamide	20.0%	100 g	590	58,160
Chlorantraniliprole	18.4%	80 mL	592	77,258

[z] Procurement and distribution records provided by the Animal and Plant Health Inspection Agency (APHIA), Ministry of Agriculture, Taiwan.

more difficult (Young 1979; Carvalho *et al*. 2013; Bateman *et al*. 2018). Therefore, timely insecticide application is particularly crucial. In Taiwan, maize is often grown in multiple cropping cycles per year. Insecticide applications typically begin when larvae first appear and are applied about four times per cycle (Huang 2025).

Although several insecticides, including spinetoram, etofenprox, flubendiamide, novaluron, and chlorantraniliprole, currently remain effective for FAW control in Taiwanese maize, their long-term sustainability will depend on appropriate rotation among compounds with different modes of action. Specifically, one to two insecticides with distinct modes of action should be used within each cropping cycle and rotated to alternative compounds in subsequent cycles to reduce selection pressure.

Future management programs should also integrate microbial control agents to reduce reliance on chemical insecticides and to delaythe evolution of resistance. For instance, *Metarhizium anisopliae* has demonstrated prolonged efficacy against FAW and strong potential for to suppress resistance while remaining environmentally compatible, particularly under low pest densities (Yao *et al*. 2023). Therefore, the development and field validation of microbial-based control strategies should be prioritized.

Additionally, as resistance is closely linked to detoxification enzymes and gene regulation (Carvalho *et al*. 2018; Gui *et al*. 2022; Guo *et al*. 2024), future research should focus on elucidating these molecular mechanisms. Such studies will support predictive resistance management and the development of evidence-based control strategies.

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臺灣秋行軍蟲 (鱗翅目：夜蛾科) 對殺蟲劑感受性變化與防治失效風險

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摘要

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秋行軍蟲 (*Spodoptera frugiperda*) 於 2019 年入侵臺灣，迅速成為玉米與高粱的重要害蟲。本研究旨在評估臺灣不同地區及時間的秋行軍蟲田間族群對多種化學殺蟲劑 (包括有機磷類、除蟲菊精類、新尼古丁類、賜諾司類、二醯胺類殺蟲劑及昆蟲生長調節劑) 及 2 種蘇力菌 (*Bacillus thuringiensis*) 製劑的敏感性。在入侵初期，秋行軍蟲族群對各測試農藥之感受性差異顯著，依據推薦濃度之防治失效可能性分析 (control failure likelihood; CFL) 顯示，賜諾特、氟大滅、諾伐隆及剋安勃的防治失效風險可忽略，而蘇力菌 NB-200 與護賽寧則具有高防治失效風險。比較 2019 與 2023 年臺灣本島採集的秋行軍蟲族群，結果顯示兩年度族群之感受性模式存在差異，2023 年族群對剋安勃與諾伐隆之半數致死濃度 (LC_{50}) 顯著較低，但對蘇力菌 ABTS-1857 的之 LC_{50} 顯著較高。至於依芬寧、賜諾特及蘇力菌 NB-200 族群間感受性差異不顯著。田間族群 YY 品系在經過 38 代未接觸殺蟲劑的實驗室內飼養後，其對氟大滅與剋安勃的感受性顯著回復，LC_{50} 分別下降 9.76 倍與 201.91 倍，顯示殺蟲劑感受性隨未接受選汰壓力時間大幅回升。綜合而言，本研究結果突顯選汰壓力在秋行軍蟲抗藥性消長動態中的關鍵作用，支持以藥劑輪用及策略性暫停使用高風險藥劑為核心之綜合害蟲管理 (integrated pest management; IPM) 策略。

關鍵詞：秋行軍蟲、殺蟲劑抗藥性、二醯胺類殺蟲劑、防治失效可能性、害蟲綜合管理。

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