

FINAL PROJECT REPORT

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Development of pest management strategies for Fall Army Worm (FAW)

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EXECUTIVE SUMMARY

This project is a continuation of one specific aspect of the previous 3-year project on fall armyworm (FAW) which was funded by the Maize Trust. The issues around insecticide resistance evolution of this pest were highlighted as an important concern for maize farmers in South Africa.

The aims of this project were, firstly, to estimate the susceptibility of FAW which established persistent populations in subtropical overwintering areas in South Africa to insecticides registered for its control in the country, and, secondly, to determine if shifts in susceptibility to insecticides occurred in FAW from this area where they are regularly sprayed with insecticides.

Maize was planted in Nelspruit in the 2020/21 and 2021/22 production seasons and FAW was sampled in February 2021 and January 2022 to establish rearing colonies for susceptibility testing of the larvae to insecticides. Susceptibility of 3rd-instar FAW larvae to insecticides was estimated in 2021 and late 2nd-instar larvae (one day younger) to the same insecticides in 2022. From the 2021 results, control failure of 3rd-instar FAW at Nelspruit was expected with beta-cypermethrin, indoxacarb and methomyl. The 2022 results confirmed the susceptibility of 2nd-instar larvae to be higher compared to 3rd-instar larvae and control failure was expected with beta-cypermethrin only. Susceptibility testing of 2nd- and 3rd-instar FAW larvae to flubendiamide showed 3rd-instar larvae to be 1.62-fold more tolerant compared to 2nd-instar larvae. Shifts in susceptibility were not found. Changes in the level of susceptibility is, however, not determined by the frequency of applications only, but also by the migration ecology of this pests. The immigration of susceptible individuals from areas where they are not subjected to selection pressure may contribute to reduce the frequency of resistance alleles in regions where there is high selection pressure.

The higher tolerance of bigger FAW larvae (later instars) to insecticides found in this study, emphasizes the difficulty in chemical control of this pest where larvae from different instars (sizes) occur simultaneously.

Introduction

The Fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is largely controlled by means of insecticides (Gutiérrez-Moreno *et al.*, 2019; Sisay *et al.*, 2019). For example, in Brazil an average of five insecticidal applications per maize cycle are required for control (Ribeiro *et al.*, 2014). In the response to *S. frugiperda* in Africa, governments purchased and distributed insecticides worth millions of dollars, often favouring cheaper and higher risk products. For example, pesticides used for *S. frugiperda* control in Africa include methomyl, methyl parathion, endosulfan and lindane, all of which are classified as highly hazardous pesticides (FAO 2018). Most African countries, until recently, had no insecticide formulations specifically recommended or registered for the protection of maize against *S. frugiperda* (Sisay *et al.*, 2019, Koffi *et al.*, 2020, Suguiyama *et al.*, 2020). In only two African countries (South Africa and Kenya) was emergency registrations of insecticides done, despite the Pesticide Emergency Use Authorization (PEUA) regulatory tool that exist in many countries (Suguiyama *et al.*, 2020). This regulatory tool allows for emergency registration of insecticides until the necessary registration process is completed. Without this due process, farmers are left with few control options other than using off-label application of older and in many cases more toxic chemical insecticides (Suguiyama *et al.*, 2020). Pesticide use therefore often occurs in a poorly regulated environment (Karungi *et al.*, 2011, Oluwole and Cheke, 2009), where input providers and farmers are uninformed regarding their appropriate use (Karungi *et al.*, 2011) and where the agrochemical industry is under-developed (Makale *et al.*, 2021).

The first reports of resistance of this pest were in 1976, in *S. frugiperda* populations in Georgia (USA) (Young and McMillian, 1979) and in 1978 in Alabama (USA) where synthetic pyrethroids could not provide effective control with standard chemical recommendations (Bass, 1978). Resistance to carbaryl, methyl parathion and trichlorfon was reported soon thereafter by Wood *et al.* (1981) after which the proverbial insecticide resistance treadmill commenced.

For decades, the main tool for *S. frugiperda* control has been the use of synthetic insecticides which lead to the evolution of resistance to at least 29 insecticidal active ingredients in six modes of action groups in the Americas (Young, 1979, Yu, 1991, 1992, Al-Sarar *et al.*, 2006, Carvalho *et al.*, 2013, Nascimento *et al.*, 2016, Blanco *et al.*, 2010, Mota-Sanchez and Wise 2017, Okuma *et al.*, 2018). There has been a rapid rise in insecticide resistance cases of *S. frugiperda* over the last five years, with 43 active ingredients in different chemical classes that have been reported in the Arthropod Pesticide Resistance Database (APRD) (<https://www.pesticideresistance.org/>). The APRD currently reports 204 cases of insecticide resistance in *S. frugiperda* globally. Some populations have developed insecticide resistance to only a few or no active ingredients from several different classes while others evolved multiple

resistance. For example, a single *S. frugiperda* population in Puerto Rico was found to have resistance against flubendiamide, chlorantraniliprole, methomyl, thiodicarb, permethrin, chlorpyrifos, zeta-cypermethrin, deltamethrin, triflumuron and spinetoram (Gutiérrez-Moreno *et al.*, 2019).

Challenges posed by chemical control are the differential susceptibility of FAW larvae from different instars to insecticides (Yu, 1983), the potential for resistance evolution (Tabashnik *et al.*, 1987; Lietti *et al.*, 2005; Shad *et al.*, 2012; Saleem *et al.*, 2016), as well as environmental and human health risks (O'Brien *et al.*, 2016). Local selection caused by intensive insecticide use is the primary driver of evolution of insecticide resistance. However, FAW is a migratory species in which resistance alleles can spread when new areas are invaded (Arias *et al.*, 2019; Yainna *et al.*, 2021; Nguyen *et al.*, 2022).

In total, 44 different products, and 22 different active ingredients (excluding *Bacillus thuringiensis* and *Beauveria bassiana*), belonging to 10 mode of action (MoA) groups were registered in South Africa for control of FAW. After the emergency registrations of these active ingredients lapsed, several were not registered for control, resulting in 17 active ingredients, belonging to 9 MoA groups currently registered for control of FAW in South Africa. Eleven of these active ingredients belong to 8 IRAC groups and are registered to be applied on their own against FAW (Agri-Intel, 2021) while registered mixtures contain various combinations from 11 active ingredients belonging to 7 groups (Agri-Intel 2021) (Table 1).

Toxicity bioassays provide base-line data for insecticides and is therefore an important part of an insecticide resistance management program (Cook *et al.*, 2004). To be able to do proper rotation of insecticides in spray programmes, base-line efficacy data for insecticides currently used against this pest, as well as shifts in susceptibility over time, which can lead to the insect evolving resistance, should be known. Once an insect has evolved resistance to insecticides, these effective insecticides are no longer able to control the pests for which they were intended (Whalon *et al.*, 2008). It is, therefore, essential to do follow-up estimates of the susceptibility of these FAW populations, using the available base lines to detect evolution of resistance.

The evolution of insecticide resistance is a natural response of a pest population exposed to selection pressure exerted by insecticides, and resistance will therefore remain a problem as long as insecticides are used in pest management programs (Zhu, 2008). Effective insecticide resistance management (IRM) is essential (Nauen *et al.*, 2019), and should be part of an Integrated Pest Management (IPM) strategy applied in crop production (<http://www.irac-online.org/>). IRM is an important aspect of sustaining the efficacy of insecticides (Nauen *et al.*,

2019). The aim of IRM is to prevent or delay the evolution of resistance to insecticides or to recover the susceptibility of an insect pest/mite population in which resistance has already evolved (Sparks and Nauen, 2015; Nauen *et al.*, 2019). With IRM, the use of insecticides is minimized and the risk of resistance development is spread over all available classes of insecticides (Phillips *et al.*, 1989). Insecticides with different modes of action (MoA) specified by the Insecticide Resistance Action Committee (IRAC) or combinations of compounds from MoA groups should therefore be altered or rotated in application sequences (Nauen *et al.*, 2019).

Table 1. Active ingredients and their respective IRAC groupings currently registered for control of fall armyworm in South Africa.

Number	Active ingredient	Class	IRAC group
1	<i>Bacillus thuringiensis</i>	<i>Bacillus</i> spp.	11
2	beta-cypermethrin	Pyrethroids	3A
3	chlorantraniliprole	Diamides	28
4	chlorpyrifos	Organophosphates	1B
5	emamectin benzoate	Avermectins	6
6	flubendiamide	Diamides	28
7	Indoxacarb	Oxadiazines	22A
8	lufenuron	Benzoylureas	15
9	mercaptotion [syn. malathion]	Organophosphates	1B
10	Methomyl	Carbamates	1A
11	pyridalyl dichloropropene-derivative	Pyridalyl	UN
12	Spinetoram	Spinosyns	5
1	benfuracarb + fenvalerate	Carbamates	1A + 3
2	chlorantraniliprole + lambda cyhalothrin	Diamide + Pyrethroid	28 + 3
3	chlorpyrifos + cypermethrin	Organophosphate + Pyrethroid	1B + 15
4	chlorpyrifos + lambda-cyhalothrin	Organophosphate + Pyrethroid +	1B + 3
5	indoxacarb + novaluron	Benzoylureas	22A + 15
6	methoxyfenozide + spinetoram	Diacylhydrazines+ Spinosyns	18 + 5

Control failure of an insecticide due to insecticide resistance is based on the significant reduction of efficacy of a (commercial) product (i.e., an insecticide formulation) used at its recommended dose/concentration but not achieving an expected control level (Guedes *et al.*, 2017). To estimate the risk or likelihood of control failure by an insecticide (i.e., the control failure likelihood) due to insecticide resistance, the recommended label rate of the insecticide and the minimum

efficacy threshold for insecticide registration (e.g., 80%) are used. The label rate is used as the discriminating concentration and the mortality achieved in the bioassay is used for comparison with the minimum efficacy threshold. This allows for the recognition of the populations likely to undergo control failure with the tested insecticide (Guedes, 2017). A desirable next step in such estimations of control failure likelihood, and also for insecticide resistance, is the recognition of the spatially dependent scale of the phenomena allowing for geographically based decision-making in resistance management (Guedes, 2017).

The climate suitability for *Spodoptera frugiperda* in Africa, as modelled by Du Plessis *et al.* (2018), indicated the most northern parts of South Africa, including the subtropical lowveld, to be potentially suitable for year-round persistence of this pest (Figure 1). The climate in the main maize production area of South Africa is therefore not suitable for overwintering of FAW. This pest does, however, persist in the lowveld where sweet corn (that do not contain Bt toxins) is cultivated and two research farms of private companies are situated. Insecticides are therefore applied on a regular basis to protect the sweet corn on commercial farms, and trial plantings on the research stations against FAW invasions. Since insecticide resistance of a pest population evolve as a result of selection, the persistence of the pest in the area, absence of vast areas planted with genetically modified Bt maize in monoculture and regular insecticide applications for control of FAW, may contribute to resistance evolution by FAW in this area.

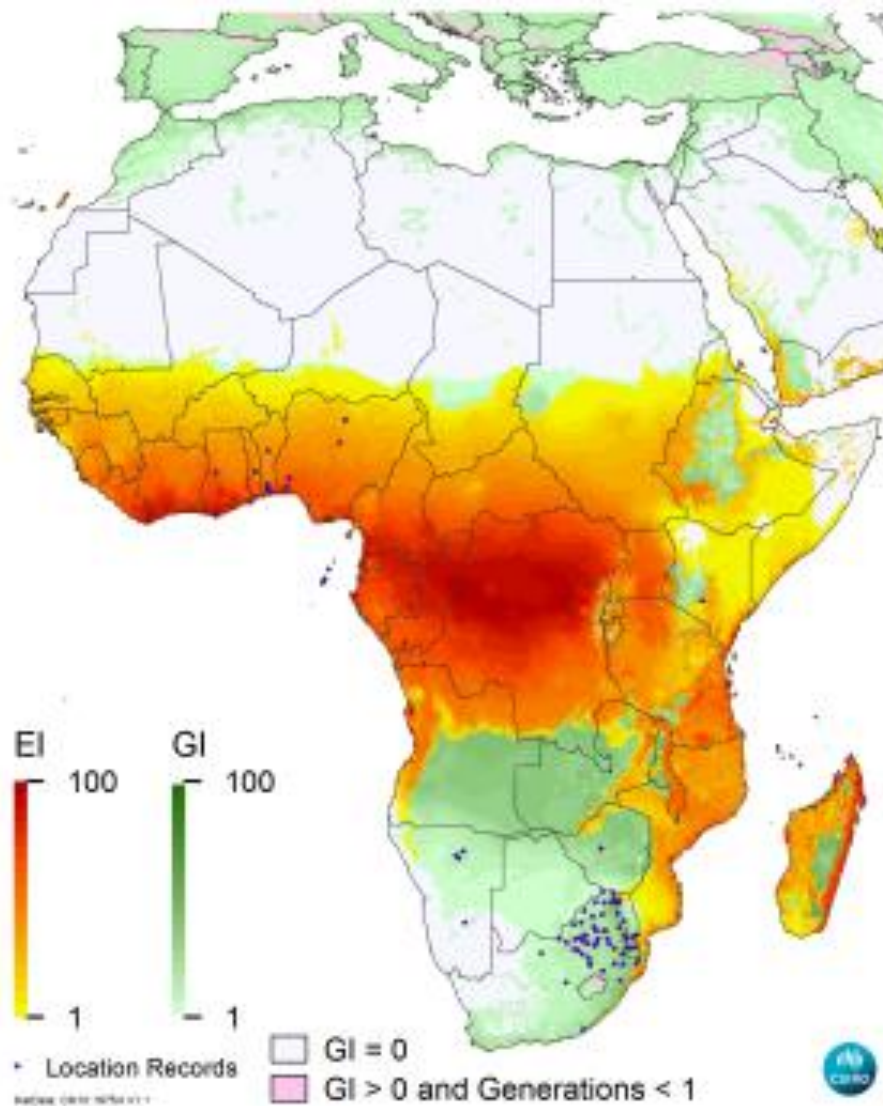


Figure 1. Climate suitability for *Spodoptera frugiperda* in Africa modelled using CLIMEX, including the spatially-explicit effects of irrigation. The Ecoclimatic Index (EI) describes the potential suitability for persistence, while the Growth index (GI) describes suitability for population growth (Du Plessis *et al.*, 2018).

The aims of this project were,

- 1) 2021 - to estimate the susceptibility of FAW which occurs in its subtropical overwintering area in South Africa, to insecticides registered for its control in South Africa
- 2) 2022 - to determine if shifts in susceptibility to insecticides occurred in a FAW population from the Nelspruit area where they are regularly sprayed with insecticides.
- 3) To determine the susceptibility of 2nd- and 3rd-instar FAW larvae to flubendiamide.

Material and methods

Fall armyworm rearing

Spodoptera frugiperda populations were collected from maize fields at Nelspruit (25°26'14.186" S; 30°59'34.598" E) (Mpumalanga province). Whorls of maize plants infested with FAW larvae were collected and placed inside containers with aerated lids (40 X 30 X 17 cm). Due to the cannibalistic nature of FAW, each larva was reared individually on Stonefly *Heliothis* premix diet (Ward's Natural Science Establishment, LLC) in small transparent plastic containers (55 mm in length x 25 mm in diameter) closed with a steel mesh-infused lid. The premix diet was mixed with water in a 1:4 ratio (diet: water) to obtain a smooth paste. Rearing was done in a rearing room at 28 ± 1 °C, 60-65% RH, and a 14L:10D h photoperiod. After emergence of the moths, 10 pairs were placed into oviposition chambers, that consisted of an aerated plastic container with a 10% sugar solution provided in a small bottle closed with a cotton plug and kept in the same rearing room as the larvae and pupae. Larvae that hatched from the egg batches laid by these moths (F1), were reared until they reached the 3rd-instar (L3) (2021) or late 2nd-instar (L2) (2022) for use in susceptibility evaluations.

Bioassays

Commercial formulations of the following insecticides, were used in this study: beta-cypermethrin (Akito, Arysta; 100 g L⁻¹), chlorantraniliprole (Coragen, FMC Corporation; 200 g L⁻¹), chlorpyrifos (Lirifos 480 EC, AECI Plant Health; 480 g L⁻¹), emamectin benzoate (Proclaim[®], Syngenta; 50 g kg⁻¹), flubendiamide (Belt, Bayer, 480 g L⁻¹), indoxacarb (Steward 150 EC, FMC Corporation; 150g L⁻¹), lufenuron (Sorba, Syngenta; 900 g kg⁻¹), methomyl (Methomex 900 SP, Adama; 900 g kg⁻¹) and spinetoram (Delegate 250 WG, Corteva; 250g kg⁻¹).

Preparation for bioassays

The susceptibility testing of late 2nd-instar *S. frugiperda* larvae were conducted for the respective active ingredients according to the protocols provided by the Insecticide Resistance Action Committee (IRAC). Susceptibility testing of the diamides, flubendiamide and chlorantraniliprole, were done by means of insecticide incorporated into artificial diet bioassays, while leaf dipping bioassays were conducted for susceptibility testing of the remaining active ingredients. Stock solutions of the respective insecticides were prepared taking into account the concentration of the active ingredients in the formulations of the insecticides. The insecticide solutions were prepared with deionised water and stirred well to homogenise the respective stock solutions. A series of 7-10 dilutions (concentrations) were prepared from each stock solution (Figure 2) and used as the insecticide treatments in the respective bioassays.



Figure 2. Dilution series (concentrations) prepared from a stock solution.

For the leaf dipping bioassay a non-ionic surfactant, Triton X-100, was added to each dilution to obtain optimal leaf coverage. A fresh stock solution was prepared for each replicate of each bioassay. Each bioassay consisted of three replicates. The stock solution was used immediately after it was prepared. Preliminary susceptibility testing (range finding) was done to determine the concentration ranges for the bioassays of each insecticide. These preliminary range findings /were done to ensure that the range include at least six serial concentrations (excluding the control) which resulted in 20 – 100% mortality.

Insecticide incorporated artificial diet bioassay

This bioassay was done according to the IRAC Susceptibility Test Methods Series no. 020. For preparation of the insecticide incorporated into artificial diet, 32 ml of the insecticide solution was added to 8 g of the Stonefly *Heliothis* artificial diet (Figure 3) and mixed to a paste. The control treatment was artificial diet prepared with deionised water. All tests were replicated three times. A spoon was used to place 2 ml of the insecticide treated Stonefly *Heliothis* or untreated diet per well of a bioassay tray (Frontier: Scientific services) (Figure 4). One late 2nd-instar (L2) FAW larva was inoculated onto the diet in each well of the bioassay trays using a fine artist brush. These bioassay trays were covered with plastic air infused lids. Each lid covered 4 wells of the

bioassay tray. The trays were placed in an incubator at $25 \pm 2^\circ\text{C}$, 60-65% RH and 16L:8D photoperiod. Larval mortality was assessed after 96 hours.



Figure 3. The dilution series transferred to the Stonefly *Heliophis* diet.

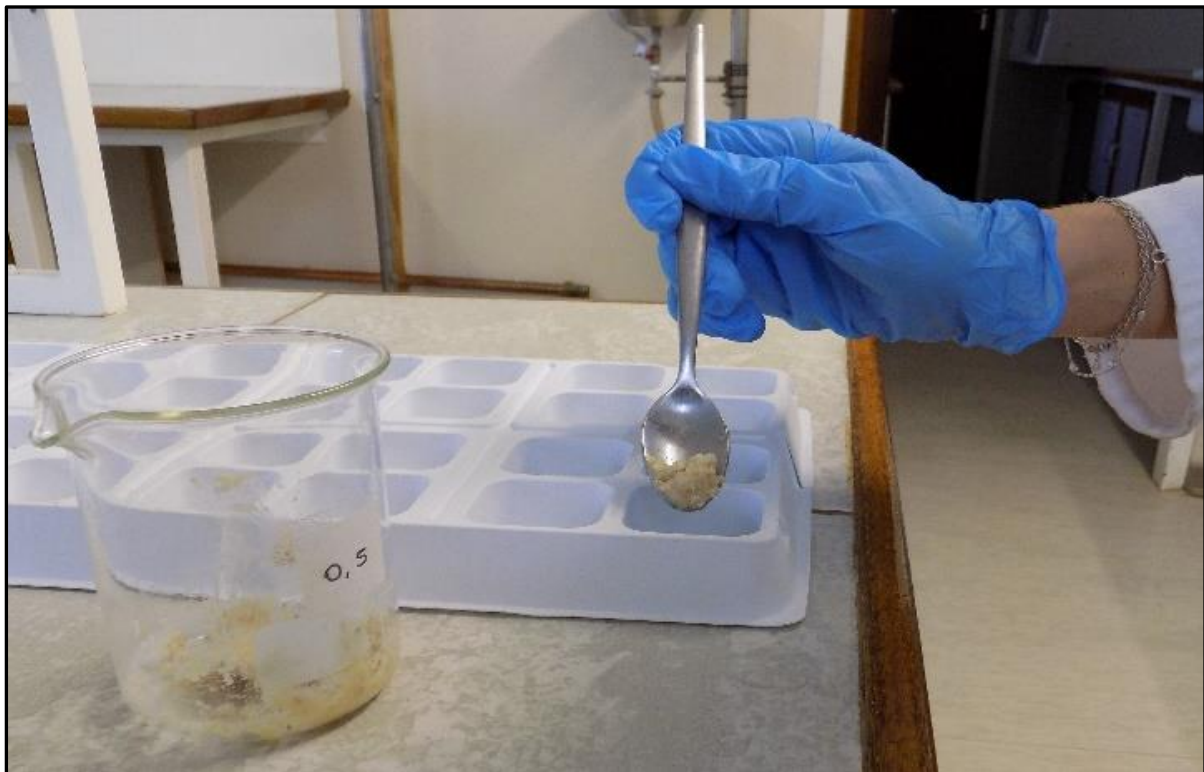


Figure 4. Artificial diet (control) or diet mixed with insecticide placed in each well of a bioassay tray using a spoon.

Insecticide leaf dipping bioassay

The leaf dipping bioassays were conducted according to the IRAC Susceptibility Test Methods Series no. 007. An agar-agar solution (1%) was prepared, and 5 mL was poured onto the bases of each cell of bioassay trays (to assist in keeping the leaf pieces turgid for the duration of the test). For each concentration of insecticide per replicate, 32 pieces of maize leaf material (3 x 3 cm) were immersed in the serial insecticide concentrations as well as in the control that consisted of deionised water and Triton X-100 solution, for five seconds ensuring that the entire surface was covered (Figure 5). Treated maize leaf pieces were placed, with the adaxial surface upwards, on a plastic wired net at room temperature and allowed to air dry and subsequently placed individually per well of the bioassay trays. The treated leaf material was placed per well for susceptibility and one late L2 larva was inoculated onto the treated leaf piece inside each well of the rearing trays, and the trays were firmly sealed with transparent ventilated adhesive lids (Frontier: Scientific services) to prevent larvae from escaping. All bioassay trays were kept in an incubator at 26 ± 2 °C, 60-65% RH and a 16L:8D photoperiod. Mortality of the larvae was assessed after 48 hours. Larvae were considered either dead or alive. Larvae that were unable to move or make coordinated movements when exposed to an external stimulus probing the insect with a fine forceps), were also considered dead.



Figure 5. Maize leaf pieces individually dipped in insecticide solution for 5 seconds with gentle stirring motion then drained of excess liquid and placed on mesh to air dry.

Data analyses

Abbott's formula was used to correct for control mortality where necessary (Abbott, 1925). Corrected mortality data from the respective dose-response bioassays were subjected to probit analysis using PoloSuite software (version 1.8) (LeOra Software). Lethal concentrations (LCs) with the corresponding 95% confidence limits (CLs) for each relationship were calculated. The

susceptibility data of the FAW larvae to the respective insecticides estimated in 2021, were compared with the responses from the larvae from the Nelspruit FAW population sampled in 2022 and were considered significantly different when the 95% CLs of the 50% lethal concentration ratios did not include the value 1 (Robertson *et al.*, 2017).

Control failure likelihood was assessed according to a method initially applied for the tomato borer, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) (Silva *et al.*, 2011). This approach compares the estimated LC₈₀ (i.e., lethal concentration for 80% of the insect population) with the recommended, registered label rate of the insecticide to recognize control failure. If the estimated LC₈₀ were higher than the label rate of the commercial formulation, control failure is expected. For insecticide formulations where an application range is recommended, the mid-concentration from the registered range was used. The 80% mortality was used as a reference because this is generally the minimum level of efficacy required for registration of an insecticidal compound and therefore the minimum expected level of control without control failure due to insecticide resistance.

The recommended application rates for control of FAW for the respective insecticides in South Africa, are summarized in table 2. The concentration of these recommended field rates for the respective insecticides was calculated using the following formula:

Recommended field rate (concentration in ppm) = [Recommended amount of product (mL or g) x Product concentration (mL/L or g/L or g/kg)]/Recommended tank water volume (L).

Table 2. Recommended application rates of insecticides for FAW control in South Africa.

Insecticide	Product (ml ha⁻¹)	Spray volume (L ha⁻¹)
Beta-cypermethrin	150	300
Flubendiamide	220	450
Indoxacarb	300	450
Lufenuron	750	500
Spinetoram	200	500
Emamectin benzoate	300	200
Chlorpyrifos	750	1000
Chlorantraniliprole	150	450
Methomyl	200	450
Pyridalyl dichloropropene-derivative	300	200

Results

The mortality data of *S. frugiperda* larvae fitted the Probit model for all insecticides. The estimated LC₅₀ and LC₈₀-values in 2021 and 2022, as well as the registered, recommended label rates for the respective insecticides tested against 2nd- and 3rd-instar FAW larvae are provided in table 3. The slopes of the regression lines in response to exposure to the respective insecticides ranged from 1.5 - 4.86 in 2021 and from 0.89 - 4.63 in 2022. Chlorantraniliprole had the highest slope in both years, and to both the larval instars. In 2021, the LC₈₀s for beta-cypermethrin, indoxacarb and methomyl were higher than the recommended label rates, viz. 50 ppm, 100 ppm and 400 ppm, respectively (Table 3). This suggested that these insecticides would not have provided the expected control of 3rd-instar *S. frugiperda* in Nelspruit in 2021. The estimated LC₈₀s for 2nd-instar FAW larvae to all insecticides was low, except for beta-cypermethrin, which was estimated higher than the recommended rate. Control of 2nd-instar larvae with these insecticides is therefore expected. However, with application of beta-cypermethrin at the recommended rate, mortality lower than 80% and control failure of 2nd-instar *S. frugiperda* with beta-cypermethrin is therefore expected at Nelspruit in 2022, similar to that of 3rd-instar larvae in 2021. The LC₈₀ of methomyl for 2nd-instar larvae was estimated lower compared to the estimation for 3rd-instar FAW larvae in 2021. Although the LC₈₀ was high, it was lower than the recommended rate and 2nd-instar larvae will therefore be controlled by methomyl.

The susceptibility of FAW to pyridalyl dichloropropene-derivative was estimated for the first time in South Africa in 2022. The LC₈₀ for 2nd-instar FAW larvae was estimated at 11.67 ppm (Table 3), compared to the recommended rate of 750 ppm (Table 2). Good control of FAW will therefore be provided by the pyridalyl dichloropropene-derivative. The susceptibility of 3rd-instar FAW larvae to flubendiamide was 1.62-fold less compared to 2nd-instar larvae (Table 4).

Discussion

The susceptibility levels of FAW larvae were different to the respective insecticides in this study, regardless of the larval instar evaluated. The difference in susceptibility of 2nd- and 3rd-instar larvae was also demonstrated by their differential susceptibility to flubendiamide, although the age difference between these larval stages, was only one day. The difference in susceptibility by different instars, is in accordance with the findings of Yu (1983). The higher tolerance of 3rd-instar larvae emphasizes the difficulties that farmers experience with chemical control of this pest where larvae from different instars occur simultaneously. The recommended application rates of the respective insecticides will control L1 and L2 larvae, but control failure of L3 larvae was, however, expected with beta-cypermethrin. Control failure of 3rd-instar larvae was also expected with indoxacarb and methomyl.

The role of natural variation in susceptibility should also not be ruled out as a factor in the different levels of insecticide susceptibility (Gutiérrez-Moreno *et al.*, 2019). Care should, however, be taken when slight decreases in susceptibility levels is ascribed to natural variation because pesticides have been continuously used for approximately seven decades (Gutiérrez-Moreno *et al.*, 2019). The long history of chemical control undoubtedly exerted selection pressure on *S. frugiperda* populations in its native areas, and consequently also the populations that invaded the Western Hemisphere. Cross-resistance due to past selection by other insecticides (Georghiou and Taylor, 1977) also influences the evolution of resistance, highlighting cross-resistance as a possible important area to investigate in *S. frugiperda* populations in newly invaded areas.

Monitoring of insecticide resistance in *S. frugiperda* populations is pivotal in terms of IRM. Although development of base-line data and monitoring for resistance have been initiated in countries such as Australia (Bird *et al.*, 2022), China (Zhang *et al.*, 2021) and India (Kulye, 2021), this is not done in most of the developing countries where this pest has become a major driver of insecticide use in smallholder agricultural systems. Furthermore, in several of the countries where *S. frugiperda* became the most important pest of grains, carbamate, organophosphate and pyrethroid insecticides are still recommended for its control, despite a long history of resistance evolution and knowledge that many of these active ingredients are hazardous to the environment and human health. The long history of insecticide exposure of *S. frugiperda* in its native region and excessive use of certain active ingredients will exacerbate the pest control challenges faced by farmers in developing countries.

The continued wide scale use of active ingredients to which many cases of resistance have been reported (e.g. lambda-cyhalothrin and methomyl) is concerning since not only are they often ineffective, they are also regarded as highly hazardous and high risk pesticides to human health and the environment (Jepson *et al.*, 2020). Seventeen cases of *S. frugiperda* resistance to lambda-cyhalothrin in six countries have been reported (APRD) (<https://www.pesticideresistance.org/>). Bird *et al.* (2022) also warned against possible control failure of *S. frugiperda* in Australia, with the pyrethroids alpha-cypermethrin and gamma-cyhalothrin, since many larvae of the invasive population survived at the diagnostic dose of these insecticides. Pyrethroids such as lambda-cyhalothrin and cypermethrin are not registered as standalone insecticides for control of FAW in South Africa. However, control failure is expected with the only pyrethroid registered as a standalone control option, i.e. beta-cypermethrin.

Insecticides from newer MoA groups are still effective although a few cases of resistance have been reported (APRD). The need therefore exists to implement resistance monitoring and IRM

strategies to delay resistance evolution against the avermectins, benzoylureas, diamides, oxadiazines and spinosyns. Comparison of insecticide susceptibility data could add predictive value to management decisions for *S. frugiperda* control, especially if these are benchmarked against the known practical significance of insecticide resistance in different populations and in other regions (Bird *et al.*, 2022).

Insecticides with older modes of action, such as AChE inhibitors, were less potent against *S. frugiperda* populations in Puerto Rico and Mexico compared to newer insecticides with other modes of action such as the insect growth regulator, triflumuron (Gutiérrez-Moreno *et al.*, 2019). In contrast, Ahissou *et al.* (2021) reported high susceptibility of *S. frugiperda* populations to AChE inhibitors (methomyl, chlorpyrifos-ethyl) in West Africa (Burkina Faso).

Resistance to chlorpyrifos was expected, based on many previous reports of resistance to this insecticide, for example in the United States (USA) (Yu 1991, 1992), Brazil (Carvalho *et al.*, 2013); Puerto Rico and Mexico (Gutiérrez-Moreno *et al.*, 2019; Boaventura *et al.*, 2020; Zhang *et al.*, 2021). High resistance ratios of *S. frugiperda* field populations to chlorpyrifos were reported from USA (25-fold) (Yu, 1991), Mexico (20-fold) and Puerto Rico (47-fold) (Gutiérrez-Moreno *et al.*, 2019), China (615-1068-fold) (Zhang *et al.*, 2021) and Brazil (> 1050-fold) (Garlet *et al.*, 2021a, b). Boaventura *et al.* (2020) reported Kenyan *S. frugiperda* populations to have a relatively high frequency of the F290V mutation in AChE, the target of organophosphate and carbamate insecticides. This further confirms that alleles conferring resistance to organophosphate and carbamate insecticides were already present at high frequency in invasive populations. The LC₈₀-values for both the 2nd- and 3rd-instar larvae in South Africa were high. The recommended application rate is, however, also high and exceeds the LC₈₀ values.

Fall armyworm is currently not a major threat to commercial maize farmers in South Africa due to the large-scale cultivation of transgenic Bt maize expressing Cry1A.105+Cry2Ab2 (stacked event) proteins for control of stem borers, but as an added advantage, also controls FAW effectively. *Spodoptera frugiperda* is, however, highly adaptable, and well known to evolve resistance against synthetic pesticides and genetically modified (GM) crops producing *Bacillus thuringiensis* (Bt) insecticidal proteins (Calles-Torrez *et al.*, 2019; Tabashnik and Carrière 2019; Carvalho *et al.*, 2013; Santos-Amaya *et al.*, 2015). Cultivation of Bt crops resulted in a reduction of 47.8% in the use of synthetic insecticide in the US (Brookes and Barfoot 2018), and it can serve as a valuable tool to manage insecticide resistance (Burtet *et al.*, 2017). This benefit is, however, lost in regions where *S. frugiperda* evolves resistance against the insecticidal proteins expressed in Bt crop plants (Blanco *et al.*, 2016).

Proper IRM is therefore important to ensure the availability of effective insecticides once this pest evolve resistance to the Bt toxins and control will rely heavily on the application of insecticides. Furthermore, in several of the countries where *S. frugiperda* became the most important pest of grains, carbamate, organophosphate and pyrethroid insecticides are still recommended for its control, despite a long history of resistance evolution and knowledge that many of these active ingredients are hazardous to the environment and human health. The long history of insecticide exposure of *S. frugiperda* in its native region and excessive use of certain active ingredients will exacerbate the pest control challenges faced by farmers in developing countries.

Evolution of insecticide resistance can be delayed by minimizing their use and employing appropriate IRM programs (Carrière *et al.*, 2020). The overall goal of IRM programs is to reduce pest pressure on the crops while simultaneously minimizing selection pressure towards any one specific group of insecticides, biological products or transgenic insect resistance traits (Sparks *et al.*, 2020). This importance of effective and proactive resistance management to maintain the efficacy of current and future insecticides has for a long time been recognized by the agrochemical industry (Jackson, 1986, Voss, 1988, McCaffery and Nauen, 2006, Sparks and Nauen, 2015).

IRM can take many forms, including the use of insecticide mixtures, mosaics or alternations / rotations (Roush, 1989, Zhao *et al.*, 2010, IRAC, 2012). The rotation of insecticide MoAs is the most commonly used and effective IRM approach. Rotation of MoA avoids treating consecutive generations of the target pest with insecticides in the same MoA group and employing the principle of MoA treatment windows which encompasses a full life-cycle of the targeted pest (Barbosa *et al.*, 2020, Sparks *et al.*, 2020). IRM strategies should be pro-active and aimed at reducing selection pressure (Bielza, 2008). The use of insecticides should be optimized and the use of insecticide mixtures with additional mode(s) of action may provide benefits for IRM when appropriately incorporated into insecticide rotation strategies. Furthermore, since the same active ingredients are often registered to control different species in a pest complex, an IRM strategy is often hampered by multiple insecticide applications against the respective pests, without taking into consideration generation time of the various pests. This often results in successive generations exposed to active ingredients from the same MoA group, enhancing the evolution of resistance.

Persistent geographic differences occur in *S. frugiperda* haplotype frequencies between west and east Africa (Nagoshi *et al.*, 2018; 2019), suggesting that transcontinental movements of large numbers of FAW by natural migration is limited (Nagoshi *et al.*, 2022). Evidence of a

second incursion of *S. frugiperda* into Africa, indicate that continued introductions are plausible, which could rapidly alter the composition of the African population with respect to pesticide resistance and host range (Nagoshi *et al.*, 2022). Nagoshi *et al.* (2019) reported that *S. frugiperda* in Africa may be a novel interstrain hybrid population, with possible novel behavioural characteristics. As a result, data on potential resistance to pesticides depending on the origin of the initial population are lacking, which could complicate its control in Africa (Nagoshi *et al.*, 2019).

The migration ecology of *S. frugiperda* populations may also have significant effects on the evolution of resistance. On the one hand, moth migration may contribute to the spread and evolution of resistance, while on the other hand, it may delay resistance evolution. The presence of an insecticide resistant population may in the first place not be due to local evolution of resistance, but to the global spread of populations which contain resistant alleles (Yainna *et al.*, 2021). Modelling the rate of resistance evolution of insect pest species with varying life history and migratory abilities showed that with high immigration, resistance can be suppressed (Helps *et al.*, 2017). For resistance to not increase over time an influx of individuals that was not subjected to selection pressure is needed into the population that is under selection pressure. This valuable role that migratory populations which are not under selection pressure can play in reducing the rate of evolution was described by Downes and Mahon (2012) for *Heliothis punctigera* (Wallengren) (Lepidoptera: Noctuidae) which remains susceptible to insecticides applied onto cotton in Australia, in contrast to *H. armigera* which does not have a seasonal influx of moths, and which is resistant to many insecticides.

The susceptibility of *S. frugiperda* to a particular insecticide in a specific region is influenced by the extent of its migration from overwintering areas into regions that are invaded on an annual basis (Pitre 1986). The seasonal influx of moths from overwintering countries in Africa, will therefore also affect the rate of insecticide resistance evolution of FAW populations in South Africa. The global spread of *S. frugiperda* may be accompanied by the spread of resistance mutations into invasive areas (Yainna *et al.*, 2021). The migration of *S. frugiperda* carrying resistance alleles to mainland United States from Puerto Rico, did, however, show the plausibility that susceptible alleles can contribute to reduce the frequency of resistance alleles in regions where there is high selection pressure with insecticides (Huang *et al.*, 2014, Camargo *et al.*, 2017).

The highly polyphagous nature of *S. frugiperda* (Montezano *et al.*, 2018) also affects the rate of resistance evolution and since wild hosts are not sprayed with insecticides, they can provide a refuge for susceptible individuals (Gutiérrez-Moreno *et al.*, 2019) to develop and contribute to

delay resistance evolution. The value of wild host plants and even minor crops on which *S. frugiperda* is not chemically controlled may however have limited value in newly invaded areas. The host range of this pest in newly invaded areas is largely limited to plant species associated with the Corn strain of this pest, i.e., maize, rice and sorghum (Juárez *et al.*, 2014, Nagoshi *et al.*, 2022). If, in future, *S. frugiperda* adapts its host range and become more polyphagous in invaded regions, integrated pest management (IPM) and IRM strategies should take advantage of these conditions to prolong the lifespan of the available control tools, similar to what was recommended by Gutiérrez-Moreno *et al.* (2019) in regions where this pest is resistant to insecticides.

MAIN FINDINGS

- Susceptibility of FAW collected at Nelspruit have been estimated for insecticides registered for its control in South Africa.
- Control failure of 3rd-instar FAW is expected with beta-cypermethrin, indoxacarb and methomyl at Nelspruit.
- Control failure of 2nd -instar FAW is expected with beta-cypermethrin.
- Third instar larvae are more tolerant to insecticides than 2nd-instar larvae.

PROJECT OUTPUTS

- **Capacity development:** Ten BSc Honours students in Integrated Pest Management were involved in this project and completed their honours projects successfully in (2021 and 2022).

One scientific paper was published:

Van den Berg, J. and Du Plessis, H. 2022. Chemical control and insecticide resistance in *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Journal of Economic Entomology*.

[page proofs attached in Appendix 1]

Table 3. Log dose probit mortality data for a *Spodoptera frugiperda* population from Nelspruit collected in 2021 and 2022 for selected insecticides.

Insecticide	Year	N	LC ₅₀	CL95%	LC ₈₀	CL95%	Slope	SE	X ²	df	Rec rate (ppm ha ⁻¹)
Beta-cypermethrin	2021	768	243.6	02-281.12	681.95	553.26-902.13	1.88	0.14	5.28	6	50
	2022	576	35.88	27.74-44.35	108.41	84.20-156.55	2.89	0.28	3.75	4	
Flubendiamide	2021	576	2.85	2.34-3.12	6.74	5.73-8.29	2.25	0.30	0.51	4	72
	2022	672	0.76	0.66-0.85	1.43	1.28-1.64	3.02	0.21	3.77	5	
Indoxacarb	2021	480	33.92	25.35-42.66	124.04	87.32-244.03	1.50	0.21	1.86	3	100
	2022	672	13.24	11.27-15.30	50.81	41.73-64.45	1.44	0.12	2.94	5	
Lufenuron	2021	576	0.26	0.22-0.31	0.57	0.49-0.70	2.51	0.23	4.56	4	125
	2022	768	0.31	0.23-0.40	1.44	1.12-2.02	1.27	0.11	6.38	6	
Spinetoram	2021	768	0.43	0.37-0.51	1.14	0.93-1.47	1.99	0.12	5.98	6	100
	2022	576	0.09	0.06-0.12	0.24	0.17-0.39	1.93	0.14	8.90	4	
Emamectin benzoate	2021	960	0.11	0.11-0.12	0.21	0.20-0.22	3.15	0.20	2.99	8	75
	2022	672	0.02	0.016-0.023	0.05	0.042-0.058	2.11	0.19	3.45	5	
Chlorpyrifos	2021	480	145.29	112.33-174.81	315.05	259.99-417.23	2.50	0.25	2.72	3	933
	2022	768	108.35	95.52-123.12	228.37	194.67-279.12	2.60	0.16	6.61	6	
Chlorantraniliprole	2021	576	0.05	0.04-0.05	0.07	0.06-0.08	4.86	0.56	4.04	4	67
	2022	768	0.07	0.07-0.08	0.11	0.10-0.12	4.63	0.29	7.00	8	
Methomyl	2021	512	224.54	183.98-267.43	629.46	514.73-815.89	1.88	0.16	5.18	6	400
	2022	768	48.83	34.60-63.23	353.87	273.06-500.13	0.98	0.11	3.39	6	
Pyridalyl dichloropropene-derivative	2022	864	1.96	1.54-2.49	11.67	8.36-18.04	1.09	0.08	7.10	7	333.33

Table 4. Log dose probit mortality data for 2nd and 3rd instar *Spodoptera frugiperda* larvae from Nelspruit collected in 2022 for selected insecticides.

Insecticide	Year	N	LC ₅₀	CL95%	LC ₈₀	CL95%	Slope	SE	X ²	df	Rec rate (ppm ha ⁻¹)
Flubendiamide	2nd	672	0.76	0.66-0.85	1.43	1.28-1.64	3.02	0.21	3.77	5	72
	3rd	864	0.98	0.86-1.12	2.32	1.99-2.77	2.25	0.12	6.78	7	

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Insecticide Resistance and Resistance Management

Chemical Control and Insecticide Resistance in *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

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Abstract

Insecticides and genetically modified Bt crops are the main tools for control of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith). Since its invasion of Africa, the Far East, and Australia where Bt crops are largely absent, insecticide use has increased and reduced susceptibility to several insecticides used for decades in its native distribution area have been reported. Poor efficacy at field-level is sometimes incorrectly ascribed to pest resistance, while numerous other factors influence efficacy at field-level. In this paper, we review the history of insecticide resistance in *S. frugiperda* and discuss the influence that life history traits, migration ecology, and chemical control practices may have on control efficacy and resistance evolution. The indirect role that poor national policies have on pesticide use practices, and indirectly on control efficacy and selection pressure is discussed. Evidence shows that local selection for resistance drives resistance evolution. Integrated pest management, rather than reliance on a single tactic, is the best way to suppress *S. frugiperda* numbers and the over-use of insecticides which selects for resistance.

Key words: Invasive pest, insecticide resistance management, pest management

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), which is native to the Neotropical areas of Central and South America (Lugbill 1928), was first reported on the African continent in 2016 (Goergen et al. 2016). Since then, it spread throughout sub-Saharan Africa (Nagoshi et al. 2022), India, Asia (Guo et al. 2018, Nagoshi et al. 2020), and Australia (Maino et al. 2021) and is now regarded as the most important pest of maize in the world. The distribution range of this pest is still expanding and its pest status will likely increase further due to climate change (Timilsena et al. 2022).

Although a huge range of yield losses due to *S. frugiperda* damage to maize have been reported in the literature, indications are that on-farm losses are over-estimated. Yield loss assessments conducted on experimental farms show that losses may be negligible (Osae et al. 2022) to as high as 90% (Evans and Stansly 1990, Hruska and Gould 1997, Overton et al. 2021, Van den Berg et al. 2021). On the other hand, farmers' perceptions of yield loss in different African countries are lower, ranging between 11 and 54% (Day et al. 2017, Rwomushana et al. 2018, Babendreier et al. 2020, De Groot et al. 2020, Kansime et al. 2019). Actual on-farm assessments recorded losses of only 11% (Baudron et al. 2019). To mitigate the impact of

S. frugiperda in Africa, governments subsidized the use of synthetic insecticides and launched emergency programs to control this pest (Rwomushana et al. 2018, Tambo et al. 2020a, Makgoba et al. 2021, Zhou et al. 2021). In newly invaded regions in Asia and the Far East, insecticide application is the main method used for its control (Li et al. 2022).

Spodoptera frugiperda is highly adaptable and well known to evolve resistance against synthetic pesticides (Huang et al. 2014, Carvalho et al. 2013, Santos-Amaya et al. 2015). Genetically modified (GM) crops producing *Bacillus thuringiensis* (Bt) insecticidal proteins are a valuable tool to reduce the use of insecticides and manage insecticide resistance (Burtet et al. 2017). For example, insecticide use for control of *S. frugiperda* and other lepidopteran pests in the USA was reduced by 47.8% following the introduction of Bt crops (Brookes and Barfoot 2018). This benefit is, however, lost in regions where *S. frugiperda* evolves resistance against the insecticidal proteins expressed in Bt crop plants (Blanco et al. 2016).

Evolution of resistance in *S. frugiperda* threatens the sustained use of pesticides. Resistance was described by Tabashnik et al. (2014) as a genetically based decrease in susceptibility to a pesticide, and the definition of 'field-evolved resistance,' as a

genetically-based decrease in susceptibility to a pesticide in a population caused by exposure to the pesticide in the field. Field-evolved resistance may result in reduced pesticide efficacy and has practical consequences for pest control (Tabashnik et al. 2014) since effectiveness of treatments is reduced and the expected level of control is not achieved even when the insecticide is used according to label recommendations. The role of natural variation in susceptibility can however not be ruled out as a factor in the different levels of insecticide susceptibility (Gutiérrez-Moreno et al. 2019). Care should therefore be taken when slight decreases in susceptibility levels are ascribed to natural variation because pesticides have been continuously used for approximately seven decades (Gutiérrez-Moreno et al. 2019). The long history of chemical control undoubtedly exerted selection pressure on *S. frugiperda* populations in its native areas, and consequently also on the populations that invaded the Western Hemisphere. Cross-resistance due to past selection by other insecticides (Georghiou and Taylor 1977) also influences the evolution of resistance, highlighting cross-resistance as a possible important area to investigate in *S. frugiperda* populations in newly invaded areas.

The first reports of resistance of this pest were in 1976, in *S. frugiperda* populations in Georgia (USA) (Young and McMillan 1979) and in 1978 in Alabama (USA) where synthetic pyrethroids could not provide effective control with standard chemical recommendations (Bass 1978). Resistance to carbaryl, methyl parathion, and trichlorfon was reported soon thereafter by Wood et al. (1981) after which the proverbial insecticide resistance treadmill commenced. There has been a rapid rise in insecticide resistance cases of *S. frugiperda* over the last five years (Fig. 1). In 2017, this pest was resistant to at least 29 insecticidal active ingredients in six mode of action groups in the Americas (Young 1979; Yu 1991, 1992; Al-Sarar et al. 2006; Carvalho et al. 2013; Nascimento et al. 2016; Blanco et al. 2010; Mota-Sanchez and Wise 2017; Okuma et al. 2018). Since then, resistance to 43 active ingredients in different chemical classes have been reported in the Arthropod Pesticide Resistance Database (APRD), <https://www.pesticideresistance.org/>. The APRD currently reports 204 cases of insecticide resistance in *S. frugiperda* globally. Of these different active substances, 32% of the cases are Cry

proteins expressed in Bt crops. Some populations have developed insecticide resistance to only a few or no active ingredients from several different classes while others evolved multiple resistance. For example, a single *S. frugiperda* population in Puerto Rico was found to have resistance against flubendiamide, chlorantraniliprole, methomyl, thiodicarb, permethrin, chlorpyrifos, zeta-cypermethrin, deltamethrin, triflumuron and spinetoram (Gutiérrez-Moreno et al. 2019).

Insecticide Use Patterns and Factors That Promote Resistance Evolution

While numerous factors influence insecticide efficacy at field-level, poor efficacy is sometimes incorrectly ascribed to pest resistance (Gutiérrez-Moreno et al. 2019, Ahissou et al. 2021). Factors that influence insecticide use, and which influence resistance evolution are listed in Table 1 and are discussed under different headings below. These factors, which are often interrelated, and include pest biology and ecology, pest management practices, insecticide application methods, and policy issues (Table 1). For example, poor infrastructure and the absence of a well-developed developed agro-chemical industry may lead to indiscriminate use of insecticides and inappropriate application methods/practices. The overestimation of risk, which is largely due to the lack of knowledge and insufficient on-farm loss assessments, together with African farmers not being familiar with insecticide use in maize (Osae et al. 2022) also contributes to unnecessary insecticide use.

Pest Biology, Ecology, and Behavior

The cryptic feeding behavior of larvae and their rapid development are likely the most important factors that impact insecticide efficacy at the field level. Insecticides provide poor control when not applied during the susceptible stages of the insect's life cycle (Yu et al. 2003) and are known to exhibit variable toxicity to different developmental stages of insects (Krambi, 2005). Larvae become more tolerant to insecticides as larval age and size increases (Yu 1983, Mink and Luttrell 1989). For example, Yu (1983) reported a decrease in *S.*

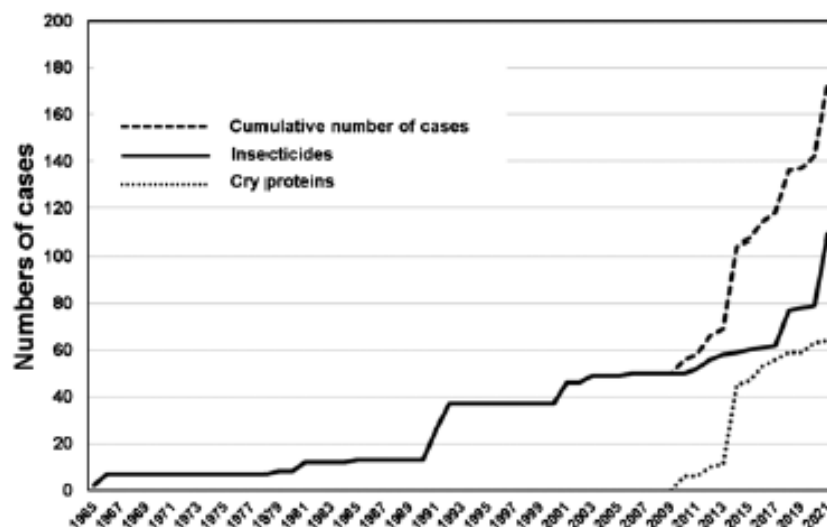


Fig. 1. The number of insecticides and Cry proteins to which resistance has been recorded for *Spodoptera frugiperda* (<https://www.pesticideresistance.org/>).

Table 1. Factors that contribute to increased risk of resistance evolution of fall armyworm to pesticides in newly invaded areas

Factor	Source
Policy issues	
Government-subsidized use of synthetic insecticides	Njuguna et al. 2021
Common and indiscriminate use of insecticides	Tambo et al. 2020a, b
Poor regulatory systems	Oluwole and Cheke 2009, Karunji et al. 2011, Goergen et al. 2016, Day et al. 2017, Bateman et al. 2018, Suguiyama et al. 2020, Jepson et al. 2020, Ahissou et al. 2021
Poor policy regarding IPM and agrochemicals	Bateman et al. 2018, Wightman 2018, Lamsal et al. 2020, Koffi et al. 2020
Over estimation of risk	Wightman 2018, Baudron et al. 2019, Van den Berg et al. 2021, Osaé et al. 2022
Pest management practices	
Disruption of existing IRM/IPM strategies for other pests	Blanco et al. 2014, Yang et al. 2021, Bird et al. 2022
Lack of economic thresholds	Overton et al. 2021, McGrath et al. 2021, Van den Berg et al. 2021
Absence of proven effective alternative control methods, e.g., Bt crops	Jepson et al. 2014, Blanco et al. 2016, Mota-Sanchez and Wise 2017, Rwomushana et al. 2018, Harrison et al. 2019, Murray et al. 2019, Chimweta et al. 2020, Osaé et al. 2022
Smallholder farmers with little previous experience of handling or applying insecticides	
Ignorance of management guidelines	Karunji et al. 2011
Uncontrolled and improper use of chemical pesticides	Lewis et al. 2016
Pest biology and invasion patterns	
Seasonal and long-distance migration	Rose et al. 1975, Sparks 1979, Pitre 1986, Johnson 1987, Arias et al. 2019, Nagoshi et al. 2022
High fecundity and fertility	Sparks 1979, Wan et al. 2021.
Cryptic feeding behavior	Diez-Rodríguez and Omoto 2001, Wan et al. 2021
Polyphagy/continuous availability and prevalence of host crops	Du Plessis et al. 2018, Wan et al. 2021
Absence of diapause, multivoltine, overlapping generations	Du Plessis et al. 2018, Early et al. 2018, Qi et al. 2020
Insecticide application methods/practices and efficacy	
Poor efficacy due to incorrect timing of insecticide applications, too large larvae, sub-lethal exposure, low-volume applications	Mink and Luttrell 1989; Yu et al. 2003, 2008; Cook et al. 2004; Kranthi 2005; Al-Sarar et al. 2006; Faretto et al. 2017; Kumela et al. 2019; Suguiyama et al. 2020; Makale et al. 2021;

frugiperda susceptibility to insecticides with increased larval age and mass, with LD₅₀ values of up to 5.6 and 236 times higher on a body weight basis, for third- and sixth-instar larvae respectively.

The efficacy of chemical control is influenced by larval behavior since they feed deep inside maize whorls, making it difficult to reach the target by means of spray applications (Young, 1979, Carvalho et al. 2013). Under such conditions, larvae may be exposed to sub-lethal doses of insecticides which select for resistance. Similarly, older larvae remain inside maize whorls, and in older plants, larger larvae can be found in leaf bases or inside maize ears where they are protected from spray applications. This behavior makes their control more difficult, especially where efficacy depends upon contact action (Bateman et al. 2018). In broad-leaf crops such as cotton, control may be difficult due to a lack of sufficient insecticide deposition in the lower region of the cotton canopy (Morrill and Greene 1973, Young 1979, Pitre 1986, Ali et al. 1989, Hardke et al. 2015). Larger instar larvae also feed inside fruiting structures further reducing their exposure to insecticide applications (Morrill and Greene 1973, Young 1979, Pitre 1986).

High reproductive potential and multi-voltinism, which is characteristic of several lepidopteran species that rapidly evolve resistance (Bernardi et al. 2015, Van den Berg et al. 2022) also contribute to increased selection pressure. Georgioui (1980) and Tabashnik and Croft (1985) showed that the shorter the generation time of a pest the faster the evolution of resistance. Pest species that thrive in warm climates have a high potential for resistance evolution since the many generations per season leads to rapid selection of resistant individuals (Farias et al. 2014, Leite et al. 2016). Furthermore, sequential planting of host crops, for example maize and sorghum

in tropical regions of Africa and Asia, followed by insecticide applications, increases pest pressure, similar to what was reported by Gutiérrez-Moreno et al. (2019) in Puerto Rico and Mexico.

The highly polyphagous nature of *S. frugiperda* (Montezano et al. 2018) also affects the rate of resistance evolution and since wild hosts are not sprayed with insecticides, they may provide a refuge for susceptible individuals (Gutiérrez-Moreno et al. 2019) to develop and contribute to delay resistance evolution. The value of wild host plants and even minor crops on which *S. frugiperda* is not chemically controlled may however have limited value in newly invaded areas. The host range of this pest in newly invaded areas is largely limited to plant species associated with the corn strain of this pest, i.e., maize, rice, and sorghum (Juárez et al. 2014, Nagoshi et al. 2022). If, in future, *S. frugiperda* adapts its host range and becomes more polyphagous in invaded regions, integrated pest management (IPM), and integrated resistance management (IRM) strategies should take advantage of these conditions to prolong the lifespan of the available control tools, similar to what was recommended by Gutiérrez-Moreno et al. (2019) in regions where this pest is resistant to insecticides.

Migration Ecology

The migration ecology of *S. frugiperda* populations may have significant effects on the evolution of resistance. Pitre (1986) reported that the susceptibility *S. frugiperda* to a particular insecticide in a specific region is influenced by the extent of its migration from overwintering areas into regions that are invaded on an annual basis. However, although gene flow may contribute to the spread

and evolution of resistance (Arias et al. 2019), it may also delay resistance evolution. For resistance to not increase over time an influx of individuals that was not subjected to selection pressure is needed into the population that is under selection pressure, and no emigration of moths back into that untreated population (Arias et al. 2019, Nagoshi et al. 2019). Modeling of the rate of resistance evolution of insect pest species with varying life history and migratory abilities showed that with high immigration, resistance can be suppressed (Helps et al. 2017). The valuable role that migratory populations which are not under selection pressure can play in reducing the rate of evolution was described by Downes and Mahon (2012) for *Helicoverpa punctigera* (Wallengren) (Lepidoptera: Noctuidae). This pest remains susceptible to insecticides applied onto cotton in Australia, in contrast to *H. armigera* which does not have a seasonal influx of moths and which is resistant to many insecticides. Although migratory populations of *S. frugiperda* which contain resistant alleles could result in the spread of resistance to newly invaded areas (Yainna et al. 2021), it is not the key factor responsible for the evolution of insecticide resistant populations. The key factors driving selection for resistance are local pest management practices and cropping strategies (Arias et al. 2019). A study conducted on gene flow between *S. frugiperda* populations in Paraguay and Brazil (Arias et al. 2019) showed that insecticide selection, dose, and frequency of application define the susceptibility landscape. The importance of regional coordination and alignment in terms of pesticide use is evident from the latter study which showed that resistant moths which immigrate into a particular region do not necessarily cause increasing LC_{50} values to a particular insecticide in a new location if that insecticide is not commonly used in the new location. Challenges to resistance management arise when the insecticides which are overused for control of the source populations of migrant moths, are also used in the areas that are invaded on a seasonal basis (Arias et al. 2019).

Although the geographic distribution of resistance mutations is poorly understood (Boaventura et al. 2020a), interesting information regarding the spread of resistance mutations have recently been published. Boaventura et al. (2020a) observed that a similar resistance mutation was frequently observed in the invasive populations in Kenya and Indonesia as well as in populations in the area of origin of the pest (Brazil and Puerto Rico), while another mutation was still only present in the Brazilian population. The presence of an insecticide resistance allele was also reported in an Indonesian population which has not previously been reported in other invasive populations (Boaventura et al. 2020a), possibly indicating local evolution. The *S. frugiperda* population that invaded China also carried resistance to organophosphates, pyrethroids (Zhang et al. 2020), and chlorantraniliprole (Lv et al. 2021).

Persistent geographic differences occur in *S. frugiperda* haplotype frequencies between west and east Africa (Nagoshi et al. 2018, 2019), suggesting that transcontinental movements of large numbers of FAW by natural migration are limited (Nagoshi et al. 2022). Evidence of a second incursion of *S. frugiperda* into Africa, indicates that continued introductions are plausible, which could rapidly alter the composition of the African population with respect to pesticide resistance and host range (Nagoshi et al. 2022). Nagoshi et al. (2019) reported that *S. frugiperda* in Africa may be a novel interstrain hybrid population, with possible novel behavioral characteristics. As a result, data on potential resistance to pesticides depending on the origin of the initial population are lacking, which could complicate its control in Africa (Nagoshi et al. 2019).

Chemical Control Practices

The excessive and off-label use of pesticides, which is described below, is the most important driver of resistance evolution (León-García et al. 2012, Carvalho et al. 2013, Gutiérrez-Moreno et al. 2019). In Brazil, chemical insecticides remain an important tool to control *S. frugiperda* in regions where it became resistant to Bt maize (Fatoreto et al. 2017). Further evidence of intensive insecticide use for *S. frugiperda* control was reported in Brazil where between three and eight insecticide applications per maize cycle may be applied (Ribeiro et al. 2014, Resende et al. 2016). In Puerto Rico up to 29 insecticide sprays from nine modes of action groups are applied per season to control *S. frugiperda* in high-value maize seed production systems (Belay et al. 2012, IRAC 2016). In Mexico, two or three applications of mostly organophosphates and pyrethroids are made against several lepidopteran species per crop cycle (Blanco et al. 2016), resulting in continuous exposure of *S. frugiperda* to insecticides. As many as 12 applications per crop cycle have been reported in Mexico (Gutiérrez-Moreno et al. 2020), leading to approximately 3,000 tons of synthetic insecticides that are applied annually to control these pests (Blanco et al. 2010).

The recent world-wide spread of *S. frugiperda* also resulted in large-scale use of synthetic pesticides to mitigate losses in Africa, India, and China (Sisay et al. 2019, Njuguna et al. 2021, Overton et al. 2021, Yainna et al. 2021). The initial response to *S. frugiperda* in sub-Saharan Africa included excessive, government-subsidized use of synthetic insecticides (Njuguna et al. 2021). For example, 60% of maize-growing households in Ghana, Rwanda, Uganda, Zambia, and Zimbabwe reported the use of insecticides (Tambo et al. 2020a). Koffi et al. (2020b) also reported that in Ghana during 2017 and 2018, 89% of farmers applied insecticides and that the frequency of number of applications ranged from two to four, while the application frequencies varied between every week to every other week. In Zambia, 277,000 liter of insecticides were acquired for control of *S. frugiperda* in the 2017 cropping season (Kassie et al. 2020). In Burkina Faso, approximately 12,000 liter of synthetic insecticides were sprayed onto 14,000 ha of *S. frugiperda* infested fields, during the 2018/2019 cropping season (MAAH 2018). Kumela et al. (2019) recorded 48% of farmers used chemical sprays in Ethiopia and Kenya. In Botswana 27% of farmers applied insecticides (Makale et al. 2021) and Cameroon 26% of farmers applied insecticides twice per week for the duration of the crop cycle, without reducing the incidence of damaged plants or severity of damage (Kuate et al. 2019). In Nigeria, cypermethrin, deltamethrin, lambda-cyhalothrin, permethrin, and chlorpyrifos are applied onto maize for control (Togola et al. 2018). Although the large-scale insecticide usage reported above cannot be extrapolated to all the affected countries in Africa, it illustrates the actions taken to mitigate the threat of *S. frugiperda* in some countries or localized regions within countries. In East Asia, including China there is large-scale use of insecticides in general (Wu 2018, Li et al. 2022) with spray frequencies of up to seven sprays per cropping cycle (Wu et al. 2020).

Insecticide Application Methodology

Poor field-level performance and repeated applications of insecticides for *S. frugiperda* control may often be ascribed to the inappropriate use of insecticides, poor calibration of spray equipment (Al-Sarar et al. 2006, Suguiyama et al. 2020, Makale et al. 2021). Reports from various African countries indicate that farmers apply pesticides at varying application rates, mix chemicals into single sprays or apply

these at incorrect dosage rates (Kansiime et al. 2019, Kassie et al. 2020, Tambo et al. 2020b).

The impact of insecticide application methodology on resistance evolution by *S. frugiperda* was highlighted by Al-Sarar et al. (2006). Spray distribution and deposition over plants differ with different types of application equipment, providing varying coverage and doses of insecticides, that select for resistance. Application rate and deposition structure on plant leaves influence selection pressure and resistance evolution. For example, insecticide droplet sizes, number, and distribution affected efficacy results with larval mortality being higher with small droplet patterns compared to large droplet patterns. Consumption by *S. frugiperda* larvae was also lower on leaves with small droplet patterns than those with large droplet patterns. Praat et al. (1996) indicated differences in larval feeding behavior on leaves with either small or large droplet patterns, which lead to larvae encountering insecticides at different dosages. In the case of small deposit patterns, larvae encounter the insecticide largely by contact and feeding, while in large deposit patterns larvae encounter sub-lethal doses, which selects for the development of resistance.

Chemical control does, however, remain largely effective if used according to label directions (Jepson et al. 2018). Insecticide application at the correct time and crop growth stage provides effective control of *S. frugiperda*, provided the pest population is not resistant to the particular pesticide. It is also important to consider that only an estimated 0.00001–1% of the pesticides that are applied, actually reaches the target pests (Pimentel 1995).

Disruption of Existing IPM and IRM Programs

Although the agrochemical industry responsibly addressed the importance of IRM during the past decades (Sparks and Nauen 2015), resistance evolution may also be affected by ecological changes that occur in pest communities. For example, a complicating factor that may increasingly contribute to resistance evolution is the disruption of existing pest management practices and insect resistance management (IRM) programs. Yang et al. (2021) described significant changes in the pest management regimes and increased dependency on insecticides following the *S. frugiperda* invasion in China. The arrival of a new pest species firstly changes the pest community composition in the crop (Krüger et al. 2008, Ntiri et al. 2019, Visser and Van den Berg 2020, Sokame et al. 2021), often by displacing or dominating the indigenous pests. In Uganda, Hailu et al. (2021) reported that *S. frugiperda* may be displacing indigenous stemborers from maize, but not from sorghum. In many cases such changes in pest complex may lead to changes in frequency of insecticide applications which disrupts existing biological control processes. For example, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) was reported to displace the indigenous African maize stemborer (*Busseola fusca* (Fuller) (Lepidoptera: Noctuidae)) (Kfir 1997) in sorghum in parts of South Africa. Management of *B. fusca* prior to *C. partellus* becoming part of the pest species complex was relatively easy, due to its highly predictable moth flight pattern (Van den Berg et al. 1991).

Similarly, *S. frugiperda* (Mutiyambai et al. 2022) is the dominating lepidopteran pest in maize in Kenya, only four years after its arrival in the country. Because farmers are unfamiliar with such new pests and the perception is that it threatens yield, it leads to increased pesticide applications. This may lead to multi-species selection for resistance if the frequency of insecticide applications increases where *S. frugiperda* co-occur with other pests. For example, in Australia,

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) occurs together with *S. frugiperda* in maize and sorghum cropping systems (Bird et al. 2022), as well as in areas where these and other host crops are grown in rotational systems and where *Helicoverpa punctigena* (Wallengren) (Lepidoptera: Noctuidae) occurs (Maino et al. 2021). A similar situation exists with the co-occurrence of *S. frugiperda* and *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) in China. In Africa, *S. frugiperda* is one of several lepidopteran pests that co-inhabit maize and sorghum crops (Ntiri et al. 2019, Sokame et al. 2021, Mutiyambai et al. 2022). Challenges in terms of insect resistance management (IRM) within a multi-species pest complex have been described by Visser and Van den Berg (2020).

Infrastructure, Insecticide Availability, and Policy Issues

In the response to *S. frugiperda* in Africa, governments purchased and distributed insecticides worth millions of dollars, often favoring cheaper and higher risk products. For example, pesticides used for *S. frugiperda* control in Africa include methomyl, methyl parathion, endosulfan, and lindane, all of which are classified as highly hazardous pesticides (FAO 2018). Most African countries, until recently, had no insecticide formulations specifically recommended or registered for the protection of maize against *S. frugiperda* (Sisay et al. 2019, Koffi et al. 2020a, Suguiyama et al. 2020). In only two African countries (South Africa and Kenya) emergency registrations of insecticides were done, despite the Pesticide Emergency Use Authorization (PEUA) regulatory tool that exists in many countries (Suguiyama et al. 2020). This regulatory tool allows for emergency registration of insecticides until the necessary registration process is completed. Without this due process, farmers are left with few control options other than using off-label application of older and in many cases more toxic chemical insecticides (Suguiyama et al. 2020). Pesticide use therefore often occurs in a poorly regulated environment (Oluwole and Cheke 2009, Karungi et al. 2011), where input providers and farmers are uninformed regarding their appropriate use (Karungi et al. 2011) and where the agrochemical industry is under-developed (Makale et al. 2021).

Effective chemical control of *S. frugiperda* largely depends on farmers' knowledge of the pest, insecticides, and application methods. Unfortunately, smallholder farmers in Africa have little previous experience in the handling and application of insecticides (Bateman et al. 2018, Jepson et al. 2020) and insect resistance management is a huge challenge (Van den Berg et al. 2022). Poor knowledge of basic biology and ecology of insect pests and the use of pesticides, especially in developing regions such as Africa and other newly invaded regions is a challenge in terms of resistance management.

Knowledge of aspects such as mode of action (MoA) and insecticide rotation programs is largely absent at farm-level in Africa (Van den Berg et al. 2021). Williamson et al. (2008) summarised the supply chain of agrochemical products in several African counties as follows: (1) authorized retail outlets of agricultural supply companies, (2) government extension services, (3) small-scale informal traders operating via local shops, (4) visitors to villages and weekly markets, and (5) bulk supplies from general markets in larger towns. The last three channels frequently repackage products, with the contents that often do not correspond to the product label. These factors, together with the poor availability of active ingredients from different insecticide groups to allow for the rotation of different MoAs, may also contribute to resistance evolution Williamson et al. (2008).

Table 2. Chemical insecticides registered for control of *Spodoptera frugiperda* in Africa. (adapted from Otim et al. 2021)

Class	IRAC Group	Active ingredient	Country
Avermectins	6	Abamectin + Emamectin benzoate	Uganda
		Abamectin	Malawi
		Emamectin benzoate	Malawi, Uganda, South Africa, Zambia
Benzoylureas	15	Lufenuron	Kenya
		Diffubenzuron*	South Africa*
Carbamates	1A	Methomyl	South Africa
		Carbosulfan	Kenya
		Cartap hydrochloride	South Africa*
Organophosphates	1B	Chlorpyrifos	Malawi, South Africa
		Profenofos	Malawi
		Mercaptothion [syn. Malathion]	South Africa
		Acephate	Kenya
Oxadiazine	22A	Indoxacarb	Malawi, South Africa, Zambia, Kenya, Sudan
Pyrethroids	3A	Beta-cypermethrin	South Africa
		Alpha-cypermethrin	Kenya
		Deltamethrin	Malawi, Zambia
		Cypermethrin	Cameroon, Malawi
		Lambda-cyhalothrin	Kenya
		Teflubenzuron + Cypermethrin	Malawi
		Gamma-cyhalothrin	Kenya
Diamides	28	Flubendiamide	Malawi, South Africa, Kenya
		Chlorantraniliprole	South Africa, Kenya, Zambia
Spinosyns	5A	Spinetoram	South Africa, Kenya
Pesticide combinations			
Avermectin + Diamide	6 + 28	Abamectin + Chlorantraniliprole	Kenya
Avermectins + Benzoylureas	15 + 6	Lufenuron + Emamectin benzoate	Malawi, Sudan
Avermectins + Benzoylureas	15 + 6	Lufenuron + Emamectin benzoate*	South Africa*
Benzoylureas + Oxadiazine	15 + 22	Novaluron + Indoxacarb	South Africa
Carbamate + Pyrethroids	1A + 3A	Benfuracarb + Fenvalerate	South Africa
Organophosphates + Pyrethroids	1B + 3A	Profenofos + Cypermethrin	Uganda
		Pirimiphos methyl + Deltamethrin	Malawi, Zimbabwe
		Chlorpyrifos + Cypermethrin	South Africa, Zambia
		Chlorpyrifos + Lambda-cyhalothrin	South Africa
		Lambda-cyhalothrin + Thiamethoxam	Uganda
		Chlorantraniliprole + Thiamethoxam	Zambia, Zimbabwe
		Chlorantraniliprole + Lambda-cyhalothrin	South Africa, Zambia
Pyrethroids + Neonicotinoids	3A + 4A	Lambda-cyhalothrin + Thiamethoxam	Uganda
Diamides + Neonicotinoids	28 + 4A	Chlorantraniliprole + Thiamethoxam	Zambia, Zimbabwe
Diamide + Pyrethroid	28 + 3A	Chlorantraniliprole + Lambda-cyhalothrin	South Africa, Zambia
Spinosyn + Benzoylureas	5A + 18	Spinetoram + Methoxyfenozide	South Africa
Spinosyn + Diamide	5A + 28	Spinetoram + Flubendiamide	Sudan

The active ingredients previously listed by Otim et al. (2021) for South Africa represented emergency registrations in 2017.

*Active ingredients of which the emergency registration received in 2017 lapsed, and which are not currently registered for control of *S. frugiperda* in South Africa (see: <https://www.agri-intel.com/label-information/search-registration-information/>).

In total, 44 different products, and 22 different active ingredients (excluding *Bacillus thuringiensis* and *Beauveria bassiana*), belonging to 10 mode of action (MoA) groups were registered in South Africa. After the emergency registrations of these active ingredients lapsed, several were not registered for control, resulting in 17 active ingredients, belonging to nine MoA groups currently registered for control of FAW in South Africa. Eleven of these active ingredients belong to 8 IRAC groups and are registered to be applied on their own against *S. frugiperda* (Agri-Intel 2021) while registered mixtures contain various combinations from 11 active ingredients belonging to 7 groups (Agri-Intel 2021) (Table 2).

The bleak picture regarding large-scale use of insecticides described above could partly be ascribed to the emergency responses of the international community and governments to address threats to food security in regions where this pest attacked a staple crop. This situation seems, however, to be changing for the better. The investment in *S. frugiperda* research in newly invaded countries over the last six years has generated a significant body of information that will improve the management of this pest. The generation of

field-data which indicate that the yield losses may be overestimated in some regions (Baudron et al. 2019, Koffi et al. 2022), is likely leading to reduced insecticide use in countries where the initial response to this pest was to subsidize the use synthetic insecticides. Farmers' perceptions of infestation levels and the threat of crop losses may also be changing, for example, farmer surveys in Zambia (Kansiime et al. 2019), Ghana (Koffi et al. 2020, Nboyine et al. 2020) and Kenya (De Groot et al. 2020) reported lower infestation levels in years following the initial observations of this pest on their farms. These observations do however differ between countries and agroecological zones and also in regions where this reduction has not been reported.

Investments in biological control programs, for example, those in Africa (Kenis et al. 2019, Chandish et al. 2021) and China (Chen et al. 2019, Xing et al. 2022) are highly likely to contribute significantly to a reduction in pest pressure over the long term, which will lead to reduced pesticide use. The many species of indigenous natural enemies that developed new associations with *S. frugiperda* in Africa (Sisay et al. 2018, Tapa-Yotto et al. 2022), China (Xing et al.

2022) and India (Chandish et al. 2021) will also in future contribute to the suppression of *S. frugiperda* populations.

Insect Resistance Management

Evolution of insecticide resistance can be delayed by minimizing their use and employing appropriate IRM programs (Carrière et al. 2020). The overall goal of IRM programs is to reduce pest pressure on the crops while simultaneously minimizing selection pressure toward any one specific group of insecticides, biological products, or transgenic insect resistance traits (Sparks et al. 2020). This importance of effective and proactive resistance management to maintain the efficacy of current and future insecticides has for a long time been recognized by the agrochemical industry (Jackson 1986, Voss 1988, McCaffery and Nauen 2006, Sparks and Nauen 2015).

IRM can take many forms, including the use of insecticide mixtures, mosaics or alternations/rotations (Roush 1989, Zhao et al. 2010, IRAC 2012). Rotating of MoAs is the most used and effective IRM approach. Rotation of MoA avoids treating consecutive generations of the target pest with insecticides in the same MoA group, and employing the principle of MoA treatment windows which encompasses a full life-cycle of the targeted pest (Barbosa et al. 2020, Sparks et al. 2020). An IRM strategy should be pro-active and aimed at reducing selection pressure (Bielza 2008). The use of insecticides should be optimized and the use of insecticide mixtures with additional mode(s) of action may provide benefits for IRM when appropriately incorporated into insecticide rotation strategies. Furthermore, since the same active ingredients are often registered to control different species in a pest complex, an IRM strategy is often hampered by multiple insecticide applications against the respective pests, without taking into consideration the generation time of the various pests. This often results in successive generations exposed to active ingredients from the same MoA group, enhancing the evolution of resistance. For this reason, regular monitoring of susceptibility levels of *S. frugiperda* to insecticides should be done.

The promotion of chemical pesticides for *S. frugiperda* control, especially in regions where the agrochemical industry is poorly developed and where there is a lack of access to appropriate spray equipment and insecticides, jeopardizes the efficacy of control and promotes resistance evolution. There is a need to make effective, low-risk products available and given that biopesticides are generally considered to be lower risk options for pest management, these promising avenues should be explored further (Bateman et al. 2018).

Ultimately, IPM, rather than reliance on a single tactic, is the best way to control *S. frugiperda*. A combination of tactics is more reliable, effective, and safe to sustainably manage *S. frugiperda* and other maize pests, while minimizing the use of broad-spectrum insecticides (Harrison et al. 2019, Murray et al. 2019, Njaguna et al. 2021, Tepa-Yotto et al. 2022).

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