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Invited Article

Special Collection: World-Scale Ecology and Management of Fall Armyworm (*Spodoptera frugiperda*)

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 (Luginbill 1928), was first reported on the African continent in 2016 (Goergen et al. 2016). Since then, it spread throughout sub-Sahara 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 Groote et al. 2020, Kansiime 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 2021, 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, chlorpyriphos, 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 agrochemical 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 (Kranthi, 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. frugiperda* susceptibility to insecticides with increased larval age and

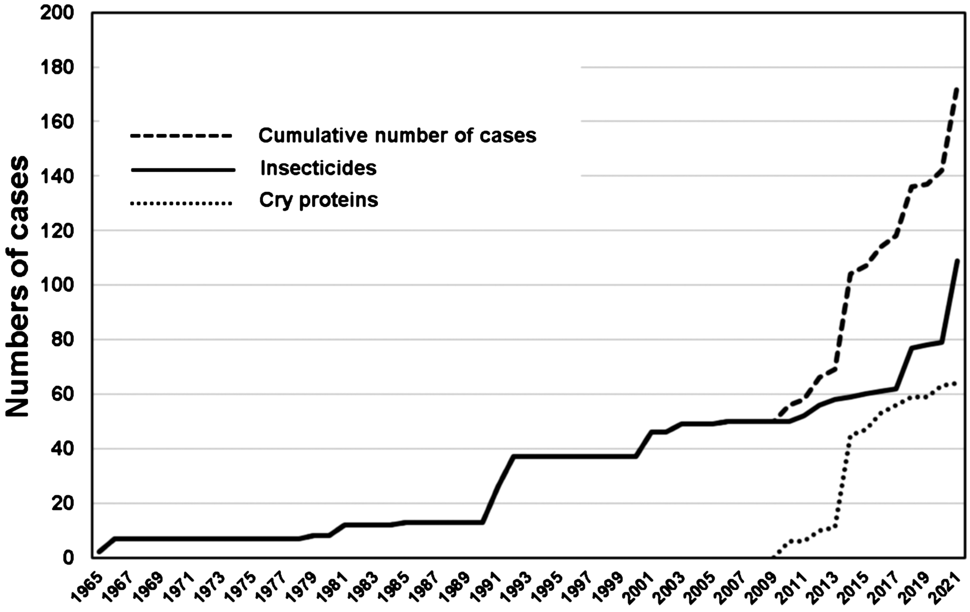

Fig. 1. The number of insecticides and *Cry* proteins to which resistance has been recorded for *Spodoptera frugiperda* (https://www.pesticideresistance.org/).

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	
Common and indiscriminate use of insecticides	Tambo et al. 2020a, b
Poor regulatory systems	Oluwole and Cheke 2009, Karungi 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. 2020a
Over estimation of risk	Wightman 2018, Baudron et al. 2019, Van den Berg et al. 2021, Osae 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
Smallholder farmers with little previous experience of handling or applying insecticides	Chimweta et al. 2020, Osae et al. 2022
Ignorance of management guidelines	
Uncontrolled and improper use of chemical pesticides	
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; Cook et al. 2004; Kranthi 2005; Al-Sarar et al. 2006; Fatoretto et al. 2017; Kumela et al. 2019; Suguiyama et al. 2020; Makale et al. 2021;

mass, with LD_{50} 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. Georghiou (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. 2020b), 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-Garcia 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 (Fatoretto 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-Sahara 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 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* (Mutyambai 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 punctigera* (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, Mutyambai 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
		Diflubenzuron[a]	South Africa[a]
Carbamates	1A	Methomyl	South Africa
		Carbosulfan	Kenya
		Cartap hydrochloride	South Africa[a]
Organophosphates	1B	Chorpyrifos	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[a]	South Africa[a]
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
Pyrethroids + Neonicotenoids	3A + 4A	Lambda-cyhalothrin + Thiamethoxam	Uganda
Diamides + Neonicotenoids	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	Spinotetramat + Flubendiamide	Sudan

The active ingredients previously listed by Otim et al. (2021) for South Africa represented emergency registrations in 2017.
[a] Active ingredients of which the emergency registration received in 2017 lapsed, and which are not currently registered for control of *S. frugiperda* 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 2022) while registered mixtures contain various combinations from 11 active ingredients belonging to 7 groups (Agri-Intel 2022) (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. 2020b, Nboyine et al. 2020) and Kenya (De Groote 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, Tepa-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 (Midega et al. 2018, Harrison et al. 2019, Murray et al. 2019, Njuguna et al. 2021, Tepa-Yotto et al. 2022).

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