SUSCEPTIBILITY OF *SPODOPTERA FRUGIPERDA* (LEPIDOPTERA: NOCTUIDAE) POPULATIONS FROM MARANHÃO, TOCANTINS, PIAUÍ AND BAHIA TO TRANSGENIC MAIZE CULTIVARS WITH CRY/VIP TOXINS FROM *BACILLUS THURINGIENSIS*

Alisson Franco T. da Silva[1], Luciana B. Silva[2], José B. Malaquias[3], Angélica S. Salustino[4], Domingos Francisco Correia Neto[5], Daniel M. Pacheco[6], Daniel B. Fragoso[7], Eliseu J. G. Pereira[8]

ABSTRACT

In some countries, the use of transgenic maize, cotton and soybean cultivars has increased significantly in recent years, reaching adoption levels above 90% in many regions, imposing intense selection pressure for resistance in the populations of the target insects. The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a polyphagous and migratory insect of global economic importance. Their populations in Brazil represent one of the main targets for the control of insecticidal proteins (toxins) of *Bacillus thuringiensis* Berliner (Bt) produced in transgenic cultivars. In addition, most of these crops receive applications of synthetic insecticides against a complex universe of insect pests and the adoption of non-Bt refuge areas is low. Several first and second generation Bt corn cultivars (with Cry toxins such as Cry1F, Cry1Ab and Cry1A.105 + Cry2Ab2) have lost efficacy against *S. frugiperda* populations by selection for resistance to Bt. Currently, reports lead to the

[1] Professor Cinobelina Elvas Campus
Federal University of Piauí
[2] Professor Cinobelina Elvas Campus
Federal University of Piauí
lubarbosabio@ufpi.edu.br
[3] Entomology Laboratory
Center for Agrarian Sciences
Federal University of Paraíba
malaquias.josebruno@gmail.com
[4] Entomology Laboratory
Center for Agrarian Sciences
Federal University of Paraíba
angelicasalustino@gmail.com
[5] Entomology Laboratory
Center for Agrarian Sciences
Federal University of Paraíba
correira.neto@ufpb.br
[6] Professor Cinobelina Elvas Campus
Federal University of Piauí
marquesdaniel@ufpi.edu.br
[7] Embrapa Tocantins
daniel.fragoso@embrapa.br
[8] Department of Entomology
Federal University of Viçosa
National Institute of Science and Technology in Plant-Pest Interactions
Bioagro
Federal University of Viçosa

suspicion that S*. frugiperda* control failures associated with the resistance event also affect the current third generation Bt corn cultivars, which jointly produce the toxins Vip and Cry. Although the Vip toxin originally showed efficacy against caterpillars resistant to Cry toxins, at least the caterpillars in the early stages, the loss of efficacy of these toxins makes Bt Vip/Cry corns more vulnerable to Bt resistance selection in *S. frugiperda populations*. Thus, it is crucial to obtain regional and reliable data on the susceptibility of insect populations to inform decision-making on management practices. The first objective in this study was to investigate the susceptibility status of field populations of *S. frugiperda from* sites with selection pressure with Bt Vip/Cry corn for more than five years. Time-mortality bioassays were used with F1 descendant third instar larvae from six populations collected in maize fields in the MATOPIBA region, a tropical agricultural frontier that covers four Brazilian states, Maranhão, Tocantins, Piauí and Bahia. The insects were evaluated in longitudinal time-mortality bioassays. The time to death of S*. frugiperda* third instar larvae was relatively short, with mortality rates of 98–100% in less than five days, regardless of the Bt corn hybrid containing three combinations of Cry1Ab, Cry1F, Cry2Ab, and Vip3Aa. However, the mean survival time (ST50) of larvae differed between populations, with the lowest and highest ST50 values occurring for the PI-Cr (42 h or 1.75 days) and PI-Ur (66–90 h or 2.75–3.75 days) populations, respectively. Therefore, the third instar larvae of the F1 generation of *S. frugiperda populations* were susceptible to corn foliage that produces Vip3Aa/Cry, and the most contrasting susceptibility occurred in insects from the state of Piauí. These results indicate that the progeny of *S. frugiperda* from areas highly pressured with Bt Vip3Aa/Cry corn hybrids is killed in the corn foliage that produces Bt Vip3Aa and Cry proteins, despite field reports of increased leaf injury by the caterpillars in some localities. In view of these results and the complaints of producers and technicians, the question arose whether there is a change in the susceptibility to Bt toxins in other larval instars of the insect, especially those that are later, supposedly more tolerant to Bt. Thus, the second chapter aimed to investigate whether there is variation in larval survival from the first to the fourth instar of *S. frugiperda* caterpillars, using the F1 generation of five geographically distinct populations collected in corn fields in the MATOPIBA region. There was a variation in susceptibility in the other instars evaluated, evidenced in the survival curves and mortality after seven days of contact of the larvae with the foliage of Bt corn. The greatest variations and the lowest percentage of mortality were found in the population of Bahia with the fourth instar and in the population of Piauí-Ur in the first and fourth instar and there was heterogeneity in the mortality pattern among the instars depending on the type of Bt corn and the population of the insect. Therefore, no decrease in the susceptibility of the insects was detected in the late instars, reinforcing the general conclusion of susceptibility of the populations collected in the states of MATOPIBA. The results of this study help to understand the risk of evolution of resistance to Vip3A and to refine mathematical models for the sustainable use of Bt crops, an insect management tool that is safe for human health and the environment. Further studies will be needed to investigate the undesirable presence and injury of *S. frugiperda* in maize crops and to generate tools for the management of *S. frugiperda resistance* to Bt maize.

Keywords: Fall armyworm. Insect management. Matopiba. Insecticidal proteins. *Zea mays*.

1 GENERAL INTRODUCTION

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae), is a polyphagous, migratory and versatile pest that attacks vegetative and reproductive stages of several crops and wild plants (Montezano *et al*., 2018; Kenis *et al*., 2023). *Spodoptera frugiperda* is a global concern due to its migratory capacity and polyphagia. Although native to the Americas, the insect has spread worldwide, recently invading Africa, Asia, and Australia and is present in more than two hundred countries (Wan *et al*., 2021; Kenis *et al*., 2023). Since the mid-2000s, transgenic corn and cotton cultivars producing insecticidal proteins with *Bacillus thuringiensis* (Bt) have been the main control method for these two crops in the Americas (ISAAA, 2019; Huang, 2021).

Prior to the use of transgenic crops, control of *S. frugiperda* in the Americas was primarily based on synthetic insecticides, and over the years, resistant populations of this insect have been selected for many major classes of insecticides (Pitre, 1988; Yu, 1991; Berta *et al*., 2000; Belay, 2012; Bernardi *et al*, 2016a; Gutiérrez-Moreno *et al*., 2019), including carbamates, organophosphates, and pyrethroids (Sogorb *et al*., 2002). Currently, many countries, especially Brazil, have adopted transgenic cultures that express Bt proteins for the management of this insect (Huang, 2021). Due to the large-scale adoption of these crops, in many regions, reaching more than 90%, the selection pressure for resistance and populations of *S. frugiperda* to Bt proteins is intense. In fact, there was a rapid emergence of resistance in populations of *S. frugiperda* to Cry1F corn (TC1507 or Herculex technology) with field control problems in Puerto Rico, in the continental USA, Brazil and Argentina. (Storer *et al.*, 2010; 2012; Would *et al.*, 2014; Huang *et al.*, 2014; Bernardi *et al.*, 2016b; Omoto *et al.*, 2016; Chandrasena *et al.*, 2018; Adam *et al.*, 2020; Huang, 2021)

Previous studies show results on the susceptibility or resistance of field populations of *S. frugiperda* in relation to characteristics of simple Bt corn (from a Bt toxin) and pyramid (containing combinations of them). There is evidence of large-scale resistance to Cry1F protein in populations of the Americas, as well as cross-resistance to Cry1A.105/Cry2Ab2 corn (PRO technology). Some studies report susceptibility to the proteins Cry2A and Vip3Aa20. For example, Li (Bernardi *et al.*, 2015; Santos-Amaya *et al.*, 2015) (Huang *et al.*, 2014) *et al*. (2016) evaluated populations of *S. frugiperda*, reporting susceptibility to Cry2A and Vip3Aa20, but resistant to Cry1A.105 and Cry1F. A similar investigation was conducted using maize, containing Vip3Aa20 and Cry1Ab, all populations were susceptible to the combinations of toxins containing Vip3Aa20. evaluated the survival and estimated the level of effective dominance of resistance of three different genotypes of

(Yang *et al.*, 2013) Zhu *et al*. (2019) *S. frugiperda*: one susceptible to Bt, one resistant to the double genes Cry1A.105/Cry2Ab2, and heterozygous F1 lines in five pyramided corn hybrids expressing Cry1A, Cry2A, Cry1F, and Vip3 proteins, concluding that Vip3Aa20 is the only protein completely active against *S. frugiperda*.

The bioassay method with corn leaf tissue is commonly used in studies related to Bt resistance. tested the efficacy of a cultivar expressing the double genes Cry1B.868 and Cry1Da_7, and experimental lines of single genes expressing Cry1B.868 or Cry1Da_7 in a susceptible S Horikoshi *et al*. (2021) *. frugiperda* population in Brazil, showing satisfactory control. Another study conducted in Brazil in 2015 determined the susceptibility of field populations of *S. frugiperda* to Cry1Ab using the leaf tissue bioassay method, with control efficacy of around 88.4% in 5 days. In the USA, Niu (Omoto *et al.*, 2016) *et al*. (2018) evaluated the performance of *S. frugiperda* exposed to the cultivar containing the proteins Cry1A.105/Cry2Ab2 using leaf tissue bioassay to assess adaptation costs and resistance dominance levels.

The sum of the investigations carried out in different parts of the world showed that the resistance to Cry1F in the caterpillars is completely overcome by the control efficiency due to the absence of cross-resistance in plants that produce Vip or in bioassays with the purified Vip protein. This was evidence to propose that the Vip protein can be used to manage Cry resistance in *S. frugiperda* and the companies opted for the strategy of "pyramiding" these proteins in plants. It is important to emphasize that the gene pyramidization strategy for resistance management requires a careful selection of Bt genes to be stacked (pyramided) in plants. (Niu *et al.*, 2013; Bernardi *et al.*, 2015; Santos-Amaya *et al.*, 2022)

Studies on the status of susceptibility and/or resistance to Bt in S*. frugiperda* populations in Brazil aim to evaluate the current levels of resistance/susceptibility in the main maize producing regions. In addition, these studies seek to analyze the correlations between resistance/susceptibility and various factors potentially associated with the selection of resistant populations. These factors include the locally occurring *S. frugiperda* race/genotype (maize versus rice breed), selection pressure of Bt crops, migration patterns, Bt crop planting history, geographic location, and insect survival habits in the off-season.

Understanding the changes in susceptibility to Bt toxins during larval development in *S. frugiperda* populations can help predict the performance of certain refuge settings and other strategies for resistance management in tropical farming areas with a high incidence of *S. frugiperda*. In the present study, we evaluated whether there are changes in susceptibility to Bt toxin during larval development of the F1 generation in different populations of *S.*

frugiperda collected in a tropical agricultural frontier region that covers four Brazilian states, Maranhão, Tocantins, Piauí and Bahia (MATOPIBA).

The first objective was to collect field populations of *S. frugiperda* in different locations of the MATOPIBA region, and to perform laboratory bioassays, with third instar larvae of the F1 generation, to determine the susceptibility to corn cultivars containing the combinations of Bt proteins (Cry1F, Cry1A.105, Cry1Ab, Cry2Ab2, Cry3Bb1, Vip3Aa20). From the results obtained, the question was raised whether there is variation in the susceptibility to Bt toxin in the different larval instars.

The knowledge generated from these studies will help in the understanding of the current status and factors related to the management of *S. frugiperda*, and thus preserve the technology of Bt cultures for the control of *S. frugiperda* in the MATOPIBA region, in Brazil and in the world.

2 EXPERIMENTAL STRATEGY

A study was carried out on the survival of *S. frugiperda* larvae in Bt Vip3Aa20/Cry corn foliage and non-Bt control in a randomized block system. For this, we used isogenic corn cultivars (i.e., which have the same genetic background, except for the transgene inserted in the Bt corn genome). Bt corn was planted in a greenhouse to be used in the bioassays. The caterpillars were collected in corn fields and kept in the laboratory, fed with an artificial diet until they completed the cycle. In the same way that the neonates were kept on an artificial diet until they reached the third instar. Populations of caterpillars collected in the region of Balsas/MA, Porto Nacional/TO, Baixa Grande/PI, Currais/PI, Uruçuí/PI and Luis Eduardo Magalhães/BA were used for the trials with third instar caterpillars. Individuals from populations in the MATOPIBA region were used for the work. This sampling effort was concentrated in the 2/2021, 1/2022 and 2/2022 harvests, which corresponds approximately to the first and second harvests in Brazil.

The survival and median lethal time of third instar larvae of the F1 generation of populations collected in the maize fields of the Matopiba region was measured, similar to the methodology of . Tavares *et al* ., (2021)

In the second stage, trials were carried out with the other instars using the same populations, with collections carried out in the 2022/2023 and 2023/2024 harvests, except for the population of Baixa Grande/PI. In this stage, survival and mortality time curves were performed to compare susceptibility between instars and between populations.

3 THEORETICAL FOUNDATION

3.1 CORN CULTIVATION

The corn crop (*Zea mays* L.) has become the most cultivated in the world. being a species belonging to the Gramineae/Poaceae family, with a great capacity to adapt to the most varied types of climate and altitude, favoring its cultivation in different parts of the world (Barros, 2014). The Aztecs, Incas and Mayans considered it as a sacred plant, being used as food and offering to the gods. The cultivation of corn in Brazil was initially practiced by the indigenous people, who used it for their food (Cruz, 2008). (Hailu *et al*., 2018; Niassy *et al*., 2021)

Corn production was leveraged from 20 million tons in the 70s to about 131 million tons in the 2022/23 harvest, with a planted area of 45.7 million hectares in the 2023/24 harvest (CONAB, 2024). Currently, corn is cultivated for both human and animal food, and about 70% of the world production and 70 to 80% of the national production of corn is used in poultry and pig feed (Cruz, 2008; CNA, 2023). The world's largest producers of corn are the United States, China, and Brazil (CONAB, 2024).

This increasing increase in the area planted with corn has led to the emergence of many pests, and the fall armyworm, *S. frugiperda*, is currently considered the main pest of corn in all continents where the crop is present. In view of the large number of pests in the corn crop, genetically modified (GM) varieties of corn were created in order to combat the attack of these insects, reducing the use of chemical products. For the planting of the 2019/2020 crop in Brazil, 196 corn cultivars were presented, 131 transgenic cultivars and 65 conventional cultivars (Schuster; Rodrigues; Linares, 2022). Insect populations resistant to active ingredients such as lambda-cyhalothrin, chlorpyrifos, spinosad, and lunofuron can be selected. (Goergen *et al*., 2016) (Burtet *et al*., 2017)

3.1.1 Bt technology

Bacillus thuringiensis (Berliner) is a rod-shaped Gram Positive bacterium that lives in the soil, producing toxins that have activities against protozoa, mites, nematodes and insects. This bacterium was discovered in Germany in 1911, and began to be used as an insecticide in France in 1938 and in the USA in the 1950s (Luthy (Baranek *et al.*, 2017) *et al.*, 1982). It is an aerobic bacterium, capable of producing insecticidal proteins during the sporulation process, such as parasporal crystals (Cry) and insecticidal vegetative proteins (VIP) that are highly specific to the target insect, and it is a biodegradable protein and safe for humans, plants, and other classes of vertebrate animals. Using this insecticidal protein, through the use of recombinant DNA technology, transgenic plants resistant to insects, such as the fall armyworm, were created. Among the toxinogenic bacteria that aim to control pest

insects, (Tetreau, 2018) (Baranek; Konecka; Kaznowski, 2017) (Monnerat *et al.*, 2006) *B. thuringiensis* is undoubtedly the most studied, certainly because it is the most used in the control of agricultural pests. (Tetreau, 2018)

This bacterium, during the sporulation process, produces a crystalline protein toxic to insects, which are toxins of high specificity that bind to receptors in the wall of the midgut of insects allowing the oligomerization of the insecticidal protein, causing the formation of pores and the consequent perforation of the intestine leading to the death of individuals. Known as Cry proteins or δ-endotoxins, these crystals are formed of one or several proteins that are toxic to various orders of insects, such as Coleoptera, Diptera, Hymenoptera and Lepidoptera. Currently, more than 70 different groups of Cry toxins are known, with more than 770 gene sequences described (Crickmore (Tetreau, 2018) *et al*., 2021). There is also secretion of insecticidal proteins produced by *B. thuringiensis*, which includes 4 groups of insecticidal vegetative protein (Vip) and one group of secreted insecticidal protein (Sip) (Crickmore *et al*., 2021).

The first genetic modification in plants took place in 1985, in tobacco plants (Martineau, 2001) and the first GM corn variety took place in 1996 to combat insect pests on the European continent. The genetic modification of the corn crop was done with the introduction of a gene from the bacterium (Storer *et al.*, 2010) *B. Thuringiensis* (Bortolotto *et al.*, 2016) . The use of Bt crops has been used since 1996, with the use of bacterial genes in maize plants to express B*. thuringiensis* proteins against insect pests, which has contributed greatly to the reduction of applications of different insecticides, reducing damage to the environment. However, some insects have been able to form populations resistant to Bt technology, which has led to increased applications of insecticides against fall armyworm in Bt corn crops (Burtet (Bortolotto *et al.*, 2016) *et al*., 2017). To reduce the speed at which this resistance develops, one of the recommended measures is to plant refuge. This involves creating areas with non-Bt crops next to areas with Bt corn (Fatoretto *et al*., 2017).

Bt insecticidal proteins Cry1Ab, Cry1F, Cry1A.105, Cry2Ab2, and Vip3Aa20 have been inserted into maize (Bt maize) plants to protect against a wide range of lepidopteran pests (ISAAA, 2023). The Bt protein Cry1Ab, in the MON810 or Bt11 corn events, was the first to be implanted in the Americas against fall armyworm. Subsequently, the event of maize TC1507 Bt, producing the insecticidal protein Cry1F from (Fatoretto *et al.*, 2017) *B. thuringiensis aizawai*, was introduced to the market. Almost simultaneously, Cry2Ab2, derived from (Storer *et al.*, 2012; Fatoretto *et al.*, 2017) *B. thuringiensis kurstaski* , and Cry1A.105, a synthetic chimera of Cry1Ab, Cry1Ac and Cry1F, were also introduced in the transgenic event MON89034 (EPA, 2012; . Finally, the Bt Vip3Aa20 protein, derived from the

AB88 strain of (Carrière *et al.*, 2020) *B. thuringiensis* and produced in a transgenic event of MIR162 corn, was launched on the market and has become increasingly adopted in Brazil since 2018, after its incorporation into elite corn hybrids. (Fatoretto *et al.*, 2017) (Schuster; Rodrigues; Linares, 2022)

The use of Bt insecticidal proteins, whether used in biopesticides or in transgenic cultivars, represent a safe pest management tool due to their specific toxicity against target organisms. However, resistance screening in pest populations is the main threat to the sustainability of Bt technologies for pest management, especially fall armyworm, which is inherently less susceptible to many Bt toxins. The efficacy of Bt corn hybrids producing Bt Cry proteins had already decreased against fall armyworm, and the structural homology of these proteins is conducive to cross-resistance between them. This is in contrast to Vip and Cry, which can bind to distinct sites on protein receptors in the insect's gut. (Raymond *et al.*, 2010; Gómez *et al.*, 2014) (Adang *et al*., 2014; Gómez *et al*., 2014; Carrière *et al*., 2016; Fatoretto *et al*., 2017) (Adang *et al*., 2014; Bernardi *et al*., 2015; Carrière *et al*., 2016) (Adang *et al.*, 2014; Carrière *et al.*, 2016; Núñez-Ramírez *et al.*, 2020)

Brazil is the second country that most uses crops expressing Bt technology in the world (52.8 million ha), with about 16.6 million hectares planted with Bt corn in 2019 (Schuster; Rodrigues; Linares, 2022), reaching total percentages of the planted area of 82, 79 and 62% of cotton, corn and soybeans, respectively. In recent years, the use of Bt crops has become more and more frequent, in the search for an alternative to combat (CIB, 2019) *S. frugiperda* (Amaral *et al*., 2020), with minimal use of chemical products.

The wide use of Bt crops in Brazil, associated with the low adoption of refuge has contributed to the rapid selection of resistance by *S. frugiperda* to Cry1 proteins. The first reports of resistance of (Santos-Amaya *et al*., 2016; Adam *et al*., 2020) *S. frugiperda* to the Cry1Fa protein in Bt corn occurred in Puerto Rico, in 2006, and were confirmed in 2010, leading to the withdrawal of corn cultivars expressing this protein from the Puerto Rican market. The insects show rates of cross-resistance to the insecticidal proteins Bt Cry1 and Cry2. (Scourge *et al*., 2018) (Amaral *et al*., 2020)

Currently, the new Vip3Aa20 technology, also originating from *B. thuringiensis*, is proving to be quite efficient in Bt corn (second generation) and cotton (third generation) crops (Yang *et al*., 2019; Amaral *et al*., 2020). So far, no cases of cross-resistance of insects to this protein and to commercially used Cry proteins have been recorded (Amaral *et al*., 2020). As insect resistance to Cry proteins has developed rapidly, it is crucial to adopt good

management practices to prevent the same from happening with the new protein (Santos-Amaya *et al*., 2016).

In Brazil, which is the second largest producer of Bt maize in the world, the large area occupied by Bt crops can hinder the uniform implementation of resistance management strategies in all regions (Santos-Amaya *et al*., 2016). However, knowing the geographic distribution of the fall armyworm resistance allele to the Vip3Aa20 protein can help companies apply resistance management strategies in a more targeted and efficient way (Amaral *et al*., 2020).

Wang *et al*. (2019) highlight the importance of technologies such as Bt in countries with tropical and subtropical climates, where these conditions favor the reproduction of fall armyworm. This insect can reproduce several times a year and on different types of plants. However, this high reproduction rate can lead to the selection of resistance, both to chemical insecticides and to Bt technology itself. Therefore, it is crucial to constantly search for new insecticidal proteins, as fall armyworm is always evolving to adapt to these control methods.

The spread and selection of fall armyworm resistance in the field can be influenced by several factors, such as the production of several generations during the year (Santos-Amaya *et al*., 2016), the migratory behavior of the insect, and inadequate management practices or insufficient planting of refuge areas (Chandrasena *et al*., 2018).

3.2 *SPODOPTERA FRUGIPERDA*

The fall armyworm, *Spodoptera frugiperda* (J.E Smith) (Lepidoptera: Noctuidae), is native to tropical and subtropical regions of the Americas and is present throughout the American Continent, having great economic importance for agriculture worldwide (Kenis, 2023). (Scourge *et al*., 2018) *S. frugiperda* is polyphagous and feeds on about 353 plant species, including corn, millet, rice, sorghum, wheat, soybean, cotton, alfalfa, among many others (Montezano *et al*., 2018). It receives the name of fall armyworm because it has a preference for the fall armyworm of corn plants. In Brazil, it has become one of the most important pests of corn, and in the larval stage, they feed, especially, on the cartridge of corn plants, and can cause damage of up to 57% in the crop. But it also feeds on corn plants at all stages of development, and can even attack the stem of young plants (Mendes (Fernandes *et al*., 2018) (Araujo *et al*., 2014) (Burtet *et al*., 2017) *et al*., 2011).

This insect has a development cycle passing through egg, caterpillar, pupa, and adults. observed that the incubation period of (Silva *et al*., 2017) Rose *et al*. (2012) *S. frugiperda* eggs at a temperature of 25 ± 1 ºC ranged from 2.8 to 3.3 days, the caterpillar

stage varied from 10.7 to 21.7 days. The pre-pupal stage lasted 1.89 days. The pupal stage lasted approximately 8.54 days and the longevity of adults ranged from around 21.41 days at a temperature of 25 ± 2 ºC. The duration of the pre-oviposition phase ranged from 0 to 10.7 days and the duration of longevity ranged from 21.3 to 45.7 days. Considering that this insect has a relatively short cycle, is polyphagous and some Brazilian regions plant up to three crops per year, these are conditions that greatly favor the reproduction of the fall armyworm throughout the year, and a single female can produce about 1,800 eggs during the adult phase of her cycle. Females usually lay their eggs on top of corn leaves and after hatching the neonates migrate to the whorl of the plant (Silva *et al*., 2017) (Pink *et al.*, 2012) (Santos-Amaya *et al.*, 2016) (Pink *et al.*, 2012) (Harrison *et al.*, 2019)

Currently, this insect has become the main pest of corn and cotton in the United States, Brazil, among other countries around the world. As of 2016, there are reports of the presence of this pest in maize fields in several countries in Africa (Goergen (Scourge *et al*., 2018) *et al*., 2016) and soon after in Asia (Rwomushana *et al.*, 2018), in 2020 it arrived in Oceania (ABC News, 2020) and in 2022 it arrived in New Zealand and some Pacific islands (CABI, 2023), causing great losses in all these places. Scoton *et al*. (2020) found significant damage in corn plants expressing Herculex® and VT PRO 3® technologies, while corn plants with Leptra® and Viptera 3® technology proved to be efficient for fall armyworm control. Damage caused by this pest in the corn crop can lead to losses of up to 53% of the production of this crop (Prasanna *et al.*, 2018).

3.2.1 Control of *Spodoptera frugiperda* in maize

For decades, the effective control of this pest was carried out mainly with the use of synthetic chemicals, such as carbamates, organophosphates, and pyrethroids (Valicente; Barreto, 2003; Barcelos; Angelini, 2018). However, the application of chemical insecticides against fall armyworm is not always efficient. This may be due to the inappropriate application method or the fact that the larvae are already at an advanced stage of development, which reduces their susceptibility to the products (Rwomushana *et al.*, 2018). With the development, after the formation of the cartridge in the corn plants, *S. frugiperda* lodges inside, making it difficult to control the chemical, which is the most used by producers, In addition, many times in the populations, individuals resistant to these products are selected and, in this sense, the technologies aimed at Bt stand out, preventing damage to the environment, to human health and delaying the development of resistance by the pest. (Yang *et al.*, 2016)

The use of chemical pesticides also has the side effect of eliminating the natural enemies of pests, which reduces the natural control over *S. frugiperda* (Burtet *et al*., 2017). In response to these challenges, biopesticides based on entomopathogenic microorganisms, such as fungi, protozoa, nematodes and viruses, have been used to control fall armyworm. Currently, more than 14 species of these microorganisms are known (Molina-Ochoa *et al*., 2007). Strategies such as the use of weeds, used by small producers, among crops should be further tested, as they can be very efficient in combating fall armyworm. They provide the environment for the emergence of nests and habitat for the natural enemies of this pest. (Harrison *et al* ., 2019) (Harrison *et al* ., 2019)

Another method of control is the use of parasitoids and predators, with more than 150 species of various orders identified worldwide (Hruska, 2019). Small producers also adopt an alternative technique, which consists of using soil, sand, ash, or sawdust on the whorl of corn plants to dehydrate caterpillars in their first stage of development (Tambo *et al*., 2020).

Currently, in addition to the alternative control methods already mentioned, the use of genetically modified plants based on *Bacillus thuringiensis genes*, popularly known as Bt plants, producing Cry and/or Vip insecticidal proteins (Angelo *et al*., 2010). The insertion of Bt genes in the corn crop conferred a high pattern of plant resistance to some lepidopteran species, such as the fall armyworm (Huang *et al*., 2002). Chemical pesticides and insecticidal proteins obtained from *B. thuringiensis*, Cry and Vip families, expressed in genetically modified (Bt) plants, have been widely used in the control of insects of the order Lepidoptera, since 1996. According to Flagel (Tabashnik *et al.* , 2008) *et al*. (2018), the introduction of the use of Bt cultures represented a significant advance, since the proteins of the Cry1 and Cry2 families proved to be very efficient against fall armyworm, especially the proteins Cry1FA, Cry1A.105, Cry2Ab2 and Cry1Ab, with lower efficacy. Monitoring the evolution of resistance of field populations of insect species is indispensable in the management of insecticide resistance (MIR) for the maintenance of the technology. (Yang *et al* ., 2017; 2020)

In view of the wide occurrence of resistance of *S. frugiperda* to the Cry1F protein, the Cry2A protein was the one that showed the most durability before the release of the plants expressing the VIP3Aa protein. The latest studies have shown that VIP3Aa proteins are highly effective in controlling *S. frugiperda* in corn and cotton and *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) in cotton. Thus, Bt corn varieties expressing Cry proteins, in some regions of Brazil, receive up to three applications of insecticides to achieve the intended result and, currently, are giving way to cultivars expressing Vip3Aa20 proteins, which still have no report of resistant insects in the field. (Chen *et al.* , 2019) (Fatoretto *et al* ., 2017)

REFERENCES

1. ABC News. (2020, 12 de fevereiro). Fall armyworm found in Torres Strait, prompting biosecurity alert amid fears for Australian crops. https://www.abc.net.au/news/2020-02-12/worm-moth-fall-armyworm-detected-found-australia-torres-strait/11957838

2. Amaral, F. S. A., Guidolin, A. S., Salmeron, E., Kanno, R. H., Padovez, F. E. O., Fatoretto, J. C., & Omoto, C. (2020). Geographical distribution of Vip3Aa20 resistance allele frequencies in Spodoptera frugiperda (Lepidoptera: Noctuidae) populations in Brazil. Pest Management Science, 76(1), 169–178. https://doi.org/10.1002/ps.5507

3. Angelo, E. A., Vilas-Bôas, G. T., & Gómez, R. J. H. (2010). Bacillus thuringiensis: Características gerais e fermentação. Semina: Ciências Agrárias, 31(4), 945–958. https://doi.org/10.5433/1679-0359.2010v31n4p945

4. Araujo, O. G., Mendes, S. M., Rosa, A. P. S. A., Marucci, R. C., Santos, C. D., Barbosa, T. A. N., Dias, A. S., & Carvalho, S. S. S. (2014). Aspectos biológicos de populações de Spodoptera frugiperda em milho Bt e arroz (Boletim de Pesquisa e Desenvolvimento 101). Embrapa Milho e Sorgo.

5. Baranek, J., Konecka, E., & Kaznowski, A. (2017). Interaction between toxin crystals and vegetative insecticidal proteins of Bacillus thuringiensis in lepidopteran larvae. BioControl, 62(5), 649–658. https://doi.org/10.1007/s10526-017-9829-8

6. Barcelos, P. H. S., & Angelini, M. R. (2018). Controle de Spodoptera frugiperda (Smith, 1797) em diferentes tecnologias Bt (Bacillus thuringiensis) na cultura do milho. Journal of Neotropical Agriculture, 5(1), 35–40.

7. Bateman, M. L., Day, R. K., Luke, B., Edgington, S., Kuhlmann, U., & Cock, M. J. W. (2018). Assessment of potential biopesticide options for managing fall armyworm (Spodoptera frugiperda) in Africa. Journal of Applied Entomology, 142(9), 805–819. https://doi.org/10.1111/jen.12565

8. Belay, D. K., Huckaba, R. M., & Foster, J. E. (2012). Susceptibility of the fall armyworm, Spodoptera frugiperda (Lepidoptera: Noctuidae), at Santa Isabel, Puerto Rico, to different insecticides. Florida Entomologist, 95(2), 476–478. https://doi.org/10.1653/024.095.0227

9. Bernardi, D., Salmeron, E., Horikoshi, R. J., Bernardi, O., Dourado, P. M., Carvalho, R. A., Martinelli, S., Head, G. P., & Omoto, C. (2015). Cross-resistance between Cry1 proteins in fall armyworm (Spodoptera frugiperda) may affect the durability of current pyramided Bt maize hybrids in Brazil. PLoS ONE, 10(10), Article e0140130. https://doi.org/10.1371/journal.pone.0140130

10. Bernardi, O., Bernardi, D., Horikoshi, R. J., Okuma, D. M., Miraldo, L. L., Fatoretto, J., Medeiros, F. C. L., Burd, T., & Omoto, C. (2016a). Selection and characterization of resistance to the Vip3Aa20 protein from Bacillus thuringiensis in Spodoptera frugiperda. Pest Management Science, 72(9), 1727–1736. https://doi.org/10.1002/ps.4236

11. Bernardi, D., Bernardi, O., Horikoshi, R. J., Salmeron, E., Okuma, D. M., & Omoto, C. (2016b). Biological activity of Bt proteins expressed in different structures of transgenic corn against Spodoptera frugiperda. Ciência Rural, 46(6), 1019–1024. https://doi.org/10.1590/0103-8478cr20150667

12. Berta, D. C., Virla, E. G., Colomo, M. V., & Valverde, E. L. (2000). Efecto en el parasitoide Campoletis grioti de un insecticida usado para el control de Spodoptera frugiperda y aportes a la bionomía del parasitoide. Revista Manejo Integrado de Plagas, 57, 65–70.

13. Bortolotto, O. C., Bueno, A. de F., Queiroz, A. P. de, & Silva, G. V. (2016). Desenvolvimento larval de Spodoptera eridania e Spodoptera frugiperda alimentadas com espigas de milho verde expressando proteínas Bt (Cry1F e Cry1F + Cry1A.105 + Cry2Ab2). Ciência Rural, 46(11), 1898–1901. https://doi.org/10.1590/0103-8478cr20160088

14. Burtet, L. M., Bernardi, O., Melo, A. A., Pes, M. P., Strahl, T. T., & Guedes, J. V. C. (2017). Managing fall armyworm, Spodoptera frugiperda (Lepidoptera: Noctuidae), with Bt maize

and insecticides in southern Brazil. Pest Management Science, 73(12), 2569–2577. https://doi.org/10.1002/ps.4660

15. CABI. (2023). Spodoptera frugiperda (fall armyworm). CABI Compendium. https://doi.org/10.1079/cabicompendium.29810

16. Chandrasena, D. I., Signorini, A. M., Abratti, G., Storer, N. P., Olaciregui, M. L., Alves, A. P., & Pilcher, C. D. (2018). Characterization of field-evolved resistance to Bacillus thuringiensis-derived Cry1F δ-endotoxin in Spodoptera frugiperda populations from Argentina. Pest Management Science, 74(3), 746–754. https://doi.org/10.1002/ps.4789

17. Chen, X., Head, G. P., Price, P., Kerns, D. L., Rice, M. E., Huang, F., Gilreath, R. T., & Yang, F. (2019). Fitness costs of Vip3A resistance in Spodoptera frugiperda on different hosts. Pest Management Science, 75(4), 1074–1080. https://doi.org/10.1002/ps.5225

18. CIB – Conselho de Informações sobre Biotecnologia. (2018). Impactos econômicos e socioambientais da tecnologia de resistência a insetos no Brasil: Histórico, análise, perspectivas e desafios futuros. https://cib.org.br/impactos-da-tecnologia-de-resistencia-a-insetos-no-brasil

19. Companhia Nacional de Abastecimento. (2024, julho). Ajustes na área de milho e soja resultam em uma produção de 295,45 milhões de toneladas na safra 2023/2024. https://www.conab.gov.br/ultimas-noticias/5531-ajustes-na-area-de-milho-e-soja-resultam-em-uma-producao-de-295-45-milhoes-de-toneladas-na-safra-20232024

20. Confederação da Agricultura e Pecuária do Brasil. (2024, 19 de agosto). Milho é um dos cereais mais nutritivos e versáteis do mundo. https://www.cnabrasil.org.br/noticias/milho-e-um-dos-cereais-mais-nutritivos-e-versateis-do-mundo

21. Crickmore, N., Berry, C., Panneerselvam, S., Mishra, R., Connor, T. R., & Bonning, B. C. (2021). A structure-based nomenclature for Bacillus thuringiensis and other bacteria-derived pesticidal proteins. Journal of Invertebrate Pathology, 186, Article 107438. https://doi.org/10.1016/j.jip.2020.107438

22. Cruz, J. C., Karam, D., Monteiro, M. A. R., & Magalhães, P. C. (2008). A cultura do milho. Embrapa Milho e Sorgo.

23. Farias, J. R., Andow, D. A., Horikoshi, R. J., Sorgatto, R. J., Fresia, P., Santos, A. C. dos, & Omoto, C. (2014). Field-evolved resistance to Cry1F maize by Spodoptera frugiperda (Lepidoptera: Noctuidae) in Brazil. Crop Protection, 64, 150–158. https://doi.org/10.1016/j.cropro.2014.06.019

24. Fatoretto, J. C., Michel, A. P., Silva Filho, M. C., & Silva, N. (2017). Adaptive potential of fall armyworm (Lepidoptera: Noctuidae) limits Bt trait durability in Brazil. Journal of Integrated Pest Management, 8(1), Article 17. https://doi.org/10.1093/jipm/pmx011

25. Fernandes, F. O., Abreu, J. Á., Martins, J. F. S., & Rosa, A. P. S. A. (2018). Desempenho de Spodoptera frugiperda (Smith, 1797) em milho expressando as proteínas Cry1A.105/Cry2Ab2 no ambiente de terras baixas (Boletim de Pesquisa e Desenvolvimento 287). Embrapa Clima Temperado.

26. Flagel, L., Lee, Y. W., Wanjugi, H., Swarup, S., Brown, A., Wang, J., Kraft, E., Greenplate, J., Simmons, J., Adams, N., Wang, Y., Martinelli, S., Haas, J., Gowda, A., & Head, G. (2018). Mutational disruption of the ABCC2 gene in fall armyworm, Spodoptera frugiperda, confers resistance to the Cry1Fa and Cry1A.105 insecticidal proteins. Scientific Reports, 8, Article 9582. https://doi.org/10.1038/s41598-018-25491-9

27. Goergen, G., Kumar, P. L., Sankung, S. B., Togola, A., & Tamò, M. (2016). First report of outbreaks of the fall armyworm Spodoptera frugiperda (J. E. Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. PLoS ONE, 11(10), Article e0165632. https://doi.org/10.1371/journal.pone.0165632

28. Gutiérrez-Moreno, R., Mota-Sanchez, D., Blanco, C. A., Whalon, M. E., Terán-Santofimio, H., Rodriguez-Maciel, J. C., & DiFonzo, C. (2019). Field-evolved resistance of the fall armyworm (Lepidoptera: Noctuidae) to synthetic insecticides in Puerto Rico and Mexico. Journal of Economic Entomology, 112(2), 792–802. https://doi.org/10.1093/jee/toy372

29. Hailu, G., Niassy, S., Zeyaur, K. R., Ochatum, N., & Subramanian, S. (2018). Maize–legume intercropping and push–pull for management of fall armyworm, stemborers, and striga in Uganda. Agronomy Journal, 110(6), 2513–2522. https://doi.org/10.2134/agronj2018.02.0110

30. Harrison, R. D., Thierfelder, C., Baudron, F., Chinwada, P., Midega, C., Schaffner, U., & van den Berg, J. (2019). Agro-ecological options for fall armyworm (Spodoptera frugiperda JE Smith) management: Providing low-cost, smallholder friendly solutions to an invasive pest. Journal of Environmental Management, 243, 318–330. https://doi.org/10.1016/j.jenvman.2019.05.011

31. Horikoshi, R. J., Bernardi, O., Godoy, D. N., Semeão, A. A., Willse, A., Corazza, G. O., Ruthes, E., Fernandes, D. S., Sosa-Gómez, D. R., Bueno, A. F., Omoto, C., Berger, G. U., Corrêa, A. S., Martinelli, S., Dourado, P. M., & Head, G. (2021). Resistance status of lepidopteran soybean pests following large-scale use of MON 87701 × MON 89788 soybean in Brazil. Scientific Reports, 11, Article 2556. https://doi.org/10.1038/s41598-021-82049-7

32. Hruska, A. J. (2019). Fall armyworm (Spodoptera frugiperda) management by smallholders. CAB Reviews, 14, Article 043. https://doi.org/10.1079/PAVSNNR201914043

33. Huang, F. (2021). Resistance of the fall armyworm, Spodoptera frugiperda, to transgenic Bacillus thuringiensis Cry1F corn in the Americas: Lessons and implications for Bt corn IRM in China. Insect Science, 28(3), 574–589. https://doi.org/10.1111/1744-7917.12860

34. Huang, F., Qureshi, J. A., Meagher, R. L., Reisig, D. D., Head, G. P., Andow, D. A., Ni, X., Kerns, D., Buntin, G. D., Niu, Y., Yang, F., & Dangal, V. (2014). Cry1F resistance in fall armyworm Spodoptera frugiperda: Single gene versus pyramided Bt maize. PLoS ONE, 9(11), Article e112958. https://doi.org/10.1371/journal.pone.0112958

35. ISAAA. (2019). Global status of commercialized biotech/GM crops in 2019 (ISAAA Brief No. 55). ISAAA. https://www.isaaa.org/resources/publications/briefs/55/default.asp

36. Kenis, M., du Plessis, H., Van den Berg, J., Ba, M. N., Goergen, G., Kwadjo, K. E., Baoua, I., Tefera, T., Buddie, A., Cafà, G., Offord, L., Rwomushana, I., & Day, R. (2023). Invasiveness, biology, ecology, and management of the fall armyworm, Spodoptera frugiperda. Entomologia Generalis, 43(2), 187–241. https://doi.org/10.1127/entomologia/2022/1659

37. Li, G., Reisig, D., Miao, J., Gould, F., Huang, F., & Feng, H. (2016). Frequency of Cry1F non-recessive resistance alleles in North Carolina field populations of Spodoptera frugiperda (Lepidoptera: Noctuidae). PLoS ONE, 11(4), Article e0154492. https://doi.org/10.1371/journal.pone.0154492

38. Lüthy, P., Cordier, J. L., & Fischer, H. M. (1982). Bacillus thuringiensis as a bacterial insecticide: Basic considerations and application. In E. Kurstak (Ed.), Microbial and viral pesticides (pp. 34–74). Marcel Dekker.

39. Martineau, B. (2001). First fruit: The creation of the Flavr Savr tomato and the birth of biotech foods. McGraw-Hill.

40. Matyjaszczyk, E. (2019). Problems of implementing compulsory integrated pest management. Pest Management Science, 75(8), 2063–2067. https://doi.org/10.1002/ps.5439

41. Mendes, S. M., Boregas, K. G. B., Lopes, M. E., Waquil, M. S., & Waquil, J. M. (2011). Respostas da lagarta-do-cartucho a milho geneticamente modificado expressando a toxina Cry1A(b). Pesquisa Agropecuária Brasileira, 46(3), 239–244. https://doi.org/10.1590/S0100-204X2011000300004

42. Molina-Ochoa, J., Lezama-Gutiérrez, R., González-Ramírez, M., López-Edwards, M., Rodríguez-Vega, M. A., & Arceo-Palacios, F. (2003). Pathogens and parasitic nematodes associated with populations of fall armyworm (Lepidoptera: Noctuidae) larvae in Mexico. Florida Entomologist, 86(3), 244–253. https://doi.org/10.1653/0015-4040(2003)086[0244:PAPNAW]2.0.CO;2

43. Monnerat, R., Martins, E., Queiroz, P., Ordúz, S., Jaramillo, G., Benintende, G., Cozzi, J., Real, M. D., Martinez-Ramirez, A., Rausell, C., Cerón, J., Ibarra, J. E., Del Rincon-Castro, M. C., Espinoza, A. M., Meza-Basso, L., Cabrera, L., Sánchez, J., Soberón, M., & Bravo, A. (2006). Genetic variability of Spodoptera frugiperda Smith (Lepidoptera: Noctuidae) populations from Latin America is associated with variations in susceptibility to Bacillus thuringiensis Cry toxins. Applied and Environmental Microbiology, 72(11), 7029–7035. https://doi.org/10.1128/AEM.01003-06

44. Montezano, D. G., Specht, A., Sosa-Gómez, D. R., Roque-Specht, V. F., Sousa-Silva, J. C., Paula-Moraes, S. V., Peterson, J. A., & Hunt, T. E. (2018). Host plants of Spodoptera frugiperda (Lepidoptera: Noctuidae) in the Americas. African Entomology, 26(2), 286–300. https://doi.org/10.4001/003.026.0286

45. Niassy, S., Agbodzavu, M. K., Kimathi, E., Mutune, B., Abdel-Rahman, E. M. F., Salifu, D., Hailu, G., Belayneh, Y. T., Felege, E., Tonnang, H. E. Z., Ekesi, S., & Subramanian, S. (2021). Bioecology of fall armyworm Spodoptera frugiperda (J. E. Smith), its management and potential patterns of seasonal spread in Africa. PLoS ONE, 16(6), Article e0249042. https://doi.org/10.1371/journal.pone.0249042

46. Niu, Y. (2018). Risk assessment of fall armyworm resistance to transgenic corn containing single or pyramided Bacillus thuringiensis genes [Doctoral dissertation, Louisiana State University]. LSU Digital Commons.

47. Niu, Y., Meagher, R. L., Yang, F., & Huang, F. (2013). Susceptibility of field populations of the fall armyworm (Lepidoptera: Noctuidae) from Florida and Puerto Rico to purified Cry1F protein and corn leaf tissue containing single and pyramided Bt genes. Florida Entomologist, 96(3), 701–713. https://doi.org/10.1653/024.096.0308

48. Omoto, C., Bernardi, O., Salmeron, E., Sorgatto, R. J., Dourado, P. M., Crivellari, A., Carvalho, R. A., Willse, A., Martinelli, S., & Head, G. P. (2016). Field-evolved resistance to Cry1Ab maize by Spodoptera frugiperda in Brazil. Pest Management Science, 72(9), 1727–1736. https://doi.org/10.1002/ps.4200

49. Pitre, H. N. (1988). Relationship of fall armyworm (Lepidoptera: Noctuidae) from Florida, Honduras, Jamaica, and Mississippi: Susceptibility to insecticides with reference to migration. Florida Entomologist, 71(1), 56–61. https://doi.org/10.2307/3494894

50. Prasanna, B. M., Huesing, J. E., Eddy, R., & Peschke, V. M. (Eds.). (2018). Fall armyworm in Africa: A guide for integrated pest management. CIMMYT/USAID. https://repository.cimmyt.org/handle/10883/19204

51. Romeis, J., Naranjo, S. E., Meissle, M., & Shelton, A. M. (2019). Genetically engineered crops help support conservation biological control. Biological Control, 130, 136–154. https://doi.org/10.1016/j.biocontrol.2018.11.007

52. Rosa, A. P. A., Trecha, C. O., Alves, A. C., Garcia, L., & Gonçalves, V. P. (2012). Biologia e tabela de vida de fertilidade de Spodoptera frugiperda (J. E. Smith) em linhagens de milho. Arquivos do Instituto Biológico, 79(1), 39–45. https://doi.org/10.1590/1808-1657v79p0392012

53. Rwomushana, I., Bateman, M., Beale, T., Beseh, P., Cameron, K., Chiluba, M., ... & Day, R. (2017). Fall armyworm: Impacts and implications for Africa. Outlooks on Pest Management, 28(5), 196–201. https://doi.org/10.1564/v28_oct_03

54. Santos-Amaya, O. F., Tavares, C. S., Monteiro, H. M., Teixeira, T. P. M., Guedes, R. N. C., Alves, A. P., & Pereira, E. J. G. (2016). Genetic basis of Cry1F resistance in two Brazilian populations of fall armyworm, Spodoptera frugiperda. Crop Protection, 81, 154–162. https://doi.org/10.1016/j.cropro.2015.12.013

55. Santos-Amaya, O. F., Rodrigues, J. V. C., Souza, T. C., Tavares, C. S., Campos, S. O., Guedes, R. N. C., & Pereira, E. J. G. (2015). Resistance to dual-gene Bt maize in Spodoptera frugiperda: Selection, inheritance, and cross-resistance to other transgenic events. Scientific Reports, 5, Article 18243. https://doi.org/10.1038/srep18243

56. Santos-Amaya, O. F., Tavares, C. S., Rodrigues, J. V. C., Santana, I. V., Queiroz, O. S., Oliveira, E. E., Guedes, R. N. C., & Pereira, E. J. G. (2022). Strong fitness costs of insect

resistance to dual-gene Bt corn are magnified on less-suitable host-crop cultivars. Agronomy, 12(3), Article 682. https://doi.org/10.3390/agronomy12030682

57. Scoton, A. M. N., Degrande, P. E., da Silva, M. B., Jacques, F. L., Lourenção, A. L. F., & de Souza, E. P. (2020). Spodoptera frugiperda (J. E. Smith, 1797) (Lepidoptera: Noctuidae) control and productive performance of Bt maize genotypes. Brazilian Journal of Agriculture, 95(1), 68–82.

58. Silva, D. M., Bueno, A. de F., Andrade, K., Stecca, C. dos S., Neves, P. M. O. J., & de Oliveira, M. C. N. (2017). Biology and nutrition of Spodoptera frugiperda (Lepidoptera: Noctuidae) fed on different food sources. Scientia Agricola, 74(1), 18–31. https://doi.org/10.1590/1678-992x-2015-0411

59. Sogorb, M. A., & Vilanova, E. (2002). Enzymes involved in the detoxification of organophosphorus, carbamate and pyrethroid insecticides through hydrolysis. Toxicology Letters, 128(1–3), 215–228. https://doi.org/10.1016/S0378-4274(01)00543-8

60. Storer, N. P., Babcock, J. M., Schlenz, M., Meade, T., Thompson, G. D., Bing, J. W., & Huckaba, R. M. (2010). Discovery and characterization of field resistance to Bt maize: Spodoptera frugiperda (Lepidoptera: Noctuidae) in Puerto Rico. Journal of Economic Entomology, 103(4), 1031–1038. https://doi.org/10.1603/EC10040

61. Storer, N. P., Kubiszak, M. E., King, J. E., Thompson, G. D., & Santos, A. C. (2012). Status of resistance to Bt maize in Spodoptera frugiperda: Lessons from Puerto Rico. Journal of Invertebrate Pathology, 110(3), 294–300. https://doi.org/10.1016/j.jip.2012.04.007

62. Tabashnik, B. E., Gassmann, A. J., Crowder, D. W., & Carrière, Y. (2008). Insect resistance to Bt crops: Evidence versus theory. Nature Biotechnology, 26(2), 199–202. https://doi.org/10.1038/nbt1382

63. Tambo, J. A., Day, R. K., Lamontagne-Godwin, J., Silvestri, S., Beseh, P. K., Oppong-Mensah, B., Phiri, N. A., & Matimelo, M. (2020). Tackling fall armyworm (Spodoptera frugiperda) outbreak in Africa: An analysis of farmers' control actions. International Journal of Pest Management, 66(4), 298–310. https://doi.org/10.1080/09670874.2019.1642862

64. Tavares, C. S., Santos-Amaya, O. F., Oliveira, E. E., Paula-Moraes, S. V., & Pereira, E. J. G. (2021). Facing Bt toxins as you grow up: The ontogeny of susceptibility to Bt corn hybrids in fall armyworm populations and the implications for resistance management. Crop Protection, 146, Article 105664. https://doi.org/10.1016/j.cropro.2021.105664

65. Tetreau, G. (2018). Interaction between insects, toxins, and bacteria: Have we been wrong so far? Toxins, 10(7), Article 281. https://doi.org/10.3390/toxins10070281

66. Valicente, F. H., & Barreto, M. R. (2003). Bacillus thuringiensis survey in Brazil: Geographical distribution and insecticidal activity against Spodoptera frugiperda (J. E. Smith) (Lepidoptera: Noctuidae). Neotropical Entomology, 32(4), 639–644. https://doi.org/10.1590/S1519-566X2003000400014

67. Wan, J., Huang, C., Li, C. Y., Zhou, H. X., Ren, Y. L., & Li, Z. (2021). Biology, invasion and management of the agricultural invader: Fall armyworm, Spodoptera frugiperda (Lepidoptera: Noctuidae). Journal of Integrative Agriculture, 20(3), 646–663. https://doi.org/10.1016/S2095-3119(20)63368-8

68. Wang, Y., Wang, J., Fu, X., Nageotte, J. R., Silverman, J., Bretsnyder, E. C., Chen, D., Rydel, T. J., Bean, G. J., Li, S., Kraft, E., Gowda, A., Nance, A., Moore, R. G., Pleau, M. J., Milligan, J. S., Anderson, H. M., Asiimwe, P., Evans, A., Moar, W. J., Martinelli, S., Head, G. P., Haas, J. A., Baum, J. A., Yang, F., & Kerns, D. L. (2019). Bacillus thuringiensis Cry1Da_7 and Cry1B.868 protein interactions with novel receptors allow control of resistant fall armyworms, Spodoptera frugiperda (J. E. Smith). Applied and Environmental Microbiology, 85(16), Article e00579-19. https://doi.org/10.1128/AEM.00579-19

69. Yang, F., González, J. C. S., Little, N., Reisig, D., Payne, G., dos Santos, R. F., Jurat-Fuentes, J. L., Kurtz, R., & Kerns, D. L. (2020). First documentation of major Vip3Aa

resistance alleles in field populations of Helicoverpa zea (Boddie) (Lepidoptera: Noctuidae) in Texas, USA. Scientific Reports, 10, Article 18698. https://doi.org/10.1038/s41598-020-75660-z

70. Yang, F., Williams, J., Porter, P., Huang, F., & Kerns, D. L. (2019). F2 screen for resistance to Bacillus thuringiensis Vip3Aa51 protein in field populations of Spodoptera frugiperda (Lepidoptera: Noctuidae) from Texas, USA. Crop Protection, 126, Article 104915. https://doi.org/10.1016/j.cropro.2019.104915

71. Yang, F., Kerns, D. L., Head, G., Brown, S., & Huang, F. (2017). Susceptibility of Cry1F-maize resistant, heterozygous, and susceptible Spodoptera frugiperda to Bt proteins used in the transgenic cotton. Crop Protection, 98, 128–135. https://doi.org/10.1016/j.cropro.2017.03.019

72. Yang, F., Kerns, D. L., Brown, S., Kurtz, R., Dennehy, T., Braxton, B., Head, G., & Huang, F. (2016). Performance and cross-crop resistance of Cry1F-maize selected Spodoptera frugiperda on transgenic Bt cotton: Implications for resistance management. Scientific Reports, 6, Article 28059. https://doi.org/10.1038/srep28059

73. Yang, F., Qureshi, J. A., Leonard, B. R., Head, G. P., Niu, Y., & Huang, F. (2013). Susceptibility of Louisiana and Florida populations of Spodoptera frugiperda (Lepidoptera: Noctuidae) to pyramided Bt corn containing Genuity®VT Double Pro™ and SmartStax™ traits. Florida Entomologist, 96(3), 714–723. https://doi.org/10.1653/024.096.0311

74. Yu, S. J. (1991). Insecticide resistance in the fall armyworm, Spodoptera frugiperda (J. E. Smith). Pesticide Biochemistry and Physiology, 39(1), 84–91. https://doi.org/10.1016/0048-3575(91)90226-Q

75. Zhu, C., Niu, Y., Zhou, Y., Guo, J., Head, G. P., Price, P. A., Wen, X., & Huang, F. (2019). Survival and effective dominance level of a Cry1A.105/Cry2Ab2-dual gene resistant population of Spodoptera frugiperda (J. E. Smith) on common pyramided Bt corn traits. Crop Protection, 115, 84–91. https://doi.org/10.1016/j.cropro.2018.09.011