Host plant resistance for fall armyworm management in maize: relevance, status and prospects in Africa and Asia

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Abstract

Key message Sustainable control of fall armyworm (FAW) requires implementation of effective integrated pest management (IPM) strategies, with host plant resistance as a key component. Significant opportunities exist for developing and deploying elite maize cultivars with native genetic resistance and/or transgenic resistance for FAW control in both Africa and Asia.

Abstract The fall armyworm [Spodoptera frugiperda (J.E. Smith); FAW] has emerged as a serious pest since 2016 in Africa, and since 2018 in Asia, affecting the food security and livelihoods of millions of smallholder farmers, especially those growing maize. Sustainable control of FAW requires implementation of integrated pest management strategies, in which host plant resistance is one of the key components. Significant strides have been made in breeding elite maize lines and hybrids with native genetic resistance to FAW in Africa, based on the strong foundation of insect-resistant tropical germplasm developed at the International Maize and Wheat Improvement Center, Mexico. These efforts are further intensified to develop and deploy elite maize cultivars with native FAW tolerance/resistance and farmer-preferred traits suitable for diverse agro-ecologies in Africa and Asia. Independently, genetically modified Bt maize with resistance to FAW is already commercialized in South Africa, and in a few countries in Asia (Philippines and Vietnam), while efforts are being made to commercialize Bt maize events in additional countries in both Africa and Asia. In countries where Bt maize is commercialized, it is important to implement a robust insect resistance management strategy. Combinations of native genetic resistance and Bt maize also need to be explored as a path to more effective and sustainable host plant resistance options. We also highlight the critical gaps and priorities for host plant resistance research and development in maize, particularly in the context of sustainable FAW management in Africa and Asia.

Abbreviations

ARIs Advanced Research Institutes
AATF African Agricultural Technology Foundation
Bt Bacillus thuringiensis
CML CIMMYT Maize Line

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DH Doubled haploid
FAW Fall armyworm
GM Genetically modified
GWAS Genome-wide association study
GEM Germplasm enhancement of maize
IRM Insect resistance management
IRMA Insect Resistant Management for Africa
IPM Integrated pest management
JA Jasmonic acid
KALRO Kenya Agricultural and Livestock Research Organization
Mb Megabase
MIRT Multiple insect-resistant tropical
MBR Multiple borer resistant
NARES National Agricultural Research & Extension System
OPVs Open-pollinated varieties
QTL Quantitative trait loci
Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae), is a migratory and highly polyphagous pest native to the Americas (Spark 1979). It is the most economically important pest of maize in South and Central America (Cruz et al. 2012; Nagoshi et al. 2014, 2015). Due to the absence of a diapause trait, in the USA, it migrates northward annually in the fall season to infest temperate maize cropping areas (Westbrook et al. 2016). FAW comprises two genetically and behaviorally separate strains that occur sympatrically throughout North and South America (Pashley 1986). The “corn” strain (C) was reported to be preferentially damaging maize, sorghum and cotton, whereas the “rice” strain (R) predominantly infests rice, alfalfa, pasture and forage grasses (Nagoshi et al. 2007; Juarez et al. 2012). These “host strains” of FAW are morphologically indistinguishable; however, polymorphisms in the mitochondrial cytochrome oxidase subunit I (COI) gene proved to be capable of consistently differentiating and identifying the C and R strains based on their haplotypes (Levy et al. 2002).

FAW was officially reported outside the Americas for the first time in West Africa in January 2016 (Goergen et al. 2016), and by January 2018, the pest was reported in over 40 African countries (Prasanna et al. 2018). In Asia, FAW was first reported in the southern Indian state of Karnataka in May 2018 (Sharanabasappa et al. 2018; Shylesha et al. 2018), and subsequently in all the maize-growing states in the country (Suby et al. 2020; Deshmukh et al. 2021). Between 2018 and 2021, the pest rapidly spread across the Asia-Pacific region and has been reported from Yemen, Bangladesh, Myanmar, China, Thailand, Sri Lanka, Nepal, Philippines, Vietnam, Indonesia, Australia, South Korea, Cambodia, Papua New Guinea, Timor Leste, New Caledonia, Jordan, Syria and the United Arab Emirates (reviewed by Prasanna et al. 2021a).

The rapid spread and establishment of FAW populations in Africa and Asia highlight two important facts: a) similar to the Americas, the pest can spread quickly across large geographic areas within a short timeframe (Prasanna et al. 2021a, b) FAW populations can persist throughout the year in the conducive tropical/subtropical climates. Thus, FAW has now become a global problem, posing a serious threat to the food and nutritional security and livelihoods of hundreds of millions of farming households, especially those dependent on maize, in both Africa and Asia. Although FAW incidence has been reported on several crops, including maize (field/sweet/waxy), sorghum, sugarcane, wheat, rice (very limited), millets, ginger, soybean, tomato, cotton, cabbage, groundnut, banana, pasture grasses and green amaranth, the pest has caused major economic damage mostly to maize across Africa and Asia, and secondarily to sorghum and sugarcane (to a limited extent). The economic impact of FAW is not only represented by the extensive yield losses caused by the pest to the affected crops like maize (Rwomushana et al. 2018; Matova et al. 2020), but also additional management costs incurred by smallholder farmers—for example, the cost of managing the pest using various technologies, especially synthetic pesticides, besides increased labor. A recent study (Yang et al. 2021) examining the response of farmers to FAW in Yunnan province in China showed that the full cost of pesticide-based crop protection increased from US$81 per hectare per crop season in 2018 to US$276 in 2020, mainly due to FAW. The study also showed that at the FAW infestation levels present, some farmers were applying, on average, as many as 6.4 pesticide applications per crop season in 2020. We still do not know the magnitude of environmental cost of such extensive pesticide applications that could potentially affect natural enemies of insect pests.

There is no single solution that can provide sustainable control of a complex pest like FAW. A wide range of technologies and management practices have been developed over the years and are available for control of FAW, including host plant resistance, cultural control, biological control, biopesticides, mating disruption technologies, synthetic pesticides and agroecological management (Prasanna et al. 2018, 2021b). However, these technologies are not equally accessible to farming communities in countries across Africa or Asia due to various reasons, including regulatory bottlenecks. More generally, efficacy, cost/affordability, safety, accessibility and scalability are all important factors to consider in assessing the potential combination of technologies or management practices for IPM of FAW. In this review, we focus on the status of host plant resistance—both native traits and transgenic FAW resistance—for FAW control in Africa and Asia, as well as future opportunities and critical needs in host plant resistance research and development.
Relevance of host plant resistance in FAW management

“Host plant resistance,” in the context of resistance to insect pests, is defined as “the collective heritable characteristics by which a plant species may reduce the probability of successful utilization of that plant as a host by an insect species” (Beck 1965). Host plant resistance is a central component of IPM strategies to control FAW (Prasanna et al. 2018, 2021c) and comprises: a) native genetic resistance: identifying/developing germplasm with resistance to FAW, and b) transgenic resistance: using a gene or combination of genes from an external source(s) (other than the recipient plant) to make the host plant resistant to FAW. FAW-tolerant/FAW-resistant varieties, whether derived through native genetic resistance or through a transgenic approach, provide a practical and economical way to minimize crop losses due to the pest. In addition, improved maize varieties with genetic resistance to FAW effectively complement other IPM interventions (Riggin et al. 1992, 1994). Seed-based technologies like host plant resistance are not only easily disseminated and readily adopted by farmers due to their visible benefits, but also require fewer applications of pesticides than the FAW-susceptible varieties.

When designing a breeding strategy to introduce FAW resistance traits into elite maize germplasm, breeders consider not only the source and strength of FAW resistance, but also the potential durability of resistance over time. Insect pests such as FAW can evolve to overcome monogenic (based on a single gene) or oligogenic (based on a few genes) resistance, as has been observed with transgenic crop varieties (Huang et al. 2014). Breeding for FAW resistance is, therefore, a continuous process, with no “finish line” to the perpetual race between the host and the evolving pest. As a general principle, breeding programs should seek to identify, utilize, and ultimately combine multiple resistance traits—whether conventional or, where approved for use, transgenic—to improve the durability of host plant resistance (Prasanna et al. 2018, 2021c).

Prasanna et al. (2018, 2021c) presented a comprehensive review of host plant resistance to FAW, especially in maize. This included information on potential sources of resistance to FAW in tropical and temperate maize germplasm identified or developed earlier by maize breeding programs in the Americas, and detailed protocols for mass rearing of FAW and screening germplasm under artificial FAW infestation. Here we (a) provide an update on the progress made in breeding for native genetic resistance to FAW in maize; (b) highlight the status of deployment of genetically modified (GM) maize (specifically Bt maize) in Africa and Asia for the control of FAW, and the need to implement effective insect resistance management (IRM) strategies for Bt maize; and (c) suggest possible next steps for making host plant resistance an integral component of an IPM-based strategy for sustainable management of FAW in sub-Saharan Africa (SSA) and Asia.

Breeding for native genetic resistance to FAW

FAW tolerance in tropical maize germplasm

CIMMYT has a wealth of diverse genetic resources in maize, including landrace accessions as well as improved germplasm with an array of traits (e.g., high yield, drought tolerance, heat tolerance, nitrogen use efficiency, and resistance to various diseases and insect-pests) that are relevant for the smallholders. The maize germplasm bank at CIMMYT, Mexico, holds nearly 27,000 accessions that provide a rich platform for identifying genetic resources for various farmer-preferred traits. Research conducted at CIMMYT in Mexico (Mihm 1997) and subsequently in Africa and Asia revealed that there are genetic variation and potential to support breeding for native genetic resistance to insect pests of maize, including stem borers (e.g., spotted stem borer, Chilo partellus; maize stalk borer, Busseola fusca; Asian corn borer, Ostrinia furnacalis; and European corn borer, Ostrinia nubilalis), FAW and post-harvest pests (weevils and large grain borer).

The work done at CIMMYT-Mexico led to the development of two major maize populations—Multiple Insect-Resistant Tropical (MIRT) and Multiple Borer Resistant (MBR)—that served as the foundation for deriving improved tropical/subtropical maize inbred lines with at least partial resistance to FAW. These insect-resistant maize populations were derived primarily from the Caribbean maize germplasm and Tuxpeño landrace accessions from Mexico (Mihm 1997). CIMMYT and partners in Africa have utilized the insect-resistant maize populations and inbred lines from Mexico and developed elite maize germplasm (hybrids and improved open-pollinated varieties or OPVs) with resistance to other lepidopteran stem borers, including the European corn borer (Ostrinia nubilalis Hbn.), the African stem borer (Busseola fusca Fuller) and the spotted stem borer (Chilo partellus Swinhoe) (Murenga et al. 2015; Tefera et al. 2016a, b). Some of these insect-resistant materials have the potential to offer resistance against FAW, which is also a lepidopteran pest.

A screenhouse complex (with 13 screenhouses, each 1000 m²) was established by CIMMYT at Kenya Agricultural and Livestock Research Organization (KALRO) Research Center in Kiboko, Kenya, in 2017–2018, for intensive screening of maize germplasm against FAW under artificial infestation and for identifying and developing promising FAW-tolerant inbred lines and hybrids (Fig. 1). Each screenhouse can accommodate 245 maize rows of 3 m length with 12 plants per row. A similar screenhouse facility has been established by CIMMYT at Hyderabad, India. When identifying materials with native
genetic resistance to FAW, it is important to consider not only foliar damage but also ear/cob damage, as FAW larvae can cause significant ear/kernel damage by entering the developing ears. CIMMYT uses a 1–9 foliar damage scale (Prasanna et al. 2018), which is a modification of the Davis et al. (1992) 0–9 scale, for assessing the responses of maize germplasm against FAW under artificial infestation. At physiological maturity (harvest), the CIMMYT team also evaluates the maize germplasm on a 1–9 ear damage scale, as described by Prasanna et al. (2018). In addition, other parameters, including percentage ear rot and number of exit holes per ear, are recorded. The cumulative foliar and ear damage scores, along with grain yield and other parameters, are considered for final rating of the germplasm and for taking selection decisions.

Starting in 2017, the CIMMYT maize breeding program in Kenya implemented intensive efforts to identify and develop maize germplasm with tolerance/resistance to FAW. FAW-tolerant maize germplasm developed earlier at CIMMYT-Mexico, as well as inbred lines, OPVs and hybrids developed by CIMMYT in Africa through the Insect-Resistant Maize for Africa (IRMA) project (Tefera et al. 2016a; Prasanna et al. 2018), were screened. Between 2017 and 2020, over 6000 maize genotypes, including inbred lines and hybrids/OPVs from diverse sources, were screened under FAW artificial infestation in the screenhouses at Kiboko. The work led to identification/validation of promising FAW-tolerant/FAW-resistant inbred lines, especially from the MBR and MIRT germplasm backgrounds, with low foliar and ear damage scores.

**FAW-tolerant/FAW-resistant CIMMYT maize inbred lines**

Several FAW-tolerant/FAW-resistant CIMMYT maize inbred lines have been developed and disseminated to interested institutions globally over the years. These inbred lines include lines identified earlier at CIMMYT-Mexico and validated under artificial infestation at CIMMYT-Kenya (e.g., CML71, CML124, CML125, CML333, CML334, CML338), as well as some of the CIMMYT maize lines that were found to offer resistance to FAW in Kenya (e.g., CML370, CML372 and CML574). Since 2018, FAW-tolerant/FAW-resistant CMLs have been disseminated to 92 institutions in 34 countries globally, including an array of NARES, advanced research institutes (ARIs) and commercial seed companies in the Americas, Europe, Africa, Asia and Australia (Table 1). These CMLs can be potentially utilized as trait donors in breeding programs of institutions.

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Table 1 Global dissemination of CIMMYT’s FAW-tolerant/FAW-resistant CMLs (since 2018)

| Type of institution          | Africa (13) | Asia (9) | Latin America (36) | North America* (5) | Europe (2) | Australia (1) | Total (34) |
|-----------------------------|-------------|----------|--------------------|--------------------|------------|---------------|------------|
| NARES/ARIs/Universities     | 14 (11)     | 9 (6)    | 14 (5)             | 3 (2)              | 1 (1)      | 2 (1)         | 43 (26)    |
| Commercial seed companies   | 11 (7)      | 10 (6)   | 22 (4)             | 2 (1)              | 4 (3)      | -             | 49 (21)    |
| Total                       | 25 (13)     | 19 (9)   | 36 (6)             | 5 (2)              | 5 (3)      | 2 (1)         | 92 (34)    |

Figures in parentheses indicate number of countries
*Mexico is included under Latin America

Seed of the FAW-tolerant CMLs can be sourced from CIMMYT Genebank at Mexico under a Standard Material Transfer Agreement (SMTA).
that are developing FAW-tolerant maize cultivars for local environments.

Several national maize breeding programs in Africa and Asia have initiated breeding programs for developing FAW-tolerant cultivars (e.g., Matova et al. 2020; Kasoma et al. 2020), especially utilizing sources of native genetic resistance from CIMMYT. Besides the CMLs mentioned above, the CIMMYT team in Africa has identified over the last two years several promising inbred lines in both yellow- and white-kernel backgrounds, with tolerance/resistance to FAW, based on low foliar damage and competitive grain yields. For example, crosses were made among the promising lines, from which progenies were selected and intercrossed to increase the frequency of resistance alleles. Doubled haploid (DH) lines were developed from F$_1$, F$_2$ and backcross (BC) source populations with resistance to FAW. In 2019–2020, a total of 2733 DH lines were produced from different source populations. From these, a set of 1400 DH lines were screened under FAW artificial infestation at the screenhouses in Kiboko, leading to identification of new FAW-resistant lines. These lines are used to make new single-crosses and three-way hybrids for further evaluation.

**Development of elite FAW-tolerant tropical maize hybrids**

Based on the results from screening of a large collection of inbred lines from different genetic backgrounds during 2017–2018, the CIMMYT maize team in Kenya formed single-cross and three-way-cross hybrids. In 2018, a set of 197 single-cross hybrids were developed and evaluated under artificial FAW infestation. The best FAW-tolerant/FAW-resistant single-crosses have been used (a) as female parents to develop three-way hybrids, (b) to make narrow-based synthetics, and (c) as source populations for DH induction to develop new FAW-resistant lines. In 2019, 88 three-way hybrids showed genetic variation for grain yield under various conditions and FAW damage parameters. Hybrids with MBR and MIRT backgrounds were among those that showed a combination of low ear damage and good grain yield across various conditions. In 2019–2020, over 500 hybrids, including single- and three-way crosses, were tested across different management conditions, including screening against FAW under artificial infestation in Kiboko. Stage gate advancement of promising maize hybrids with native genetic resistance is implemented by considering both foliar damage and ear damage scores below specific thresholds ($\leq 5.0$ and $< 3.0$, respectively), in addition to significantly higher grain yield than FAW-susceptible commercial checks (WE3106 and DK777).

Based on the results of on-station screenhouse trials against FAW in Kiboko during 2017–2019, the CIMMYT maize team in Africa further evaluated in 2020 a set of eight promising white-grained hybrids (four early-maturing and four intermediate-maturing) against four widely used commercial hybrids (two early-and two intermediate-maturing) as checks under different management conditions. Of particular importance are “no-choice trials” under FAW artificial infestation in screenhouses in Kiboko, Kenya (Fig. 2), which provide a clear assessment of the ability of the genotype to “resist” the pest and provide acceptable yield. In this trial, each entry was planted in 40 rows in a separate screenhouse compartment (“no-choice”) and each plant was infested with seven FAW neonates 14 days after planting.
Foliar damage was assessed 7, 14, and 21 days after infestation, followed by ear damage and grain yield at harvest.

In addition, promising entries were also evaluated for their performance under managed drought stress, managed low-nitrogen stress and for their responses to key diseases (Turcicum leaf blight, Maize streak virus, Maize lethal necrosis, ear rots, etc.). The hybrids and their parents were also characterized on-station for their seed production characteristics, including maximum flowering time difference between parents and single-cross female parent seed yield. Besides on-station trials, the test hybrids along with commercial checks were evaluated under farmers’ management conditions (without any insecticide spray) at 16 on-farm sites in Kenya. Each entry was planted in 20-row plots and data were recorded on natural FAW infestation. Foliar damage was assessed 7, 14, 21, 28 and 35 days after germination together with insect incidence. Ear damage and percent ear damage were also recorded, as well as grain yield and other agronomic parameters. Based on data collected from the on-station and on-farm trials, three promising FAW-tolerant elite maize hybrids were announced by CIMMYT in December 2020 (https://www.cimmyt.org/news/announcing-cimmyt-derived-fall-armyworm-tolerant-elite-maize-hybrids-for-eastern-and-southern-africa/) for partners, especially in SSA. National performance trials (NPTs) of the three FAW-tolerant elite maize hybrids are presently undertaken by several countries in SSA.

**FAW resistance in temperate maize germplasm**

The USDA-ARS Corn Host Plant Resistance Research Unit (CHPRRU) in Mississippi, USA (https://www.ars.usda.gov/southeast-area/mississippi-state-ms/crop-science-research-laboratory/corn-host-plant-resistance-research/) has a long history of conducting research on native genetic resistance to FAW, especially with temperate maize germplasm. During the late 1980s and throughout the 1990s, USDA-ARS and CIMMYT (Mexico) collaborated extensively on developing FAW-resistant maize germplasm in Mexico (Williams and Davis 1997). USDA-ARS researchers developed protocols for infesting maize plants with neonates and evaluating the resulting damage and thus identified temperate maize inbred lines with resistance to FAW (e.g., Mp705) (Prasanna et al. 2018). In addition to USDA-ARS, temperate maize germplasm with native genetic resistance to FAW has been developed by Embrapa-Brazil, University of Florida, USA, and the Germplasm Enhancement of Maize (GEM) project (Table 2).

**Genetic and molecular bases of native genetic resistance to FAW in maize**

In the context of insect pests, “resistance” is the capacity to minimize feeding damage through mechanisms such as antibiosis and/or antixenosis, while “tolerance” is the ability to limit economic damage even in the presence of the pest (outside/inside the host). Native resistance in maize to FAW is polygenic and quantitative in nature, conferring partial resistance. The quantitative and polygenic nature of native genetic resistance is less vulnerable to resistance evolution in the targeted FAW populations than if native resistance was high level and or monogenic. Although we do not know comprehensively the genetic, biochemical and molecular bases of native genetic resistance in maize, some interesting insights are available and are summarized below.

Resistance to an insect pest may involve a combination of antibiosis, antixenosis, and/or tolerance (Painter 1958). Earlier studies evaluating FAW-resistant maize germplasm showed that the mechanisms could be quite varied, with some showing non-preference and others antixenosis (Wise-man et al. 1982). Non-preference could be due to distinct morphological traits (e.g., leaf thickness/toughness, very tight husk cover, kernel hardness) that minimize foliar or ear damage by FAW. Ni et al. (2008) showed that CML333 (with moderate silk maysin), CML336 (with low silk maysin) and CML338 (with high silk maysin) were resistant to FAW at the seedling stage, and CML335 (without silk maysin) was susceptible. CML338 and Mp708 were categorized as tolerant to insect herbivory because uninested and injured plants

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Fig. 3 Photographs from a field trial in Vietnam showing A FAW-damaged conventional (non-Bt) maize hybrid with extensive foliar damage and B Bt maize (MON 89034) hybrid expressing the Cry1A.105 and Cry2Ab2 proteins with no FAW damage. Note: Bt maize was planted as a blend containing 5% non-Bt seed (Source: Bayer Crop Science, Vietnam)
Table 2  Some potential sources of FAW resistance in temperate maize germplasm identified or developed by maize breeding programs in the Americas

| Germplasm | Description | References |
|-----------|-------------|------------|
| Mp496; Mp701-Mp708, Mp713; Mp714; Mp716 | Temperate maize inbred lines with resistance to FAW developed in the USA by USDA-ARS (Mississippi). Of these, Mp496, and Mp701 to Mp708, were derived from Caribbean accessions—Antigua Gp1, Antigua Gp2D, Guadalupe Gp1A, and Republica Dominica Gp1. Mp713 and Mp714 were developed from CIMMYT’s Multiple Insect-Resistant populations | Scott and Davis (1981); Scott et al. (1982); Williams and Davis (1980, 1982, 1984, 2000, 2002); Williams et al. (1990) |
| B49; B52; B64; B68; B96 | Corn borer-tolerant inbreds generated by Iowa State University, USA, through introgression of Maiz Amargo from Argentina into temperate maize. The most important inbred line among these was B68, which became widely used by the seed industry in the USA | Walter Trevisan, personal communication |
| Three GEM (Germplasm Enhancement of Maize) inbreds, including XL370A | Derived from the introgression of germplasm from Uruguay, Cuba, and Thailand; showed resistance to FAW in the southern USA | Ni et al. (2014); Abel et al. (2020) |
| CMS14C; CMS23 (Antigua x Republica Dominica); CMS24; MIRT (Multiple Insect Resistance Tropical) race Zapulote Chico, Sintetico Spodoptera, Caatingueiro Spodoptera, and Assum Preto Spodoptera | Since 1975, Embrapa-Brazil identified and described several sources of resistance to FAW in maize, while also investigating the chemical compounds that underlie these native resistance traits | Walter Trevisan, personal communication |
| Brazilian maize lines with potential resistance to FAW | In work conducted from 1986 to 1993, Embrapa-Brazil identified potential sources of resistance to FAW based on evaluation of maize accessions in the Brazilian germplasm bank | Viana and Guimaraes (1997) |

*Source: Modified based on Prasanna et al. (2018)*
showed no differences in photosynthetic rate, light response curves or photosynthetic rate in the A/Ci curves (net CO₂ assimilation rate, A, versus calculated substomatal CO₂ concentration, Ci).

Shivaji et al. (2010) analyzed whether constitutive levels of jasmonic acid (JA) and other octadecanoid compounds were elevated prior to herbivory in a maize genotype Mp708 with documented resistance to FAW and other lepidopteran pests. The inbred Mp708 had approximately threefold higher levels of JA prior to herbivore feeding than the susceptible inbred Tx601. In addition, the constitutive expression of JA-inducible genes, including those in the JA biosynthetic pathway, was higher in Mp708 than in Tx601. In response to herbivory, Mp708 generated higher levels of hydrogen peroxide and NADPH oxidase transcripts before and after FAW larval feeding. The authors concluded that Mp708 could have a portion of its defense pathway primed resulting in constitutive defenses and the ability to mount a stronger defense when FAW larvae attack. Analysis of volatiles released by the FAW-resistant Mp708 and FAW-susceptible Tx601 in the presence and absence of FAW larvae led to the identification of (E)-β-caryophyllene, a terpenoid associated with FAW resistance, released constitutively in Mp708 (Smith et al. 2012). Israni et al. (2020) recently demonstrated that FAW utilizes specific UDP-Glycosyltransferases to detoxify or inactivate maize defensive benzoxazinoids.

Malook et al. (2021) identified a Chinese maize inbred line Xi502 that was able to mount effective defense in response to FAW attack. Comparative transcriptomics analyses, phytohormonal measurements and targeted benzoxazinoid quantification demonstrated significant inducible defense responses in Xi502 but not in the susceptible reference inbred line B73. The study also showed that Xi502 accumulates higher levels of benzoxazinoids effective against FAW than B73.

There is still a lot to learn about the genetic architecture of native genetic resistance to FAW in maize, although a few studies carried out in recent years have given some insights. Brooks et al. (2007) used 91 simple sequence repeat (SSR) markers on 213 F₂:3 families and detected quantitative trait loci (QTLs) on chromosomes 1, 2, 6, 7, and 9. Womack et al. (2018) evaluated 231 F₂:3 families from the cross of Mp704 (resistant) × Mo17 (susceptible) and genotyped with both SSR and single-nucleotide polymorphism (SNP) markers. This study revealed QTLs in chromosome bins 1.09, 2.08, 3.08, 6.02, 7.04, 8.03, 9.03, 10.02 and 10.04. Womack et al. (2020) developed a bi-parental mapping population, comprising 243 F₂:₃ families from the cross Mp705 (resistant) × Mp719 (susceptible), and evaluated this population for FAW leaf-feeding damage under artificial infestation over 3 years in the USA. QTL analyses led to identification of two major QTLs in bins 4.06 and 9.03 that together explained 35.7% of the phenotypic variance over all environments. The QTL identified in bin 9.03 co-located with a previously identified QTL associated with resistance to leaf-feeding damage in maize by FAW and other lepidopteran insects, while the QTL in bin 4.06 is a new source of resistance to FAW leaf-feeding damage identified in this study. Badji et al. (2020) evaluated a set of 316 tropical maize lines under natural FAW pressure in Uganda and identified 14 SNPs through genome-wide association study (GWAS). These SNPs are distributed on all chromosomes except chromosomes 6 and 7. Several FAW resistance QTLs discovered in earlier studies (Brooks et al. 2005, 2007; Womack et al. 2018) co-localized with 6 of the 14 SNPs reported by Badji et al. (2020).

Kamweru et al. (2022) recently undertook GWAS on a set of 423 CIMMYT maize lines to dissect the genetic basis of native resistance to FAW. The lines were evaluated, based on foliar and ear damage scores, against FAW under artificial infestation at Kiboko, Kenya, in 2020 and 2021. All the screened lines were genotyped with the DArTseq genotyping-by-sequencing platform (Diversity Arrays Technology/DArT). The study revealed 56 significant marker–trait associations and the predicted functions of the putative candidate genes varied from a defense response to several genes of unknown function. Chromosome 4 accounted for the highest number (15%) of the SNP markers associated with foliar damage. One major effect QTL on chromosome 9 in bin 9.03, reported in previous studies (Womack et al. 2018, 2020), coincided with SNP DT9_96875821, detected for the foliar damage score on the 14th day after infestation. Another major QTL detected on bin 4.06 coincided with SNP DT4_167218393, detected for the foliar damage score 21 days after infestation. Another SNP (DT8_165270110) located on chromosome 8 contributed the strongest estimated effect size (6.50) for the expression of the leaf feeding damage resistance trait. Overall, the study revealed that native genetic resistance to FAW is quantitative in nature and is controlled by many loci with minor effects. Genomic selection/prediction could play an important role in improving native genetic resistance to FAW in maize.

Transgenic resistance to FAW

Development of Bt maize technologies and their use against FAW

The first GM crops developed in the late 1980s and 1990s expressed lepidopteran-active insecticidal proteins from *Bacillus thuringiensis* Berliner (and hence are known as Bt crops) (Fischhoff et al. 1987; Perlak et al. 1990). These proteins had been used previously in formulations of microbial products to control insect pests worldwide (US EPA 1998a, b; Huang et al. 2007; Hammond and Koch 2012). The efficacy and safety to humans and non-target organisms of these
insecticidal proteins made them the optimal candidates for the development of GM crops (Koch et al. 2015; Romeis et al. 2019). By 2019, Bt crops expressing one or more Bt proteins for pest control were grown on 56 million hectares globally (ISAAA 2019), reflecting the economic and environmental benefits accrued by farmers due to the high efficacy of Bt crops (Carrière et al. 2003; Mendelsohn et al. 2003; Wu et al. 2008; Hutchinson et al. 2010; Dively et al. 2018) and their potential to reduce insecticide use (Zhang et al. 2018).

As a key lepidopteran maize pest in South America, Bt maize technologies have been successfully used to reduce FAW larval feeding injury in Brazil, Argentina, Paraguay and other major maize-growing countries (Fatoretto et al. 2017). Although the first generation of Bt maize technologies available in the region was based on the Cry1Ab protein, which has limited activity against FAW, these Bt maize hybrids still offered average protection against FAW that was superior to conventional insecticides. The behavior of FAW larvae to feed within the whorl of maize plants typically reduces the success of insecticidal sprays to manage FAW (Burtet et al. 2017). Moreover, resistance to various classes of synthetic insecticides including pyrethroids and organophosphates (Díez-Rodríguez and Omoto 2001; Carvalho et al. 2013), larval growth inhibitors (Nascimento et al. 2016), spinosyns (Okuma et al. 2018) and recently diamides (Bolzan et al. 2019; Boaventura et al. 2020) has been documented in FAW in Brazil. The highly destructive nature of FAW and the limited efficacy to insecticidal sprays favored the early adoption of Bt maize technologies by farmers in Brazil and surrounding countries. For instance, MON 810 hybrids containing Cry1Ab were commercially deployed in 2008 in Brazil and were perceived as an important contribution to more effective IPM for FAW (Waquil et al. 2013). Subsequently, the deployment of Bt maize hybrids expressing Bt proteins with significantly higher activity against FAW (Cry1F, Cry1A.105 and Cry2Ab2, and Vip3Aa20) led to higher adoption of Bt maize; Bt maize hybrids currently represent approximately 80% of the maize area in Brazil (Waquil et al. 2013; Marques et al. 2019; Moscardini et al. 2020). Extensive cultivation of Bt maize had no significant effect on non-target organisms, including parasitoids and predators of FAW (Comas et al. 2014; Resende et al. 2016; Bertho et al. 2020).

The same Bt maize technologies developed and commercialized for lepidopteran pest control in the Americas have been tested for their efficacy against key African and Asian maize pests to determine their fit for those regions. Where they promise good control of these pests, now including FAW, these technologies could be an important additional tool for farmers. However, a prerequisite for Bt maize technologies to be legally cultivated by farmers is assessment of the safety of the transgenic event to humans, non-target organisms and the environment and approval by national regulatory authorities. This in turn requires the presence of suitable regulatory frameworks and assessment capacity, which do not exist in many African and Asian countries. Where the capacity is present, regulatory approvals typically take many years and represent a significant barrier to the adoption of Bt maize. This situation contrasts with the simple and rapid process for registering hybrids with the sort of novel native traits described in the previous sections. Not surprisingly, the countries cultivating the largest areas of Bt crops globally typically have regulatory frameworks for Bt crops that are expeditious, transparent, and relatively simple to comprehend and comply with (Levin, 1994; ISAAA 2020; Turnbull et al. 2021). Because of the regulatory hurdles, political barriers and other factors, experience with Bt maize in Africa and Asia still is relatively limited, as summarized in the following sections.

### Bt maize in Africa

In South Africa, the first Bt maize hybrids (MON 810 with Cry1Ab) were planted commercially in 1997. In 2010, MON 89,034 hybrids with the Cry1A.105 and Cry2Ab2 proteins were introduced. These technologies were grown to control the stem borers, *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Crambidae). As in the Americas, these technologies have provided economic and environmental benefits to farmers, including regions comprised largely of smallholders (Keetch et al. 2005; Muzhinji and Ntuli 2020; Ala-Kokko et al. 2021). The area planted to GM maize in 2017 was estimated at 1.96 million ha, representing 85% of the total maize area (approximately 2.3 million ha) (FAOSTAT 2021). Of this area, 1.62 million ha was planted with Bt maize hybrids containing the Cry1Ab protein (MON 810) or the Cry1A.105 and Cry2Ab2 proteins (MON 89,034) (ISAAA 2017).

Since 2016, FAW has become a major pest in parts of the South African maize-growing area. After its invasion into South Africa in early 2016, FAW was included as a target pest of MON 89034 (Botha et al. 2019). Consistent with experience in the Americas, MON 89034 was observed to provide high levels of protection against FAW with superior yields in South Africa (Chingombe 2020). In contrast, the MON 810 maize event confers partial resistance to FAW.

South Africa is currently the only African country where Bt maize is grown commercially. However, the National Agricultural Research Organizations of Kenya, Ethiopia, Nigeria, Tanzania, Uganda and Mozambique are testing the performance of Bt maize technologies introgressed into locally adapted African maize hybrids under the TELA® Maize project (AATF 2021). The TELA maize project was launched in 2018 as a public–private partnership led by the African Agricultural Technology Foundation (AATF). The
TELA maize project is working to enhance food security in sub-Saharan Africa (SSA) through the release of high yielding insect-protected (TELA®) maize hybrids.

**Bt maize in Asia**

In Asia, experience with Bt maize has been broader than in Africa but is still limited. Bt maize technologies were first approved for cultivation in the Philippines in 2002 and Vietnam in 2014. The primary target pest for Bt maize in these countries is the Asian corn borer (Ostrinia furnacalis Guenée) (ACB), while secondary target pests include the common cutworm (Spodoptera litura Fabricius) (CCW), the corn earworm (Helicoverpa armigera Hübner) (CEW) and more recently FAW. Bt maize is also approved but not yet commercially planted in Pakistan, where the primary target pest is the maize stem borer (Chilo partellus Swinhoe). In addition, Bt maize is in the testing and approval process in China, the largest maize-growing country in Asia.

In the Philippines, Bt maize products have been cultivated since 2002 when the first Bt maize event, MON 810 (Yieldgard™), containing the Cry1Ab protein, was approved for commercial use. The approval of the first pyramided insect-resistant maize hybrid containing the MON 89034 event was received by Monsanto Philippines in 2010 (Table 3), followed by approval of Intrasect® hybrids from Pioneer Hi-Bred Philippines, containing the TC1507 × MON 810 events for insect resistance. The maize products containing the MON 810, Bt11, MON 89034 and TC1507 × MON 810 events have demonstrated excellent control of ACB over the 18 years of cultivation (Afidchoa et al. 2013; Thompson et al. 2010; Caasi-Lit et al. 2018). Maize in the Philippines is planted on about 2.5 million ha, of which Bt maize hybrids occupied close to 0.66 million in 2019–20 (PSA 2020; USDA-GAIN 2021). GM maize (including herbicide-tolerant traits stacked with Bt traits) reached a peak of 0.730 million ha during 2012 and are planted on 0.6–0.7 million ha every year (USDA-GAIN 2020a). The high adoption of Bt maize in the Philippines has led to significant socioeconomic benefits (Yorobe and Quicoy 2006; Yorobe and Smale 2012; Gonzalez et al. 2013; Afidchoa et al. 2013). FAW was first reported in the Philippines in 2019 (Navasero et al. 2019) and was reported to infest an area of 8,000 ha, mostly conventional maize, as of June 2020 (https://www.da.gov.ph/da-allots-p150m-to-help-farmers-control-fall-armyworm/). One possible reason for low infestations and delayed spread could be the adoption and cultivation of Bt maize (USDA-GAIN 2020a). There are no more recent estimates from the Philippines of FAW infestations.

The evaluation of Bt maize in Vietnam began in 2010 and since then three Bt maize events (MON 89034, Bt11 and TC1507) have been approved for environmental release (Table 3). Based on the biosafety approval given by MONRE, the Ministry of Agriculture and Rural Development approved Bt maize hybrids containing the MON 89034 (Fig. 3) and Bt11 events. In 2015, when they were first planted, Bt maize events occupied 3,500 ha and in 2019 they covered 92,000 ha, which was 10.2% of the total maize area (USDA-GAIN 2020b; Brookes and Dinh 2021). Brookes and Dinh (2021) highlighted the economic and environmental benefits of GM maize cultivation in Vietnam. FAW was documented in Vietnam in 2019 and was reported to have affected 35,000 ha in the country. However, in 2020, FAW infestations were reduced in earlier affected areas and this may be related to an increase in planting of Bt maize hybrids (USDA-GAIN 2020c).

In Pakistan, conventional maize was grown on 1.413 million hectares in 2019, with a consistent increase in area and production over the last 10 years (FAOSTAT 2021). Maize stem borer is the primary pest of maize (Arabjafari and Jalali 2007) in Pakistan, followed by armyworm species (Spodoptera spp., Mythimna spp.) and shoot fly (Atherigona soccata) which can reduce yield by 10–30% (Naz et al. 2003; Ahmed et al. 2003). FAW was first reported in 2019–20 in the maize growing districts of Sindh and Faisalabad, with Infestation levels of up to 80% (Naeem-Ullah et al. 2019; Gilal et al. 2020; Khan et al. 2020). Considering the management challenges with key maize pests, the evaluation of Bt maize events started in 2009. After seven years of evaluation, in 2016, the National Biosafety Committee of the Ministry of Climate Change approved stacked GM maize expressing insect resistance and herbicide tolerance traits for commercial cultivation. The GM maize products approved include stacked events with MON 810, MON 89034, TC1507 and TC1507 × MON 810. However, the varietal registration of the above-mentioned GM hybrids is pending approvals by the Federal Seed Certification Authority.

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**Table 3** Bt maize events approved for cultivation in the Philippines and Vietnam (Sources: Bureau of Plant Industry, Philippines and Ministry of Natural Resources and Environment (MONRE), Vietnam)

| Technology Provider   | Bt maize event | Bt gene(s) expressed | Country—year of approval for cultivation |
|-----------------------|----------------|----------------------|------------------------------------------|
| Bayer Crop Science    | MON 810        | cry1Ab               | Philippines—2002                         |
|                       | MON 89034      | cry1A.105 + cry2Ab2  | Philippines—2010, Vietnam—2014           |
| Pioneer Hi-bred       | TC1507         | cry1F                | Philippines—2013, Vietnam—2016           |
| Syngenta              | Bt11           | cry1Ab               | Philippines—2005, Vietnam—2015           |
|                       | MIR162         | vip3Aa20             | Philippines—2018                         |
Table 4 List of GM maize events offering control of lepidopteran insects that have been approved by the Ministry of Agriculture and Rural Affairs (MARA) in China

| Event name | Genes         | Targeted insects       | Technology developer                        |
|------------|---------------|------------------------|---------------------------------------------|
| DBN9501    | vip3Aa19, pat | Fall armyworm          | Beijing Da Bei Nong Biotech Ltd             |
| DBN9936    | cry1Ab, epsps | Asian corn borer       | Beijing Da Bei Nong Biotech Ltd             |
| Ruifeng125 | cry1Ab/cry2Aj, g10evo-epsps | Asian corn borer       | Hangzhou Ruifeng Biotech Ltd and Zhejiang University |

Source: MARA, China

Maize is planted over approximately 40 million ha in China (FAOSTAT 2021). The major lepidopteran pests of maize are ACB and CEW, causing 10–30% yield losses every year (Wang et al. 2000, 2021; Shen et al. 2016; Liu et al. 2016) with ACB alone causing an estimated 6–9 million tons of lost yield annually (He et al. 2003). Adding to these production constraints, FAW was first documented in China in 2019 (Sun et al. 2021a; Wu et al. 2019) and was observed in all maize-growing regions of China by mid-2019 (Jiang et al. 2019; NATESC 2019; Yang et al. 2021). By late 2019, FAW had damaged a total of 1.08 million ha of crops, mainly maize (Jiang et al. 2019). Qin et al. (2020) estimated that the potential economic losses to maize by FAW in China could be at least US$5.8 billion annually, of which US$3.95 billion can be managed with effective control measures in place. Most of the Bt maize events developed in China express Cry1 and/or Cry2 class proteins, as reviewed by Liu et al. (2016). These include events expressing single genes e.g., Cry1Ab (Wang et al. 2015) and fusion proteins such as Cry1Ab/Zip3A (Chang et al. 2013a, b) and Cry1Ab/Cry1Ie (Yang et al. 2012). All these events demonstrated efficacy against ACB under laboratory and field conditions. In a recent published study by Sun et al. (2021b), three Bt maize events—Ruifeng 125 (expressing Cry1Ab/Cry2Aj), DBN9936 & DBN9978 (expressing Cry1Ab)—were evaluated and found to be highly efficacious against ACB, including a Cry1C-resistant strain (Sun et al. 2021b). The invasion of FAW in 2019 triggered evaluations of available and new Bt maize events across China. FAW populations that invaded China were found to be susceptible to commonly used Bt proteins, e.g., Cry1, Cry2 and Vip3 classes (Li et al. 2019, 2020), and maize events, e.g., DBN9936 (expressing Cry1Ab protein) and the pyramided events, e.g., DBN3608 and DBN3601 (expressing Cry1Ab + Vip3A proteins) (Zhang and Wu 2019). There are three Bt maize event approvals (biosafety certificates) given by MARA in China since 2020 (Table 4), but no Bt maize hybrid approvals have been given yet.

Additional countries with potential for cultivation of Bt maize to manage FAW in Asia

India and Indonesia are the two largest maize-growing countries after China in Asia. Maize reached a peak of 8.7–9.9 million ha during 2018–19 in India, while in Indonesia an area of 4.5–5.7 million ha was planted in the past few years (FAOSTAT 2021). In both India and Indonesia, lepidopteran pest pressure, including from FAW, is high with heavy economic impacts and Bt maize should be considered as part of the IPM toolbox. However, no Bt maize events have been approved in either country.

In India, the stem borers, C. partellus and Sesamia inferens (Walker), are the major pests limiting maize production (Kumar et al. 2013). C. partellus alone was reported to cause yield losses up to 80% in some regions (Singh and Sajjan 1982; Chatterji et al. 1969). FAW was first detected in India in mid-2018, when Ganiger et al. (2018) reported it in southern India. By August 2019, FAW was reported from all maize-growing states (Sharana basappa et. al. 2018; ICAR-NBAIR, 2018; Bhavani et al. 2019; Suby et al. 2020; Sharma 2021). Balla et al. (2019), using rainfall patterns, remote sensing and imaging, predicted yield losses from FAW infestation could be up to 33%.

In Indonesia, the major production constraint for maize is insect pests including ACB and CEW (Swastika et al. 2004). ACB has been the primary pest and causes significant damage to maize plants (Trisyono et al. 2020). ACB alone was reported to cause yield losses up to 80% in some regions (Singh and Sajjan 1982; Chatterji et al. 1969). FAW was first detected in India in mid-2018, when Ganiger et al. (2018) reported it in southern India. By August 2019, FAW was reported from all maize-growing states (Sharana basappa et. al. 2018; ICAR-NBAIR, 2018; Bhavani et al. 2019; Suby et al. 2020; Sharma 2021). Balla et al. (2019), using rainfall patterns, remote sensing and imaging, predicted yield losses from FAW infestation could be up to 33%. In the last two years, FAW has gained economic importance after being first documented in mid-2019. The first report of FAW occurrence observed FAW on 100% of maize plants in the Lampung area, Sumatra (Trisyono et al. 2019). Supartha et al. (2021) surveyed FAW infestations in Bali province and reported that infestations began in the 2nd week of planting (19.12%), peaked at 4th week of planting (66.41%) and remained above 10% until 8th week. This
indicates the continued presence of FAW and the potential impact on maize yields.

**Field-evolved Bt resistance in FAW populations**

The primary threat to the sustainable use of *Bt* maize technologies is the evolution of insect resistance. The first case of documented field-evolved resistance to *Bt* maize in FAW was for Cry1F-based maize hybrids in Puerto Rico (Storer et al. 2010, 2012a). Several factors apparently drove the evolution of FAW resistance in Puerto Rico, including the island setting limiting insect migration and the tropical climate conducive to year-round cultivation of maize (Storer et al. 2010). Subsequently, field resistance to Cry1F maize was also detected in the southeastern USA (Niu et al. 2013; Huang et al. 2014) and in the Brazilian state of Bahia, in the latter case approximately three years after first commercial plantings (Farias et al. 2014a, b). Low compliance with IRM recommendations seems to be a major cause of the rapid onset of resistance to Cry1F in FAW in Brazil (Farias et al. 2014b). Bernardi et al. (2015a) also detected partial cross-resistance among Cry1 proteins in FAW, meaning that the Cry1F resistance conferred some resistance to Cry1A.105 and Cry1Ab. However, no significant cross-resistance was found between Cry1F and Cry2Ab2. The potential cross-resistance between Cry1F, Cry1A.105 and Cry1Ab in FAW was previously shown through in vitro assays by Hernández-Rodríguez et al. (2013). Omoto et al. (2016) documented the evolution of field-relevant resistance in FAW to Cry1Ab in Brazil, potentially due to either selection from the use of MON 810 and/or cross-resistance to Cry1F.

The use of *Bt* maize hybrids with less-than-ideal IRM fit (e.g., less-than-high-dose technologies, components of *Bt* pyramids with cross-resistance to other *Bt* proteins in the landscape) combined with low compliance with IRM recommendations seems to be a common theme across the FAW resistance cases in South America (Farias et al. 2014a; Chandrasena et al. 2017). The deployment of MIR162-based maize technologies (expressing Vip3Aa20) carrying an effective new mode of action to counter FAW resistance to *Bt* maize technologies in South America has been an important addition to the “toolbox” for FAW control. However, poor compliance with IRM recommendation was a critical contributor to the observed cases of FAW resistance to *Bt* proteins in South America (Farias et al. 2014a; Chandrasena et al. 2017) and continues to be a threat to the sustainability of *Bt* maize technologies in the region.

Insect resistance management (IRM) for *Bt* maize

The proactive implementation of effective IRM plans can delay resistance evolution to *Bt* maize in FAW populations. The central components of an IRM strategy for *Bt* crops are the “dose” of the *Bt* technology and ensuring that the “refuge” is present refuge needs of the product are met, typically via the planting of structure refuges. The dose of a *Bt* technology refers to the level of control of susceptible and heterozygous-resistant insects; ideally, a *Bt* technology should control nearly all heterozygotes in the pest population of the pest and thereby eliminate most of the resistance alleles from the target pest population (Gould 1998). A refuge ensures that a sufficient population of susceptible insects is available to mate with the few homozygous-resistant insects that may survive in *Bt* maize fields. The combination of high-dose products to control heterozygous individuals and sufficient refuge can significantly dilute the frequency of resistance alleles in the insect population over time, thereby delaying the evolution of insect resistance (Gould 1998; Tabashnik and Carrière 2017; Van den Berg et al. 2021).

Therefore, an effective IRM plan should include:

1. **Removal of resistance alleles/genes from the insect population through *Bt* technologies with effective dose or high-dose expression of *Bt* proteins**
2. **Sufficient refuge for *Bt*-susceptible target insects**
3. **Deploy *Bt* technologies expressing two or more *Bt* proteins with independent modes of action against the target insect species**
4. **Educate and train farmers and relevant stakeholders on practices to manage resistance**
5. **Monitor the development of insect resistance**

Although MIR162 expressing the Vip3Aa20 protein is currently the most effective *Bt* gene maize event, i.e., has the highest measured dose against FAW larvae (Bernardi et al. 2015b), the latest generations of *Bt* maize combining at least two *Bt* proteins active against FAW and representing unique and independent modes of action characterize a robust alternative to manage this species (Horikoshi et al. 2016, 2021; Moscardini et al. 2020; Tavares et al. 2021). These products, known as *Bt* pyramids, combine robust protection against larval feeding injury of FAW (Waquil et al. 2013; Moscardini et al. 2020) and improved IRM value (Roush 1998; Storer et al. 2012b). *Bt* maize products with two or more effective *Bt* proteins with distinct modes of action significantly improve the likelihood of delaying resistance; however, sustaining reasonable compliance with structured refuge recommendations is also essential.
for sustained management of FAW. Failure to maintain adequate compliance with structure refuge recommendations was one of the main causes for FAW resistance to Bt maize technologies in South America. Among the reasons for the low levels of compliance are the economic and opportunity costs of refuge plantings. The use of seed mixtures of Bt and non-Bt seeds in the same package can transfer the responsibility of ensuring compliance to manufacturers instead of relying on farmers to plant a structured refuge (Carroll et al. 2012). Despite the benefits of seed mixtures in ensuring refuges are present within Bt maize fields, larval movement between Bt and non-Bt plants in a seed mix field can increase the risk of resistance evolution. FAW larvae not receiving a lethal dose that move off Bt plants onto adjacent non-Bt plants, and movement of larger and less susceptible larvae from non-Bt to adjoining Bt plants, could increase heterozygote fitness and intensify selection for resistance (Carroll et al. 2012). In addition, movement of susceptible FAW larvae off non-Bt plants onto neighboring Bt plants reduces refuge effectiveness by reducing the number of susceptible insects produced by refuge plants (Carroll et al. 2012). Although FAW larvae are highly mobile (Pannuti et al. 2016; Malaquias et al. 2017; Sokame et al. 2020), the use of effective Bt maize pyramids can reduce these risks associated with seed mix refuges for FAW (Bernardi et al. 2015b; Dimase et al. 2021; Horikoshi et al. 2021; Tavares et al. 2021).

Once the resistance risk of a Bt maize technology is properly assessed and a refuge recommendation is defined, it is fundamental to integrate the IRM recommendation into business plans and ensure resources are available to: a) implement training and education programs for farmers and other key stakeholders; b) track adoption and use patterns of a Bt maize technology and the level of compliance with structured refuge by farmers (if structured refuge is part of the IRM recommendation); c) monitor the development of resistance in populations of the target pest and d) follow up on the cases of unexpected injury to the technology and recommend remediation practices (Head and Greenplate 2012).

**Host plant resistance to FAW: critical gaps, challenges and priorities**

**Critical gaps and challenges**

- An array of FAW-tolerant/FAW-resistant germplasm in diverse genetic backgrounds needs to be developed and deployed in both Africa and Asia. A major obstacle to breeding crop varieties with FAW resistance using conventional breeding is the low frequency of resistant genotypes in germplasm collections. Therefore, it is imperative both to widen the search for sources of native genetic resistance to FAW and to discover, validate and ultimately deploy genomic regions conferring resistance to FAW using either marker-assisted breeding or genomic selection, as appropriate, depending on presence/absence of major haplotypes conferring resistance to FAW.
- It must be noted that farming communities need elite crop varieties with not only FAW tolerance/resistance, but also a package of other traits relevant for that specific agroecology or market segment, including high yield, abiotic stress tolerance, disease resistance, nutrient and water use efficiency, nutritional enhancement, etc. Often the sources of genetic resistance to FAW may not be directly useful as elite parental lines of commercial hybrids/varieties. Therefore, intensive and accelerated breeding efforts are required to transfer native resistance from validated sources of resistance into diverse, Africa-adapted and Asia-adapted elite maize products (inbreds/hybrids/OPVs) for deployment to farming communities. Similar efforts are needed in other major crops, such as sorghum and millets, affected by FAW in Africa and Asia.
- Lack of adequate investment in accelerated and intensive breeding for native genetic resistance to FAW in Africa and Asia is hampering progress by the international agricultural research centers and national partners to come out with solutions for FAW management based on host plant resistance.
- Another important gap that needs urgent attention is the stacking of transgenic insect-resistant traits with native genetic resistance and the combined value they could generate, ensuring sustainable yield protection from pests such as FAW.
- Deploying improved maize varieties with genetic resistance to FAW (native or transgenic) has significant potential to reduce the use of pesticides by farmers. Studies should be done to empirically quantify the reduction in pesticide use together with the increase in resilience and productivity that comes with deployment of host plant resistance.
- Functional and effective management of intellectual property seems to be a challenge in parts of Africa and Asia, likely impacting investments on transgenic research to address issues insect control in those regions. This would require policies in place to ensure there is return on the investments made by the private and or public sectors in developing these technologies.
- Regulatory systems that are restrictive for the research and cultivation of transgenic crops in countries in Africa and Asia are limiting farmers access to technologies to manage FAW. Consumer acceptance of transgenic crops and or limited technical capacity to evaluate safety of these products seems to be the main drivers of this bottleneck. These technologies
have been proven safe to humans, non-target organisms and the environment. Therefore, it is critical to work across stakeholders to understand the causes and how to improve the functionality of the regulatory systems in Africa and Asia. Moreover, capacity building on biosafety may be necessary in several countries in Africa and Asia to enable the development of science-based and efficient regulatory frameworks to assess the safety of Bt crops in the region.

Priorities

In terms of native genetic resistance to FAW, the key priorities are:

1. Varietal release and widespread deployment of “first-generation” white maize hybrids with FAW resistance, developed recently by CIMMYT and now available to partners, especially in SSA; these hybrids can also be potentially tested in Asian countries where white maize varieties are grown and consumed by local populations.

2. Fast-tracked introgression of sources of native genetic resistance to FAW into Africa-and Asia-adapted germplasm, and release of next-generation products with native genetic resistance to FAW in Africa and Asia.

3. Discovery/validation of genomic regions for resistance to FAW in maize using appropriate populations and exploring the possibility of genomic prediction for developing novel Africa-adapted/Asia-adapted FAW-tolerant/FAW-resistant maize varieties.

4. Strengthening the capacity of NARES institutions in Africa and Asia in breeding and deploying improved maize varieties with resistance to FAW and other important adaptive and agronomic traits relevant for the smallholders.

Regarding transgenic resistance to FAW, the major priorities are:

1. Accelerated testing and deployment of Bt maize with proven efficacy, biosafety and environmental safety with appropriate support from policy makers and regulatory authorities.

2. Pyramiding transgenes with different modes of action (e.g., cry + vip genes), instead of single-gene deployment, as a part of IRM strategy.

3. Implementing IRM and proper stewardship wherever Bt maize varieties have been deployed in Africa and Asia, to ensure sustainable protection against the pest.

Conclusion

Sustainable control of FAW is best achieved when farmers use host plant resistance as part of an IPM strategy, together with good agricultural practices, pest scouting, biological control, agro-ecological management and judicious use of environmentally safer pesticides. Intensive efforts are being made in Africa by CIMMYT and partners to identify, validate and develop elite maize germplasm with native genetic resistance to FAW. These efforts need to be further accelerated and intensified in both Africa and Asia to derive elite tropical/subtropical germplasm suitable for different agro-ecologies and market segments. Such products must combine FAW resistance with other desirable and relevant traits for resource-constrained smallholder farmers in the target geographies.

In addition, Bt maize hybrids carrying lepidopteran-specific transgene(s), wherever released in Africa or Asia, can become an important tool in the IPM toolbox for FAW management. Bringing the benefits of Bt-based solutions for FAW management more extensively into Africa and Asia would, however, require overcoming existing regulatory, political and consumer acceptance hurdles. In countries where Bt maize is already commercialized, it is important to devise and implement effective IRM strategies. Combinations of native genetic resistance and Bt maize also need to be explored as a path to more effective and sustainable host plant resistance options.

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**References**

AATF (2021) https://www.aatf-africa.org/tela-maize-project/

Abel CA, Coates BS, Millard M, Williams WP, Scott MP (2020) Evaluation of XL370A-derived maize germplasm for resistance to leaf feeding by fall armyworm. Southwest Entomol 45:69–74.

Afidchoa MM, Mustersa CJM, de Snooa GR (2013) Asian corn borer (ACB) and non-ACB pests in GM corn (Zea mays L.) in the Philippines. Pest Manag Sci 69:792–801.

Ahmed S, Anjum S, Naem M, Ashraf M (2013) Molecular characterization of the inheritance of resistance of *Zea mays* due to fall armyworm infestation and potential IoT-based interventions for its control. J Entomol Zool Stud 7(5):920–927.

Beck SD (1965) Resistance of plants to insects. Annu Rev Entomol 10:207–232.

Bernardi O, Bernardi D, Amado D, Sousa RS, Fattorato J, Medeos FC, Convijile J, Burd T, Omoto C (2015b) Resistance risk assessment of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and *Diatraea saccharalis* (Lepidoptera: Crambidae) to Vip3Aa20 insecticidal protein expressed in corn. J Econ Entomol 108:2711–2719. https://doi.org/10.1093/jee/tov219

Bhavani B, Chandra Sekhar V, Varma PK, Bharatha Lakshmi M, Jamuna P, Swapan B (2019) Morphological and molecular identification of an invasive insect pest, fall armyworm, *Spodoptera frugiperda* occurring on sugarcane in Andhra Pradesh. J Entomol Zool Stud 7(4):12–18.

Boaventura D, Bolzan A, Padovez FEO, Okuma DM, Omoto C, Nauen R (2020) Detection of a cyanodine receptor target-site mutation in diamide insecticide resistant fall armyworm, *Spodoptera frugiperda*. Pest Manag Sci 76:47–54. https://doi.org/10.1002/ps.5505

Bolzan A, Padovez FEO, Nascimento ARB, Kaiser IS, La EC, Amaral FSA, Kanno RH, Malaquias JB, Omoto C (2019) Selection and characterization of the inheritance of resistance of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) to chlorantraniliprole and cross-resistance to other diamide insecticides. Pest Manag Sci 75:2682–2689. https://doi.org/10.1002/ps.5376

Botha AS, Erasmus A, du Plessis H, Van den Berg J (2019) Efficacy of *Bt* maize for control of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in South Africa. J Econ Entomol 112:1260–1266. https://doi.org/10.1093/jee/toz048

Brookes G, Dinh TX (2021) The impact of using genetically modified (GM) corn/maize in Vietnam: results of the first farm-level survey. GM Crops & Food 12:71–83. https://doi.org/10.1080/22237747.2010.1031677

Brooks TD, Wilcox MC, Williams WP, Buckley PM (2005) Quantitative trait loci conferring resistance to Fall armyworm and Western corn borer leaf feeding damage. Crop Sci 45:2430–2434. https://doi.org/10.2135/cropsci2004.0656

Brooks TD, Bushman BS, Williams WP, McMullen MD, Buckley PM (2007) Genetic basis of resistance to Fall armyworm (Lepidoptera: Noctuidae) and Western corn borer (Lepidoptera: Crambidae) leaf-feeding damage in maize. J Econ Entomol 100(4):1470–1475.

Burgett LM, Bernardi O, Melo AA, Pes MP, Strahl TT, Guedes JVC (2017) Managing fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), with *Bt* maize and insecticides in southern Brazil. Pest Manag Sci 73:2569–2577. https://doi.org/10.1002/ps.4660

Caasi-Lit MT, Manalo NAQ, Suyat EA, Dacuba RH, Benigno EA (2018) Response of second instar Asian corn borer, *Ostrinia furnacalis* (Gueneé) (Crambidae: Lepidoptera), to *Bt* transgenic maize, MON 89034. Philipp Entomol 32:107–111.

Carrière Y, Ellers-Kk C, Sisterson M, Antilla L, Whitlow M, Dennehy TJ, Tabashnik BE (2003) Long-term regional suppression of pink
bollworm by Bacillus thuringiensis cotton. Proc Nat Acad Sci USA 100:519–1523. https://doi.org/10.1073/pnas.0436708100

Carroll MW, Head G, Caprio MA (2012) When and where a seed mix refuge makes sense for managing insect resistance to Bt plants. Crop Prot 38:74–79. https://doi.org/10.1016/j.cropro.2012.02.015

Carvalho RA, Omoto C, Field LM, Williamson MS, Bass C (2013) Investigating the molecular mechanisms of organophosphate and pyrethroid resistance in the fall armyworm Spodoptera Fagraeidae. Plos One 8:e62268. https://doi.org/10.1371/journal.pone.0062268

Chandrasena DI, Signorini AM, Abratti G, Storer NP, Olacegui ML, Alves AP, Pilcher CD (2017) Characterization of field-evolved resistance to Bacillus thuringiensis-derived Cry1F δ-endotoxin in Spodoptera frugiperda populations from Argentina. Pest Manag Sci 74:746–754

Chang X, Liu G, He K, Shen Z, Peng Y, Ye G (2013a) Efficacy evaluation of two transgenic maize events expressing fused proteins to Cry1Ab-susceptible and-resistant Ostrinia farnacula (Lepidoptera: Crambidae). J Econ Entomol 106:2548–2556

Chang X, Wang W, Shen Z, Ye G (2013b) Evaluation of transgenic cry1Ab/cry2Aj maize for its resistance to Ostrinia farnacula. Acta Phytopathologica Sinica 40:339–344

Chatterji SM, Young WR, Sharma GC, Sayi IV, Chahal BS, Khare BP, Rathore YS, Panwar VPS, Siddiqui KH (1996) Estimation of loss in yield of maize due to insect pests with special reference to borers. Ind J Entomol 31:109–115

Chingeble PN (2020) Efficacy of MON 89034 Bt trait in conferring fall armyworm resistance in high yielding three-way and single-cross maize hybrids. Dissertation, University of KwaZulu-Natal, Pietermaritzburg, Republic of South Africa

Comas C, Lumbierres B, Pons X, Albajes R (2014) No effects of Bacillus thuringiensis maize on nontarget organisms in the field in southern Europe: a meta-analysis of 26 arthropod taxa. Transgenic Res 23:135–143. https://doi.org/10.1007/s11248-013-9737-0

Cruz I, Figueiredo MLC, Silva RB, Silva IF, Paula CS, Foster J (2012) Using sex pheromone traps in the decision-making process for pesticide application against fall armyworm (Spodoptera frugiperda [Smith] [Lepidoptera: Noctuidae]) larvae in maize. Int J Pest Manag 58(1):83–90. https://doi.org/10.1080/09670874.2012.655702

Davies FM, Williams WP (1992) Visual rating scales for screening whorl-stage corn for resistance to fall armyworm. Mississippi Agricultural & Forestry Experiment Station, Technical Bulletin 186, Mississippi State University, MS, USA

Deshmukh SS, Prasanna BM, Kalleshwarswamy CM, Jaba J, Choudhary B (2021) Fall armyworm (Spodoptera frugiperda). In: Omkar. (ed) Polyphagous pests of crops. Springer, Singapore, pp 349–372. https://doi.org/10.1007/978-981-15-8075-8_8

Díez-Rodríguez GI, Omoto C (2001) Inheritance of lambda-cyhalothrin resistance in Spodoptera frugiperda (J.E. Smith) [Lepidoptera: Noctuidae]. Neotrop Entomol 30:311–316. https://doi.org/10.1590/S1519-566X2001000200016

Dimase M, Brown S, Head GP, Price PA, Walker W, Yu W, Huang F (2021) Performance of Bt-susceptible and-heterozygous dual-gene resistant genotypes of Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) in seed blends of non-Bt and pyramided Bt maize. Insect Sci 28(4):1147–1158. https://doi.org/10.1111/1744-7917.12850

Dively GP, Venugopala PD, Bean D, Whalen J, Holmstrom K, Kuhar TP, Doughty HB, Patton T, Cissel W, Hutchison WD (2018) Regional pest suppression associated with widespread Bt maize adoption benefits vegetable growers. Proc Natl Acad Sci USA 115:3320–3325. https://doi.org/10.1073/pnas.1720692115

FAOSTAT (2021) http://www.fao.org/faostat/en/#data/QCL

Farias JR, Andow DA, Horikoshi JR, Sorgatto RJ, Fresia P, Santos AC, Omoto C (2014a) Field-evolved resistance to Cry1F maize by Spodoptera frugiperda (Lepidoptera: Noctuidae) in Brazil. Crop Prot 64:150–158

Farias JR, Horikoshi JR, Santos AC, Omoto C (2014b) Geographical and temporal variability in susceptibility to Cry1F toxin from Bacillus thuringiensis in Spodoptera frugiperda (Lepidoptera: Noctuidae) populations in Brazil. J Econ Entomol 107(6):2182–2189

Fataoretto JC, Michel AP, Silva Filho MC, Silva N (2017) Adaptive potential of fall armyworm (Lepidoptera: Noctuidae) limits Bt trait durability in Brazil. J Integrated Pest Manag 8:17. https://doi.org/10.1093/jipm/pmx011

Fischhoff BA, Bowdish KS, Perrak FJ, Marrong PG, McCormick SM, Niedermeyer JG, Dean DA, Kusano-Kretzmer K, Mayer EJ, Rochester DE, Rogers SG, Fraley RT (1987) Insect tolerant transgenics tomato plants. Bio/technology 5:807–813. https://doi.org/10.1038/nb08870-807

Ganiger PC, Yeshwanth HM, Muralimohan K, Vinay N, Kumar ARV, Chandrashekara K (2018) Occurrence of the new invasive pest, fall armyworm, Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae), in the maize fields of Karnataka. India Curr Sci 115(4):25

Gili AA, Bashir L, Faheem M, Rajput A, Soomro JA, Khanbar S, Mirwani AS, Zahra T, Mastoi GS, Sahito JGM (2020) First record of invasive fall armyworm (Spodoptera frugiperda [Smith] (Lepidoptera: Noctuidae) in corn fields of Sindh, Pakistan. Pak J Agric Res 33(2):247–252. https://doi.org/10.17582/journal.pjar/2020/33.2.247.252

Goergen G, Kumar PL, Sankung SB, Togola A, Tamo 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):e0165632

Gonzales LA, Elca C, Paningbatan B, Umali R, Gonzales A, Ignacio JL (2013) Micro–Macro Impacts of Technological Change: The GM (Bt) Corn Experience in the Philippines. Final Report. SIKAP/ STRIVE, Los Baños, Philippines

Gould F (1998) Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. Annu Rev Entomol 43:701–726. https://doi.org/10.1146/annurev.ento.43.1.701

Hammond BG, Koch MS (2012) A review of the food safety of Bt crops. In: Sansenbein (ed) Bacillus thuringiensis Biotechnology. Springer, New York, pp 305–325

He KL, Wang ZY, Zhou DR, Wen LP, Song YY, Yao ZY (2003) Evaluation of transgenic Bt corn for resistance to the Asian corn borer (Lepidoptera: Pyralidae). J Econ Entomol 96:935–940

Head GP, Greenplate J (2012) The design and implementation of insect resistance management programs for Bt crops. GM Crops & Food 3:144–153

Hernández-Rodríguez CS, Hernández-Martínez P, Van Ric J, Escrich B, Ferré J (2013) Shared midgut binding sites for Cry1A.105, Cry1Aa, Cry1Ab, Cry1Ac and Cry1Fa proteins from Bacillus thuringiensis in two important maize pests, Ostrinia nubilalis and Spodoptera frugiperda. PLoS One. https://doi.org/10.1371/journal.pone.0068164

Horikoshi JR, Vertuan H, Castro AA, Morrell K, Griffith C, Evans A, Tan J, Asimwe P, Anderson H, José OMA, Donrado PM, Berger G, Martinelli GH (2021) A new generation of Bt maize for control of fall armyworm (Spodoptera frugiperda). Pest Manag Sci 77(8):3727–3736. https://doi.org/10.1002/ps.6334

Horikoshi RJ, Bernardi D, Bernardi O, Malagquis JB, Okuma DM, Mallo LD, Amalar FS de A, Omoto C (2016) Effective dominance of resistance of Spodoptera frugiperda to Bt maize and cotton varieties: implications for resistance management.
Huang DF, Zhang J, Song FP, Lang ZH (2007) Microbial control and biotechnology research on Bacillus thuringiensis in China. J Invertebr Pathol 95:175–180. https://doi.org/10.1016/j.jip.2007.02.016

Huang F, Qureshi JA, Meagher RL et al (2014) Cry1F resistance in fall armyworm Spodoptera frugiperda: single gene versus pyramided Bt maize. PLoS One. https://doi.org/10.1371/journal.pone.0112958

Hutchinson WD, Burkness EC, Mitchell PD, Moon RD, Leslie TW, Fleischer SJ, Abrahamson M, Hamilton KL, Stetty KL, Gray ME, Hellmich RL, Kaster LV, Hunt TE, Wright RJ, Pecinovsky K, Rabaeu TL, Flood BR, Raun ES (2010) Areawide suppression of European corn borer with Bt maize reaps savings to non-Bt maize growers. Science 320:222–225. https://doi.org/10.1126/science.1190242

ICAR-NBAIR (2018) Indian Council of Agricultural Research—National Bureau of Agriculturally Important Insect Newslet-t, X (3), https://www.nbair.res.in/sites/default/files/2019-03/NBAIR%20Newsletter%20%28September%202018%29-09.pdf

ISAAA (2017) Global status of commercialized biotech/GM crops in 2016. ISAAA, Ithaca, NY

ISABA (2017) Global status of commercialized biotech/GM crops in 2017: biotech crop adoption surges as economic benefits accumulate in 22 Years. ISAAA Brief 53: 25–26

ISAAA (2019) International Service for the Acquisition of Agri-Bio-tech Applications. Global status of commercialized biotech/GM Crops: Biotech crops drive socio-economic development and sustainable environment in the new frontier. ISAAA Brief No. 55. ISAAA, Ithaca, NY

ISAAA (2020) ISAAA Brief 55–2019: Executive Summary. Available Online at: https://www.isaaa.org/resources/publications/briefs/55/executivesummary/default.aspx (accessed October 6, 2021)

Israni B, Wouters FC, Luck K, Seibel E et al (2020) The fall armyworm Spodoptera frugiperda utilizes specific UDP-glycosyltransferases to inactivate maize defensive benzoazinoids. Front Physiol 11:604754. https://doi.org/10.3389/fphys.2020.604754

Jiang YY, Liu J, Xie MC, Li YH, Yang JJ, Zhang ML, Qiu K (2019) Observation on law of diffusion damage of Spodoptera frugiperda in China in 2019. Plant Prot 45:10–19

Kamweru I, Anani BY, Beyene Y, Makumbi D, Adetimirin VO, Prasanna BM, Gowda M (2022) Genomic analysis of resistance to fall armyworm (Spodoptera frugiperda) in CIMMYT maize lines. Genes 13:251. https://doi.org/10.3390/genes13020251

Kasoma C, Shimelis H, Laing M, Shayanowako AIT, Mathew I (2020) Screening of inbred lines of tropical maize for resistance to two stem borers species, Busseola fusca and Chilo partellus. J Plant Breed Crop Sci 8:23–33

Keech DP, Webster JW, Ngąka A, Akanbi R, Mahlanga P (2005) Bt maize for small scale farmers: a case study. Afr J Biotech 4(13):1505–1509

Khan HA, Ali N, Farooq MU, Gill NA, Ahmad T, Khalique U (2020) First authentic report of fall armyworm presence in Faisalabad Pakistan. J Entomol and Zool Stud 8(4):1512–1514

Koch MS, Ward JM, Levine SL, Baum JA, Fleischer SJ, Stetty KL, Gray ME, Hellmich RL, Kaster LV, Hunt TE, Wright RJ, Pecinovsky K, Rabaeu TL, Flood BR, Raun ES (2010) Areawide suppression of European corn borer with Bt maize reaps savings to non-Bt maize growers. Science 320:222–225. https://doi.org/10.1126/science.1190242

Levy HC, Garcia-Marinua A, Maruniak JE (2002) Strain identification of Spodoptera frugiperda (Lepidoptera: Noctuidae) insects and cell line: PCR-RFLP of cytochrome oxidase subunit II gene. Fla Entomol 85:186–190. https://doi.org/10.1653/0015-4040(2002)085[186:SOFIL2]2.0.CO;2

Li GP, Ji T, Sun X, Jiang Y, Wu K, Feng HQ (2019) Susceptibility evaluation of invaded Spodoptera frugiperda population in Yunnan province to five Bt proteins. Plant Prot 45(3):15–20

Li Y, Wang Z, Romeis J (2020) Managing the invasive fall armyworm through biotech crops: a Chinese perspective. Trends Biotechnol 39:105–107

Liu Q, Hallerman E, Peng Y, Li Y (2016) Development of Bt Rice and Bt Maize in China and their efficacy in target pest control. Int J Mol Sci 17:1561

Malaqius JB, Godoy WAC, Garcia AG, Ramalho FS, Otomo C (2017) Larval dispersal of Spodoptera frugiperda strains on Bt cotton: a model for understanding resistance evolution and consequences for its management. Sci Rep 7:16109. https://doi.org/10.1038/s41598-017-1699-x

Malook S, Xiao-Feng Liu X-F, Liu W, Qi J, Zhou S (2021) The race goes on: a fall armyworm resistant maize inbred line influences insect oral secretion elicitation activity and nullifies herbivore suppression of plant defense. BioRxiv. https://doi.org/10.1101/2021.05.17.444416

Marques LH, Santos AC, Castro BA, Moscardini VF, Rossetto J, Silva OABN, Babcock JM (2019) Assessing the Efficacy of Bacillus thuringiensis (Bt) pyramided proteins Cry1F, Cry1A.105, Cry2Ab2, and Vip3Aa20 expressed in Bt maize against lepidopteran pests in Brazil. J Econ Entomol 112:803–811. https://doi.org/10.1093/jee/toy380

Matova PM, Kamutindo CN, Magorokosho C, Kutywayo D, Gutsa F, Labuschagne M (2020) Fall armyworm invasion, control practices and resistance breeding in Sub-Saharan Africa. Crop Sci 60:2951–2970. https://doi.org/10.1002/csc2.20317

Mendelsohn M, Kough J, Vaituzis Z, Matthews K (2003) Are Bt crops safe? Nat Biotechnol 21:1003–1009. https://doi.org/10.1038/nbt0903-1003

Mihm JA (ed.) (1997) Insect Resistant Maize: Recent Advances and Utilization; Proceedings of an International Symposium held at CIMMYT, 27 November-3 December, 1994. Mexico, D.F.: CIMMYT

Moscardini VF, Marques LH, Santos AC, Rossetto J, Silva OABN, Rampazzo PE, Castro BA (2020) Efficacy of Bacillus thuringiensis (Bt) maize expressing Cry1F, Cry1A.105, Cry2Ab2 and Vip3Aa20 proteins to manage the fall armyworm (Lepidoptera: Noctuidae) in Brazil. Crop Prot. https://doi.org/10.1016/j.cropro.2020.105269

Muringa M, Derera J, Mugo S, Tongoona P, Gichuru L (2015) Evaluation of tropical maize inbred lines for resistance to two stem borer species, Busseola fusca and Chilo partellus. J Plant Breed Crop Sci 8:23–33

Muzhinji N, Ntuli V (2020) Genetically modified organisms and food security in Southern Africa: model and regulations. Shar Biotechnol Regul Exp West Hemisph, 127

Nagoshi RN, Silvie P, Meagher RL Jr, Hay-Roe Thomas JMG, Murua GM (2015) Larval dispersal of Spodoptera frugiperda populations from Mexico with those in China in 2019. Plant Prot 45:10–19

Nagoshi RN, Rosas-Garcia NM, Meagher RL, Fleischer SJ, Westbrook JK, Sappington TW, Hay-Roe Thomas JMG, Murgua GM (2015) Larval dispersal of Spodoptera frugiperda populations from Mexico with those in China in 2019. Plant Prot 45:10–19

Naeem-Ullah U, Ansari AM, Iqbal N, Saeed S (2019) First authentic report of Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) an alien invasive species from Pakistan. Appl Sci Business Econ 6(1):1–3

Nagoski RN, Silvie P, Meagher RL Jr (2007) Comparison of hapolotype frequencies differentiate fall armyworm (Lepidoptera: Noctuidae) corn-strain populations from Florida and Brazil. J Econ Entomol 100:954–961. https://doi.org/10.1603/0222-0493(2007)100[954:cohfdf]2.0.CO;2

Nagoski NN, Meagher RL, Hay-Roe M (2014) Assessing the resolution of hapolotype distributions to delineate fall armyworm (Lepidoptera: Noctuidae) migratory behaviors. J Econ Entomol 107(4):1462–1470. https://doi.org/10.1093/jee/tec14124

Nagoski RN, Rosas-Garcia NM, Meagher RL, Fleischer SJ, Westbrook JK, Sappington TW, Hay-Roe Thomas JMG, Murgua GM (2015) Hapolotype profile comparisons between Spodoptera frugiperda (Lepidoptera: Noctuidae) populations from Mexico with those in China in 2019. Plant Prot 45:10–19

Prasanna BM, Gowda M (2022) Genomic analysis of resistance to fall armyworm (Spodoptera frugiperda) in CIMMYT maize lines. Genes 13:251. https://doi.org/10.3390/genes13020251

Theoretical and Applied Genetics (2022) 135:3897–3916

Springer
from Puerto Rico, South America, and the United States and the implications to migrant behavior. J Econ Entomol 108(1):135–144. https://doi.org/10.1093/jee/too044

Nascimento ARB, Farias JR, Bernardi D, Horikoshi RJ, Omoto C (2016) Genetic basis of Spodoptera frugiperda (Lepidoptera: Noctuidae) resistance to the chitin synthesis inhibitor lufenuron. Pest Manag Sci 72:810–815. https://doi.org/10.1002/ps.4057

NATEG (2019) National Agricultural Technology Extension Service Center-recent reports of fall armyworm in China and neighbouring countries. Plant pathogen and pest information. 2019-4-4

Navasero MV, Navasero MM, Burgonio GAS, Ardez KP et al (2019) Detection of the fall armyworm, Spodoptera frugiperda, (JE Smith) (Lepidoptera: Noctuidae) using larval morphological characters, and observations on its current local distribution in the Philippines. Philipp Ent 33(2):171–184

Naz F, Hussain M, Faridullah DM (2003) Insect Pests of Maize and their Losses. Asian J Pl Sci 2(5):412–414

Ni X, Da K, Buntin GD, Brown SL (2008) Physiological basis of fall armyworm (Lepidoptera: Noctuidae) resistance in seedlings of maize inbred lines with varying levels of silk maysin. Florida Entomol 91:537–545

Ni X, Xu W, Blanco MH, Williams PW (2014) Evaluation of fall armyworm resistance in maize germplasm lines using visual leaf injury rating and predator survey. Insect Sci 21:541–555

Niu Y, Meagher RL Jr, 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 Entomol 96:701–713

Okuma DM, Bernardi D, Horikoshi RJ, Bernardi O, Silva AP, Omoto N, Niu Y, Meagher RL Jr, 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 Entomol 96:701–713

Okuma DM, Bernardi D, Horikoshi RJ, Bernardi O, Silva AP, Omoto C (2018) Inheritance and fitness costs of Spodoptera frugiperda (Lepidoptera: Noctuidae) resistance to spinosad in Brazil. Pest Manag Sci 74:1441–1448. https://doi.org/10.1002/ps.4829

Omoto C, Bernardi O, Salmeron E, Sargott RJ, Dourado PM, Crivellari A, Carvalho RA, Willse A, Martinelli S, Head GP (2016) Field-evolved resistance to Cry1Ab maize by Spodoptera frugiperda in Brazil. Pest Manag Sci 72:1727–1736. https://doi.org/10.1002/ps.4201

Painter RH (1958) Resistance of plants to insects. Annu Rev Entomol 3:267–290. https://doi.org/10.1146/annurev.en.03.010158.001411

Pannuti ER, Baldin ELL, Hunt TE, Paula-Moraes SV (2016) On-Plant Larval Movement and feeding behavior of fall armyworm (Lepidoptera: Noctuidae) on reproductive corn stages. Environ Entomol 45(1):192–200. https://doi.org/10.1093/ee/cnv019

Pashley DP (1986) Host-associated genetic differentiation in fall armyworm (Lepidoptera: Noctuidae): a sibling species complex? Ann Entomol Soc Am 79:898–904. https://doi.org/10.1093/eea/79.6.898

Perlak FJ, Deaton RW, Armstrong TA, Fuchs RL, Sims SR, Greenplate JT, Fischhoff DA (1990) Insect resistant cotton plants. Biotechnology 8:939–943. https://doi.org/10.1016/0010-9217(90)90011-0

Prasanna BM, Bruce A, Winter S, Otin M, Asea G, Sevgan S, Ba M, van den Berg J, Beiger R, Gichuru L, Trevisan W, Williams P, Oikeh S, Edge M, Huesing JE, Powell T (2018) Host plant resistance to fall armyworm. In: Prasanna BM et al (eds) Fall armyworm in Asia: a guide for integrated pest management. Mexico, CIMMYT, pp 99–113

Prasanna BM, Huesing JE, Peschke VM, Eddy R (2021b) Fall Armyworm in Asia: A Guide for Integrated Pest Management. Mexico, CIMMYT

PSA (2020) Philippine Statistics Authority. https://opensat.psa.gov.ph/DataBank/Agriculture-Forestry-Fisheries. Accessed 20 September 2021

Qin YJ, Yang DC, Kang DL, Zhao ZH, Zhao ZH, Yang PY, Li ZH (2020) Potential economic loss assessment of maize industry caused by fall armyworm (Spodoptera frugiperda) in China. Plant Prot 46:69–73

Resende DC, Mendes SM, Marucci RC, de Carvalho SA, Campanha MM, Waquil JM (2016) Does Bt maize cultivation affect the non-target insect community in the agro ecosystem? Revista Brasileira De Entomologia 60:82–93. https://doi.org/10.1016/j.rbe.2015.12.001

Riggin TM, Wiseman BR, Isenhour DJ, Espelie KE (1992) Incidence of fall armyworm (Lepidoptera: Noctuidae) parasitoids on resistant or susceptible corn genotypes. Environ Entomol 21:888–895

Riggin TM, Wiseman BR, Isenhour DJ, Espelie KE (1994) Functional response of Cotesia marginiventris (Cresson) (Hym., Braconidae) to Spodoptera frugiperda (J.E. Smith) (Lep., Noctuidae) on meridic diet containing resistant or susceptible corn genotypes. J Appl Entomol 117:144–150

Romeis J, Naranjo SE, Meisle M, Shelton AM (2019) Genetically engineered crops help support conservation biological control. Biol Control 130:136–154. https://doi.org/10.1016/j.biocontrol.2018.10.001

Routh RT (1998) Two-toxin strategies for management of insecticidal transgenic crops: Can pyramiding succeed where pesticide mixtures have not? Phil Trans R Soc Lond Ser B 353:1777–1786

Rwomushana I, Bateman M, Beale T, Beseh P, et al. (2018). Fall armyworm: impacts and implications for Africa. Evidence note update, October 2018. Wallingford, UK: CABI

Scott GE, Davis FM (1981) Registration of Mp496 inbred of maize. Crop Sci 21:353

Scott GE, Davis FM, Williams WP (1982) Registration of Mp701 andMp702 germplasm lines of maize. Crop Sci 22:1275

Sharanabasappa KCM, Asokan R et al (2018) First report of the fall armyworm, Spodoptera frugiperda (JE Smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India. Pest Manag Hort Ecosystems 24:23–29

Sharma SK (2021) First report of fall armyworm, Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) incidence in Himachal Pradesh (H.P.). India J Entomol Res 45(1):159–164

Shen P, Zhang Q, Lin Y, Li W, Li A, Song Q (2016) Thinking to promote the industrialization of genetically modified corn of our country. China Biotech 36:24–29

Shivaji R, Camas A, Ankala A, Engelberth J, Tumlinson JH, Williams WP, Wilkinson JR, Luthe DS (2010) Plants on constant alert: elevated levels of jasmonic acid and jasmonate induced transcripts in caterpillar-resistant maize. J Chem Ecol 36:179–191

Shylesha AN, Jalali SK, Gupta A et al (2018) Studies on new invasive pest Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) and its natural enemies. J Biol Control 32:1–7

Singh J, Sajjan SS (1982) Losses in maize yield due to different grades (1 to 9 scale) caused by maize borer, Chilo partellus (Swinhoe). Ind J Entomol 44:41–48

Smith WE, Shivaji R, Williams WP, Luthe DS, Sandoya GV, Smith CL, Sparks DL, Brown AE (2012) A maize line resistant to herbivory constitutively releases (E)-β-caryophyllene. J Econ Entomol 105:120–128

Springer
Sokame BM, Subramanian S, Kilalo DC, Juma G, Calatayud PA (2020) Larval dispersal of the invasive fall armyworm, Spodoptera frugiperda, the ectoxic stemborer, Chilo partellus, and indigenous maize stemborers in Africa. Entomol Exp Appl 168:322–331. https://doi.org/10.1111/eea.12899

Storer NP, Babock JM, Schlenz M, Made T, Thompson GD, Bing JW, Huckaba RM (2010) Discovery and characterization of field resistance to Bt maize: Spodoptera frugiperda (Lepidoptera: Noctuidae) in Puerto Rico. J Econ Entomol 103:1031–1038

Storer NP, Kubiszak ME, King JE, Thompson GD, Santos AC (2012a) Status of resistance to Bt maize in Spodoptera frugiperda: lessons from Puerto Rico. J Invertebrate Pathol 110:294–300

Storer NP, Thompson GD, Head GP (2012b) Application of pyramided traits against Lepidoptera in insect resistance management for Bt crops. GM Crop & Food 3(3):154–162

Subiadi S, Trisyono YA, Martono E (2014) Aras kerusakan ekonomi (AKE) larva Ostrinia furnacalis (Lepidoptera: Crambidae) pada tiga fase pertumbuhan tanaman jagung. Jurnal Entomologi Indonesia 11(1):19–26

Suby SB, Soujanya PL, Yadava P et al (2020) Invasion of fall armyworm (Spodoptera frugiperda) in India: nature, distribution, management and potential impact. Curr Sci 119:44–51

Sun D, Quan Y, Wang Y, Wang Z, Kanglai HE (2021a) Resistance of transgenic Bt maize (Ruifeng 125, DBN9936 & DBN9978) to Asian corn borer. Plant Prot 3:206–211

Sun XX, Hu CX, Jia HR, Wu QL, Shen XJ, Zhao SY, Jiang YY, Wu KM (2021b) Case study on the first immigration of fall armyworm, Spodoptera frugiperda invading into China. J Integr Agric 20:664–672

Supartha IW, Susila IW, Sunari AAA, Febri Mahaputra IG, Yudha IKW, Wiradana P (2021) Damage characteristics and distribution patterns of invasive pest, Spodoptera frugiperda (J.E Smith) (Lepidoptera: Noctuidae) on maize crop in Bali, Indonesia. Biodiversitas J Biol Diversity. https://doi.org/10.13057/biodiv/d220645

Swastika DKS, Kasim F, Suhariyanto K, Sudana W, Hendayana R, Gerpacio RV, Pingali PL (2004) Maize in Indonesia: Production Systems, Constraints, and Research Priorities. Mexico, D.F.: CIMMYT

Tabashnik BE, Carrière Y (2017) Surge in insect resistance to transgenic crops and prospects for sustainability. Nat Biotechnol 35:926–925. https://doi.org/10.1038/nbt.3974

Tavares CS, Santos-Amaya OF, Olivea EE, Paula-Moraes SV, Perea EJG (2021) Facing Bt toxins growing up: developmental changes of susceptibility to Bt corn hybrids in fall armyworm populations and the implications for resistance management. Crop Prot. https://doi.org/10.1016/j.cropro.2021.105664

Tefera T, Mugo S, Beyene Y (2016a) Developing and deploying insect resistant maize varieties to reduce pre-and post-harvest food losses in Africa. Food Security 8:211–216

Tefera T, Mugo S, Mwimali M et al (2016b) Resistance of Bt-maize (MON 810) against the stem borers Busseola fusca (Fuller) and Chilo partellus (Swinhoe) and its yield performance in Kenya. Crop Prot 89:202–208

Thompson GD, Dalmacio SC, Criador AR, Alvarez ER, Hechanova RF (2010) Field performance of TC1507 transgenic maize hybrids against Asian corn borer in the Philippines. Philipp Agric Sci 93:375–383

Trisyono YA, Suputa AYF, Hartaman MM, Jumari, (2019) Occurrence of Heavy Infestation by the Fall Armyworm, Spodoptera frugiperda., a New Alien Invasive Pest, in Corn in Lampung Indonesia. Jurnal Perlindungan Tanaman Indonesia 23:156–160

Trisyono YA, Aryuwandari VEF, Andika IP, Hanjelina NG (2020) Assessment on the economic importance of corn borers in Indonesia. Report submitted to CropLife Asia

Turnbull C, Lillemo M, Hvoslef-Eide TAK (2021) Global regulation of genetically modified crops amid the gene edited crop boom—a review. Front Plant Sci. https://doi.org/10.3389/fpls.2021.630396

US EPA (1998a) R.E.D. FACTS: Bacillus thuringiensis. EPA-738-F-98-001. Washington, DC: United States Environmental Protection Agency

US EPA (1998b) Reregistration Eligibility Decision (RED): Bacillus thuringiensis. EPA738-R-98–004. Washington, DC: United States Environmental Protection Agency

USDA-GAIN (2020a) Agricultural Biotechnology Annual, Report number: RP2019–0036

USDA-GAIN (2020b) Agricultural Biotechnology Annual, Report number: VM2020b-0114

USDA-GAIN (2020c) Fall Armyworm Update, Report number: VM2020c-0061

USDA-GAIN (2021) Grain and Feed Update, Report number: RP2021–0031

Van den Berg J, Prasanna BM, Midega CAO, Ronald PC, Carrière Y, Tabashnik BE (2021) Managing fall armyworm in Africa: can Bt maize sustainably improve control? J Econ Entomol 114:1934–1949. https://doi.org/10.1093/jee/toab161

Viana PA, Guimaraes PEO (1997) Maize resistance to lesser corn stalk borer and fall armyworm in Brazil. In: Insect resistant maize: recent advances and utilization; Proceedings of an International Symposium held at CIMMYT, 27 November-3 December, 1994. Mexico, D.F.: CIMMYT, 112–116

Wang ZY, Lu X, He KL, Zhou DR (2000) Review of history, present situation and prospect of the Asian maize borer research in China. J Shenyang Agric Univ 31:402–412

Wang Y, Yang S, Yin Y, Liu Y, Li N, Liu Q, Yu Z, Liu X, Feng S, Hao D (2015) Rational mutation of Cry protein and the insect resistance assessment in the transgenic maize. J Maize Sci 23:27–34

Wang Y, Wang Z, He K, Guo J (2021) Transgenic maize and its potential commercialization in China. In: Gujar G, Trisyono YA, Chen M (eds) Genetically modified crops in Asia Pacific. CSIRO Publishing, Australia, pp 107–118

Waqul JM, Dourado PM, Carvalho RA, Oliveira WS, Berger GU, Head GP, Martinelli S (2013) Manejo de lepidópteros-praga na cultura do milho com o evento Bt pamidado Cry1A.105 e Cry2Ab2. Pesq Agropec Bras 48:1529–1537. https://doi.org/10.1590/ s0100-204X2013001200007

Westbrook JK, Nagoshi RN, Meagher RL, Fleischer SJ, Jaam S (2016) Modeling seasonal migration of fall armyworm moths. Int J Biometeorol 60:255–267. https://doi.org/10.1007/s00484-015-1022-x

Williams WP, Davis FM (1980) Registration of Mp703 germplasm line of maize. Crop Sci 20:418

Williams WP, Davis FM (1982) Registration of maize germplasm line of maize. Crop Sci 22:1269–1270

Williams WP, Davis FM (1984) Registration of Mp705, Mp706, and Mp707 germplasm lines of maize. Crop Sci 24:1217

Williams WP, Davis FM (2000) Registration of maize germplasm lines Mp713 and Mp714. Crop Sci 40:584

Williams WP, Davis FM (2002) Registration of maize germplasm line Mp716. Crop Sci 42:671–672

Williams WP, Davis FM, Windham GL (1990) Registration of Mp708 germplasm line of maize. Crop Sci 30:757

Williams WP, Davis FM (1997) Mechanisms and bases of resistance in maize to Southwestern Corn Borer and Fall Armyworm. In: Mihm JA (ed.) Insect resistant maize: recent advances and utilization; Proceedings of an International Symposium held at CIMMYT, 27 November-3 December, 1994. Mexico, D.F.: CIMMYT, pp. 25–36
Wiseman WR, Davis WWP, FM, (1982) Fall armyworm: resistance mechanisms in selected corns. J Econ Entomol 74:622–624. https://doi.org/10.1093/jee/74.5.622

Womack ED, Warburton ML, Williams WP (2018) Mapping of quantitative trait loci for resistance to fall armyworm and southwestern corn borer leaf-feeding damage in maize. Crop Sci 58:1–11

Womack ED, Williams WP, Smith JS, Warburton ML, Bhattaramakki D (2020) Mapping Quantitative Trait Loci for resistance to Fall Armyworm (Lepidoptera: Noctuidae) leaf-feeding damage in maize inbred Mp705. J Econ Entomol 113:956–963

Wu KM, Lu YH, Feng HQ, Jiang YY, Zhao JZ (2008) Suppression of cotton bollworm in multiple crops in China in areas with Bt toxin-containing cotton. Science 321:1676–1678. https://doi.org/10.1126/science.1160550

Wu QL, Jiang YY, Wu KM (2019) Analysis of migration routes of the fall armyworm Spodoptera frugiperda (J. E. Smith) from Myanmar to China. Plant Prot 45:1–6

Yang Z, Lang Z, Zhang J, Song F, He K, Huang D (2012) Studies on insect-resistant transgenic maize (Zea mays L.) harboring Bt cry1Ah and cry1He genes. J Agric Sci Technol 14:39–45

Yang X, Wyckhuys KAG, Jia X, Nie F, Wu K (2021) Fall armyworm invasion heightens pesticide expenditure among Chinese smallholder farmers. J Environ Manag 282: 111949

Yorobe J, Quicoy C (2006) Economic impact of Bt corn in the Philippines. Philipp Agric Sci 89:258–267

Yorobe J, Smale M (2012) Impacts of Bt maize on smallholder income in the Philippines. AgBio Forum 15(2):152–162

Zhang D, Wu K (2019) The bioassay of Chinese domestic Bt-Cry1Ab and Bt-(Cry1Ab+Vip3Aa) maize against the fall armyworm, Spodoptera frugiperda. Plant Prot 45:54–60

Zhang W, Lu Y, van der Werf W, Huang J, Wu F, Zhou K, Deng X, Jiang Y, Wu K, Rosegrant MW (2018) Multidecadal, county-level analysis of the effects of land use, Bt cotton, and weather on cotton pests in China. Proc Natl Acad Sci USA 115:E7700–E7709. https://doi.org/10.1073/pnas.1721436115

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