CHAPTER 04

Host Plant Resistance in Maize to Fall Armyworm

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Note: Throughout the chapter, we discuss host plant resistance to FAW using maize as an example, since considerable work has been done on maize. However, the principles of host plant resistance remain the same in other major crops (*e.g.*, sorghum, millets) affected by FAW.

1. Introduction

Host plant resistance, in the context of resistance to insect pests, was originally 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). It is indeed a central component of the integrated pest management (IPM) strategy to control the fall armyworm (FAW) (Prasanna *et al.* 2018), and comprises:

- **Native genetic resistance:** Identifying/developing germplasm with resistance to an insect pest; and
- **Transgenic resistance:** Using a gene (or genes) from an external source(s) (other than the recipient plant species) to make the host plant resistant to an insect pest.

FAW-tolerant/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. Improved maize varieties with genetic resistance to FAW will effectively complement other IPM interventions (Riggin *et al.* 1992, 1994). Seed-based technologies such as host plant resistance are not only easily disseminated and readily adopted by farmers due to their visible benefits, but will also require far fewer applications of pesticides than FAW-susceptible varieties, thus saving smallholder farmers resources (financial and labor), while mitigating negative environmental impact.

When designing a breeding strategy to introduce FAW resistance traits into elite maize germplasm, breeders should 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 demonstrated particularly in transgenic crop varieties (Huang *et al*. 2014). Breeding for insect-pest 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).

Prasanna *et al.* (2018) presented a comprehensive review of host plant resistance to FAW, especially in maize (FAW IPM Guide For Africa). This included information on potential sources of resistance to FAW in maize germplasm identified or developed earlier by maize breeding programs in the Americas, and detailed protocols for (a) mass rearing of FAW and (b) screening germplasm under artificial and natural FAW infestation. These will not be repeated in this chapter. Here we will (a) provide an update on progress with regard to breeding for native genetic resistance to FAW in maize; (b) highlight the status with regard to deployment of genetically modified (GM) maize (specifically *Bt* maize) in Asia for the control of FAW, and the need for implementing a well-coordinated insect resistance management (IRM) strategy in Asia; 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.

2. Breeding for Native Genetic Resistance to FAW

2.1. FAW Resistance in CIMMYT's Tropical Maize Germplasm

The International Maize and Wheat Improvement Center (CIMMYT) has a wealth of diverse genetic resources in maize, including improved germplasm for an array of traits (*e.g.,* high yield, drought tolerance, heat tolerance, nitrogen use efficiency, disease resistance, etc.) relevant for smallholders in Africa, Asia, and Latin America. In addition, the maize germplasm bank at CIMMYT-Mexico (https://www.genebanks.org/genebanks/cimmyt/) holds over 28,000 accessions that provide a rich platform for identifying genetic resources for client-preferred traits. Throughout the 1970s to 1990s, research conducted at CIMMYT in Mexico (Mihm 1997) revealed that there is genetic variation and potential to support breeding for native genetic resistance to FAW insect-pests of maize, including stem borers, FAW, and post-harvest pests (weevils and large grain borer).

The work done at CIMMYT-Mexico led to development of two major 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. CIMMYT's insect-resistant maize populations were derived primarily from the Caribbean maize germplasm and Tuxpeño landrace accessions from Mexico (Mihm 1997). Most native resistance in maize to FAW is polygenic (based on multiple genes) and quantitative in nature, conferring "partial resistance". The quantitative or polygenic nature of native genetic resistance also offers the opportunity to minimize selection pressure on FAW and prevents emergence of new resistant strains.

CIMMYT and partners in Africa have utilized the insect-resistant maize populations and inbred lines from Mexico and developed elite maize germplasm with resistance to other lepidopteran stem borer pests, including the European corn borer (*Ostrinia nubilalis* Hbn.), the African stem borer (*Busseola fusca* Fuller), and the spotted stem borer (*Chilo partellus* Swinhoe) (Beyene *et al.* 2012; 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.

FAW mass rearing: The CIMMYT team, together with the Kenya Agricultural and Livestock Research Organization (KALRO), adopted and further optimized the USDA-ARS-based FAW mass-rearing protocol at KALRO-Katumani, for a steady supply of neonate larvae for artificial infestation of maize germplasm in screenhouses. This is important for identifying reliable sources of resistance to the pest. A colony of FAW was established and maintained at KALRO Insectary at Katumani, Kenya, on artificial diet as described by Prasanna *et al.* (2018). The larvae and pupae were originally collected from Kiboko (02°21'S, 037°70'E, 945 m.a.s.l.) and Machakos (01°57'S, 027°25'E, 1568 m.a.s.l.) in the eastern part of Kenya. The FAW rearing facility at the Katumani Center has the capacity to supply 500,000-800,000 neonates per year, which are used for germplasm screening experiments under artificial infestation at Kiboko, Kenya.

Artificial infestation of maize plants in screenhouses: A screenhouse complex (with 13 screenhouses, each 1000 m^2) was established by CIMMYT at KALRO Research Center at Kiboko, Kenya, in 2017-2018, for intensive screening of maize germplasm against FAW under artificial infestation (Figure 1), and for identifying and developing promising FAW-tolerant inbred lines and hybrids. Each screenhouse can accommodate 245 maize rows of 3 m length. Similar screenhouse facilities are being established by CIMMYT at Hyderabad, India.

Figure 1. Screenhouse complex established by CIMMYT at KALRO Research Center at Kiboko, Kenya, for screening maize germplasm under artificial FAW infestation.

The neonates produced in the laboratory are used for artificial infestation of maize plants in the screenhouse. To infest a plant, a camel-hair brush is used to pick the neonates from a container and put them in different nodes of maize plants to avoid cannibalism (Figure 2) (Prasanna *et al.* 2018). Infestation is carried out either early in the morning (7-9 am) or in the evening (4-6 pm) to allow the neonates to acclimatize to the environment since sudden changes of conditions may desiccate the neonates, especially if infestation is done during dry, hot conditions. Based on optimization experiments, the CIMMYT team at Kiboko, Kenya, typically uses five (5) neonates for infesting inbred lines at the V5 stage (three weeks after planting), and seven (7) neonates for infesting hybrids at the V3 stage (two weeks after planting).

Figure 2. Infestation of a maize plant with FAW neonates using a camel-hair brush.

Data recording: When identifying germplasm with native genetic resistance to FAW, it is important to consider not only the foliar damage score but also the ear damage score, as FAW larvae can cause significant ear/kernel damage by burrowing into the developing ears. CIMMYT uses a 1-9 scale (Prasanna *et al.* 2018), which is a modification of the Davis *et al.* (1992) 0-9 scale, for assessing maize germplasm against FAW under artificial infestation for the foliar damage. At physiological maturity (harvest), the CIMMYT team also assesses the ear damage of the maize germplasm due to FAW on a 1-9 scale, as described by Prasanna *et al.* (2018). In addition, other parameters including percentage ear rot and number of exit holes per ear, are also recorded. The average score of foliar and ear damage rating, besides grain yield and other parameters are considered for final rating of the germplasm.

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, open-pollinated varieties (OPVs), and hybrids developed by CIMMYT in Africa through the Insect Resistant Maize for Africa (IRMA) project were some of those that were screened. Between 2017 and 2020, over 6,000 maize genotypes, including 3,000 inbred lines and 3,000 hybrids/OPVs from diverse sources were screened under artificial FAW infestation in the screenhouse complex at Kiboko. The work has led to identification of some promising FAW-tolerant/resistant* inbred lines, especially from the MBR and MIRT germplasm backgrounds, with low foliar and ear damage scores.

The **FAW-tolerant/resistant CIMMYT maize inbred lines** include CML71, CML124, CML125, CML338, CML333, CML334, CML338, CML370, CML372, and CML574. Since 2018, FAW-tolerant/resistant CIMMYT Maize Lines (CMLs) have been disseminated to 92 institutions in 34 countries globally, including an array of National Agricultural Research and Extension Systems (NARES), advanced research institutes (ARIs) and commercial seed companies (Table 1). The FAW-tolerant/

Table 1. Global dissemination of CIMMYT-developed FAW-tolerant/resistant CMLs since 2018 (until August 2021).

Type of Institution	Africa	Asia	Latin America	North America*	Europe	Australia	Total
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)**

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

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* In the context of insect pests, "resistance" is the capacity to minimize the damage through mechanisms such as antibiosis and/or antixenosis, while "tolerance" is the ability to restrict the economic damage even in the presence of the pest (outside/inside the host). Resistance to an insect pest, thus, may involve a combination of antibiosis, antixenosis, and/or tolerance (Painter 1958). Earlier studies evaluating FAW-resistant maize germplasm showed that the mechanisms contributing to native genetic resistance in these materials could be quite varied: for example, some lines showed higher levels of metabolites such as silk maysin and terpenoids, while some lines have morphological traits (*e.g.*, very tight husk cover) that minimize the ear damage by FAW. As of now, we do not have firm evidence whether the promising inbreds/hybrids developed recently at CIMMYT can be considered as "resistant/tolerant" to FAW, as we still do not know the underlying mechanisms; this requires further studies. Therefore, in this chapter, we have used the term "FAW-tolerant/resistant hybrids".

resistant CMLs can be potentially utilized as trait donors in breeding programs of partner institutions that are aiming to develop FAW-tolerant maize cultivars suitable for local environments. These CMLs can be sourced through a Standard Material Transfer Agreement (SMTA) from CIMMYT Genebank at Mexico. Several national maize breeding programs in Africa and Asia have initiated breeding programs for development of FAW-tolerant cultivars (*e.g.*, Matova *et al.* 2020; Kasoma *et al.* 2020), especially utilizing sources of native genetic resistance developed and disseminated by CIMMYT.

Besides the promising CMLs mentioned above, the CIMMYT team in Africa has also identified over the last two years several promising inbred lines (materials under development) in both yellow- and white-kernel backgrounds, with tolerance/resistance to FAW for both foliar and ear damage as well as combining ability for grain yield under FAW artificial infestation. For example, based on the data from germplasm screening during 2017-2018, several crosses were made among the promising FAW-tolerant/resistant lines, from which progenies were selected and intercrossed to increase the frequency of favorable resistance alleles. Doubled haploid (DH) lines were developed from F1, F2, and backcross (BC) source populations that showed promising levels of resistance to FAW. In 2019-20, a total of 2733 DH lines were produced from different source populations. In 2020, a set of 1400 DH lines were screened against FAW under artificial infestation at Kiboko (Figure 3), leading to identification of new lines with resistance to FAW. Such lines are being used to make new single-cross and three-way hybrids for further evaluation in 2021 and beyond.

Figure 3. Variability for FAW foliar feeding under artificial infestation in a screenhouse at Kiboko, Kenya (2019-2020). The figure shows a FAW-resistant doubled haploid (DH) line (left), developed from a MIRT population, side-by-side with a FAW-susceptible DH line (right).

Development of FAW-tolerant maize hybrids with high yield potential and other agronomic and adaptive traits: Based on results from screening of a large collection of inbred lines from different genetic backgrounds during 2017-2018, the CIMMYT 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/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 at Kiboko under artificial FAW infestation. 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 (≤5.0 and <3.0 Davis scores, respectively), in addition to significantly higher grain yield than the FAW-susceptible commercial checks. On average, the FAW-tolerant pre-commercial maize hybrids produced 47% to 77% higher grain yield than the FAW-susceptible commercial checks.

2.2. FAW-tolerant Elite Maize Hybrids for Africa

Based on the results of on-station screenhouse trials against FAW (under artificial infestation) conducted at 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. The experimental conditions and the main findings are summarized below:

- **"No-choice" trial under FAW artificial infestation in screenhouses in Kiboko, Kenya:** Each entry was planted in 40 rows in a separate screenhouse compartment ("no-choice"), and each plant infested with seven FAW neonates 14 days after planting. Foliar damage was assessed 7, 14, and 21 days after infestation. Ear damage due to FAW in each plot was also recorded, in addition to grain yield and other agronomic parameters. Significant differences were observed between three FAW-tolerant hybrids (FAWTH2001, FAWTH2002, FAWTH2003) and the commercial benchmark hybrid checks at the vegetative and grain-filling stages and at harvest (Figure 4). In the FAW artificial infestation trial, the three FAWTH hybrids yielded 7.05 to 8.59 t/ha while the commercial checks yielded 0.94 to 1.03 t/ha.

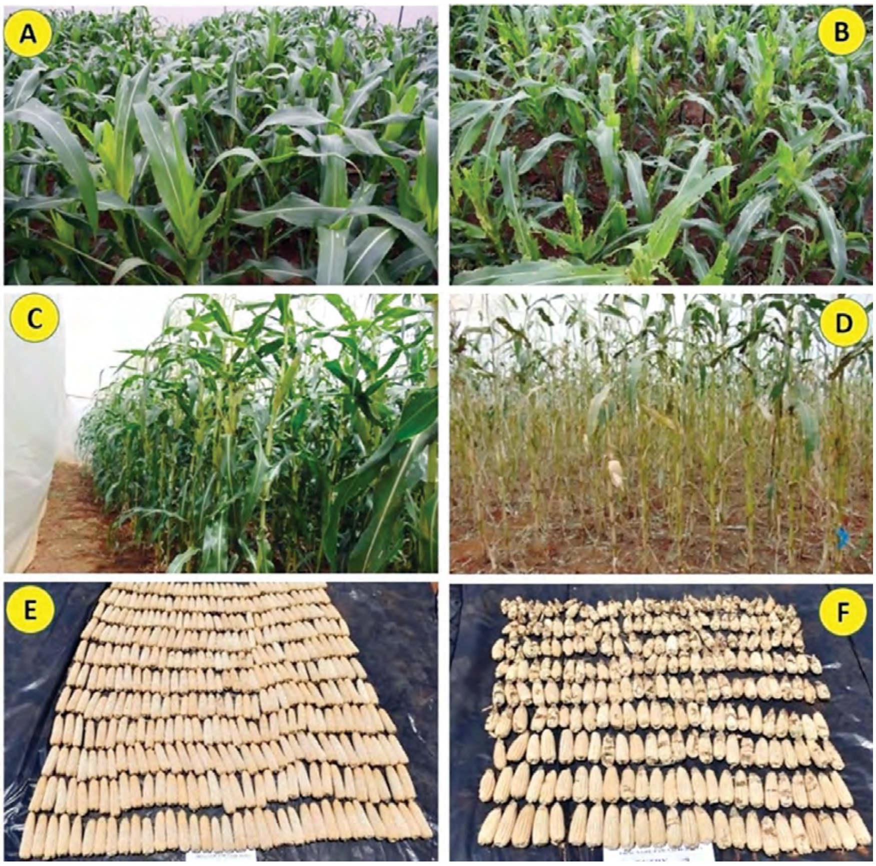

Figure 4. Responses of CIMMYT-derived FAW-tolerant hybrids (left) versus susceptible commercial checks (right) at the vegetative stage (**A & B**) and at the reproductive stage (**C & D**), after artificial infestation of FAW under "no-choice" conditions in screenhouses at Kiboko, Kenya. Note the difference in the yield of a FAW-tolerant hybrid (**E**) versus one of the susceptible commercial hybrid checks (**F**), as well as the extent of damage caused by FAW to the ears of the susceptible check (visible as blackish spots with no grains in the ears).

- **On-station trials in East Africa**: The trials, including the eight test entries and four commercial checks, were conducted at six locations in Kenya during the maize cropping season in 2020. The purpose of these regional trials was to collect data on agronomic performance across a range of environments. Entries were evaluated for their performance under managed drought stress, managed low-nitrogen stress, and artificial inoculation for Turcicum leaf blight (TLB) and Gray leaf spot (GLS) diseases. The three-way cross CIMMYT test 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. In addition to the above, the eight test entries with FAW tolerance were also evaluated in regional on-station trials (comprising a total of 58 entries) at 28 locations in Kenya and Tanzania. No significant differences were observed between the three selected FAWTH hybrids and the commercial checks for grain yield and other important traits evaluated under optimum conditions, managed drought stress, low-nitrogen stress, and TLB and GLS disease pressure. The three selected FAWTH hybrids recorded excellent synchrony in terms of flowering between the female and male parents, and very good female parent seed yield.
- **On-farm trials in Kenya**: The eight test hybrids and four 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. There were significant differences in terms of foliar damage ratings between the FAWTH hybrids and the commercial checks. For ear damage, the differences were not statistically significant. The grain yields did not vary significantly under natural infestation in the on-farm trials because of the very low incidence of FAW at most sites.

Based on the stage-gate advancement process, including rigorous review of the complete set of on-station and on-farm trial data (described below), the three promising FAW-tolerant elite maize hybrids (FAWTH2001, FAWTH2002, FAWTH2003) 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.

Note: Native genetic resistance to FAW in maize is partial, though quite significant in terms of yield protection under severe FAW infestation, as compared to the susceptible commercial checks. Sustainable control of FAW is best achieved when farmers use host plant resistance as part of an IPM program, including good agricultural practices, pest scouting (**Chapter 2**), and judicious use of safer-use pesticides (**Chapter 3**) only when needed to encourage conservation biological control.

2.3. FAW Resistance in IITA's Tropical Maize Germplasm

Considering the importance of FAW as an emerging major pest of maize in West Africa, the International Institute of Tropical Agriculture (IITA) began screening genotypes under naturally occurring FAW infestation in 2016, and later under artificial infestation with FAW larvae, to identify tolerant synthetics, hybrids, and inbred lines from existing adapted germplasm. Among the 365 yellow and 212 white lines screened at IITA, 13 yellow and 20 white lines exhibited minimal damage symptoms and had well-filled ears under severe natural infestation. As cyclical/recurrent breeding methods have been used to accumulate desirable genes for resistance to FAW (Welcker 1993; Welcker *et al.* 1997), equal quantities of seeds of the self-pollinated ears from each of the white and yellow lines were used to form balanced bulks, which were planted to form a white synthetic (AWSYN-W) and a yellow (AWSYN-Y) synthetic. After one generation of recombination, the two synthetics were improved using an S1 selection scheme under artificial infestation with FAW larvae.

A modest FAW rearing facility has also been established at IITA for artificial infestation and has been further upgraded with support from the Consultative Group for International Agricultural Research (CGIAR) Research Program MAIZE to enable screening large numbers of inbred lines under artificial infestation. The IITA maize team has screened more than 20 stress-tolerant and provitamin A–enriched synthetics, about 60 drought-tolerant and *Striga*-resistant hybrids being tested in regional trials, and more than 200 advanced stress-tolerant maize inbred lines, all under FAW natural infestation in the screenhouse. Some promising synthetics and hybrids were tested in multiple locations under natural FAW infestation to confirm their performance. These materials are suitable candidates for extensive field testing under both natural and artificial infestation to identify the best products for further testing and sharing with partners. To boost the levels of resistance to FAW in adapted germplasm, several FAW-resistant inbred lines from the USA have also been introduced as donors and backcrosses have been made (Abebe Menkir, IITA, personal communication).

2.4. 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 within temperate maize germplasm. During the late 1980s and throughout the 1990s, USDA-ARS and CIMMYT (Mexico) collaborated extensively on developing maize germplasm with resistance to FAW damage 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) (Williams and Davis 1984, 2002; Prasanna *et al*. 2018). Several maize inbred lines (Mp496, Mp701, Mp704, Mp706, and Mp708) developed at USDA-Mississippi were based on CIMMYT maize germplasm, especially Caribbean-based, as source populations. 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 (Prasanna *et al*. 2018).

2.5. Genomic Analysis of Resistance to FAW in Maize

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 $F_{2:3}$ families and detected quantitative trait loci (QTLs) on chromosomes 1, 2, 6, 7, and 9. Womack *et al.* (2018) evaluated 231 $F_{2:3}$ 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 $F_{2:3}$ 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 insect pressure for FAW 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).

The CIMMYT team in Africa recently undertook GWAS and joint linkage association mapping on a set of 285 lines and about 485 DH lines developed from seven FAW-tolerant lines. These lines were evaluated for their responses to FAW artificial infestation at Kiboko, Kenya, in 2017 and 2018. Foliar damage was scored 7, 14, and 21 days after artificial infestation on a modified Davis scale (1-9) (Prasanna *et al.* 2018). Ear damage was also rated on a 1-9 scale, based on the protocol described by Prasanna *et al.* (2018). All the screened lines were genotyped with the DArTseq genotyping-by-sequencing platform (Diversity Arrays Technology/DArT). A set of 20,000 SNPs were used for association mapping on 285 lines, and around 1000 SNPs were used on DH populations, for linkage and joint linkage association mapping. The study revealed a very weak and non-significant correlation between foliar and ear damage scores. GWAS revealed 22 SNPs significantly associated with foliar damage, distributed on all 10 chromosomes. Only one SNP, *S4_186497220* on chromosome 4, was significantly associated with ear damage. Seven SNPs distributed on chromosomes 4, 5, 7, 8, and 9 were significantly associated with grain yield under FAW infestation.

Even though there were no common SNPs identified across the GWAS panel used by CIMMYT and that by Badji *et al.* (2020), several markers were consistently present in the same bins on chromosomes 8, 9, and 10. QTLs on chromosome 4 (17.28 Mb and 183.82 Mb) and chromosome 9 (at 8.05 Mb) are consistent with bi-parental population-based QTL mapping in the CIMMYT study, as well as earlier studies (Womack *et al.* 2018, 2020). These regions appear important for developing markers for resistance to foliar damage by FAW.

In CIMMYT's GWAS panel, ridge regression–based genomic prediction correlations were 0.61, 0.53, 0.31, and 0.30 for early foliar damage, late foliar damage, ear damage, and grain yield, respectively, under FAW artificial infestation. In contrast, prediction correlations as high as 0.69 to 0.71 were reported for foliar damage (under FAW natural infestation) in a set of 316 lines by Badji *et al.* (2021). Overall, considering both foliar and ear damage, the role of specific QTLs on chromosomes 4 and 9 needs further investigation, while genomic prediction could possibly play an important role in improving native genetic resistance to FAW.

3. Transgenic Resistance to FAW

Deploying transgenic or genetically engineered/modified (GE/GM) maize hybrids that express lepidopteran resistance genes is an important component of an IPM strategy to effectively control FAW. FAW-resistant transgenic maize hybrids typically have insecticidal crystal protein genes (*cry* genes) and/or *vip* genes encoding vegetative insecticidal proteins (Vip), isolated from a soil bacterium, *Bacillus thuringiensis* (*Bt*). Numerous transgenic maize hybrids, with various combinations of *cry* (*cry1Ab, cry1F, cry1A.105 + cry2Ab2*) and *vip* (*vip3A*) genes, are commercially available in Brazil and North America, where over 80% of the total maize production area is cultivated with *Bt* maize (Horikoshi *et al.* 2016; ISAAA 2019).

3.1. *Bt* Maize Status in Africa

In Africa, *Bt* maize is currently being commercialized only in South Africa, where regulatory authorities have overseen multiple approvals, with more than 15 years of deployment of such products. Kenya is presently undertaking national performance trials of MON810 (*cry1Ab*)-based *Bt* maize hybrids. In South Africa, *Bt* maize hybrids expressing the *cry1Ab* gene (MON 810) and the *cry1A.105+cry2Ab2* genes (MON 89034) have been planted on over 1.62 million hectares, comprising 71% of the total maize area (ISAAA 2017). After the documentation of FAW invasion into Africa during early 2016, it has been included as a target pest of MON 89034 (Botha *et al.* 2019). MON 89034 is particularly recommended for FAW control due to its high efficacy against the pest, as well as the resistance management value of "pyramided" insect-resistant *Bt* genes expressing the Cry1A.105 and Cry2Ab2 proteins. The MON 810 maize event, which has been cultivated in South Africa since 1997 and is intended to primarily manage the larval feeding damage caused by stem borers (*e.g., Chilo partellus*, *Busseola fusca*), confers partial resistance to FAW.

Beyond South Africa, under the TELA® Maize project the National Agricultural Research Organizations of Kenya, Ethiopia, Nigeria, Tanzania, Uganda, and Mozambique are testing the performance of *Bt* and stacked *Bt* + Drought Tolerance (DT) transgenes introgressed into Africa-adapted maize genetic backgrounds. The TELA Maize Project is a public-private partnership led by the African Agricultural Technology Foundation (AATF) working towards the release of transgenic drought-tolerant and insect-protected (TELA®) maize hybrids, in partnership with Bayer, CIMMYT, and National Agricultural Research System (NARS) institutions in Ethiopia, Kenya, Mozambique, Nigeria, South Africa, Tanzania, and Uganda.

3.2. *Bt* Maize Status in Asia

In Asia, *Bt* maize is currently grown in the Philippines and Vietnam, and *Bt* maize events are approved in Pakistan. The primary target pests are the Asian corn borer (*Ostrinia furnacalis* Guenée) in the Philippines, Vietnam, Indonesia, and China, and the maize stem borer (*Chilo partellus* Swinhoe) in Pakistan. Other secondary target pests include the common cutworm (*Spodoptera litura* Fabricius), the corn earworm (*Helicoverpa armigera* Hübner), and FAW. The experiences with *Bt* maize in different Asian countries are discussed in more detail below.

Philippines: The cultivation of *Bt* maize in the Philippines began with the approval of the insect-resistant event MON 810 in 2002. This was followed by approvals of Bt11 in 2005, MON 89034 in 2010, TC1507 in 2013, and MIR162 in 2018. Insect-resistant event MIR162 contains the *vip3Aa20* gene, which encodes the insecticidal protein Vip3Aa20; Bt11 expresses the Cry1Ab protein; and TC1507 expresses the Cry1F protein. In 2019, commercial products with these insect resistance events were estimated to occupy over 45% (0.66 million hectares of the total 1.415 million hectares) of the yellow maize hectarage (USDA-GAIN 2020a).

FAW invaded the Philippines in mid- to late-2019 with nearly 8000 hectares affected, mostly conventional maize, in the regions of Cagayan Valley, Soccsksargen, Northern Mindanao, and Zamboanga Peninsula, as of June 2020 (Department of Agriculture (DoA), Philippines; https://www.da.gov.ph/da-allots-p150m-to-help-farmers-control-fall-armyworm/). Currently, the list of products approved for the control of FAW in maize from the Fertilizer and Pesticide Authority (FPA) of the Department of Agriculture (DoA) in the Philippines includes MON 89034 and TC1507 × MON 810. The FAW-resistant hybrids include DK8719S, DK8899S, DK9118S, DK9132S, DK9919S, DK6919S, DK6999S, P3530YHR, P3774YHR, P4097YHR, and P4124YHR.

Vietnam: *Bt* maize has been commercialized in Vietnam since 2015. In 2019, *Bt* maize occupied 92,000 hectares, which was about 10.2% of the total crop) (Crop Protection Department of the Ministry of Agriculture and Rural Development: CPD MARD, Brookes and Dinh 2021). The approved *Bt* maize hybrids include stacked events, *viz.*, MON 89034 × NK603 and Bt11 × GA21. *Bt* maize hybrids carrying MON 89034 × NK603 include DK9955S, DK6919S, DK8868S, DK6818S, and CP501S; those carrying Bt11 × GA21 include NK66 BT/GT, NK67 BT/GT, NK4300 BT/GT, and NK7328 BT/GT (Brookes and Dinh 2021).

After the invasion of FAW in Vietnam in 2019, the pest was reported to have affected 35,000 hectares. However, in 2020, there was a reduction in heavily affected areas as well as an increase in planting of insect-resistant *Bt* maize hybrids (USDA-GAIN 2020b; Figure 5). One of the *Bt* maize hybrids, DK6919S, planted by farmers of Nghi Xuân, Hà Tĩnh province, was resistant to FAW, and reportedly led to an increased yield of 5.5-6.0 tons/hectare as compared to conventional varieties/hybrids (https://www.sggp.org.vn/giong-ngo-dk-6919-s-cho-nang-suat-cao-tren-vung-dat-nghi-xuan-660427.html [in Vietnamese]).

Pakistan: Currently, conventional maize is grown on 1.4 million hectares in Pakistan, with an increase in area from 1.0 to 1.4 million hectares in the last two decades. The production also has increased from 1.7 to 7.2 million metric tons due to the introduction of elite genetics and improved agronomics (http://www.fao.org/faostat/en/#home). The evaluation of GM maize events started in 2009 in Pakistan, and the approval of stacked GM maize expressing insect resistance and herbicide tolerance traits for

Figure 5. (A) FAW-damaged conventional (non-*Bt*) maize hybrid in Vietnam with extensive foliar damage; (B) *Bt* maize (MON 89034) hybrid expressing Cry1A.105 and Cry2Ab2 proteins with no FAW damage. *Note: Bt* maize (MON 89034) planted in the field is a blend containing 5% non-*Bt* seed. (Source: Bayer Crop Science, Vietnam).

commercial cultivation was given by the National Biosafety Committee (NBC) of the Ministry of Climate Change (MOCC) in 2016. The products approved include MON 89034 × NK603, MON 810 × NK603, TC1507 × NK603, and TC1507 × MON 810 × NK603. As part of the regulatory requirement for varietal registration by the Federal Seed Certification and Registration Department, Ministry of National Food Security and Research (MNFS&R) in 2017-18, field performance trials of GM maize hybrids were conducted. Commercialization of biotech maize in Pakistan will happen once MNFS&R registers the tested GM hybrids. Other products being tested include Bt11 × GA21 and Bt11 × MIR162 × GA21.

Other countries in Asia: *Bt* maize is undergoing testing and approval processes in Indonesia and China. Events with insect resistance genes such as *cry1Ab*, *cry1F*, *cry1A.105*, *cry2Ab2*, and *cry1b-cry2Aj fusion* are in various stages of the approval process. In January 2021, China's Ministry of Agriculture and Rural Affairs granted a biosafety certificate for *Bt* maize event DBN9501 (*vip3Aa-19*), developed by Beijing Dabeinong Technology Group, conferring resistance to FAW. A biosafety certificate was granted in January 2020 to "double-stacked 12-5" (*cry1e* + *cry1Ab-cry2Aj*) maize, which was co-developed by Hangzhou Ruifeng Biotech Co. Ltd. and Zhejiang University. In a recent study, Li *et al.* (2019) demonstrated that the FAW population invading China is highly susceptible to the commonly used Cry1, Cry2, and Vip3 proteins, with the highest susceptibility to Vip3A, Cry1Ab, and Cry1F. In another study, Zhang and Wu (2019) showed that pyramided events DBN3608 and DBN3601 (Cry1Ab + Vip3A) have high resistance to FAW. Recent publications from China (Li *et al.* 2020, 2021) highlighted the need to deploy pyramided events in China as an effective strategy for delaying resistance evolution in target pests, including FAW to *Bt* maize.

3.3. Field-evolved *Bt* Resistance in FAW

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 were central to the evolution of FAW resistance in Puerto Rico, including the island setting, which limited insect migration; the tropical climate conducive to year-round cultivation of maize; and drought conditions in 2006/2007, which reduced the availability of alternative hosts for FAW (Storer *et al.* 2010). Subsequently, field resistance to Cry1F maize was detected in the southeastern USA (Niu *et al.* 2013; Huang *et al.* 2014) and in the Brazilian state of Bahia, three years after being deployed in Brazil (Farias *et al.* 2014a). A significant decrease in susceptibility to Cry1F was detected in FAW across Brazil between 2010 and 2013, especially in areas with intensive maize production and high adoption of *Bt* technologies (Farias *et al.* 2014b). Low compliance with non-*Bt* structured refuge recommendations was one of the root causes for resistance to Cry1F in Brazil (Farias *et al.* 2014b).

Bernardi *et al.* (2015) 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. MON 89034 maize (expressing the Cry2Ab2 and Cry1A.105 proteins) in combination with appropriate management practices continues to provide effective control of FAW in Brazil (Bernardi *et al.* 2015). Omoto *et al.* (2016) documented the evolution of field-relevant Cry1Ab *Bt* resistance in FAW in Brazil, potentially due to either direct 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 expression, components of *Bt* pyramids with cross-resistance to other *Bt* proteins in the landscape) combined with low compliance with the structured refuge recommendation seems to be a common theme across the resistance cases with FAW in South America (Farias *et al.* 2014a; Chandrasena *et al.* 2017). A consequence of these is a reduction in the number of effective modes of action to manage FAW. However, the deployment of MIR162 (Vip3Aa20) maize represents an effective new mode of action added to the maize cropping system to counter FAW.

3.4. Insect Resistance Management (IRM) for *Bt* Maize

The primary threat to the sustainable use of *Bt* maize is the selection for resistance in the target pests. It is important to note that, to date, there is no evidence that *Bt* resistance alleles were transferred from the Americas to Africa and Asia with the current invasive FAW population (see also **Chapter 1**). This evidence includes the fact that MON810 performed as expected across Africa. However, good stewardship practices encourage deploying the best IRM strategies regardless. Therefore, proactive

IRM programs are needed to delay resistance in the FAW populations. A sound IRM plan varies with the crop and pest combination, but generally considers:

1) Lowering the frequency of resistance alleles/genes in the insect population, which can be accomplished via an effective dose or high-dose expression of *Bt* proteins in *Bt* maize.
2) Providing refuge plants for the target insect pest to reduce selection pressure.
3) Ensuring “redundant killing” with products expressing two or more proteins that provide multiple modes of action against the targeted insect pests.
4) Rigorous scouting and surveillance for potential development of insect resistance above a baseline level determined prior to introduction of the GM crop.

For *Bt* maize, the critical components of an IRM strategy are the refuge strategy and refuge compliance, which drive the durability of the product. The refuge ensures that a sufficient population of susceptible insects is available to mate with the few resistant insects that may evolve in the *Bt* maize-planted areas. This significantly dilutes the frequency of resistance alleles in the insect population, thereby delaying the evolution of insect resistance to the *Bt* traits. Refuge plantings are recommended for use with all *Bt* maize products.

In addition, the latest generations of *Bt* maize express at least two *Bt* proteins for FAW control with unique modes of action. These products, known as *Bt* pyramids, are characterized by more robust insect protection and improved IRM value (Horikoshi *et al.* 2016; Roush 1998; Storer *et al.* 2012b). Studies undertaken in the USA and Brazil suggest that pyramiding multiple transgenes (in the same plant) is more effective in terms of FAW control than single-gene-based resistance (Huang *et al.* 2014; Horikoshi *et al.* 2016). This also calls for introgression of different transgenic resistance traits (*e.g.,* different *cry* genes, or *cry* + *vip3A*) into a maize genetic background, preferably one with native genetic resistance to the insect pest. The biggest advantage of this type of pyramid is that if the pest overcomes the transgenic resistance trait(s), the native resistance of the conventional genetic background (even if partial) can potentially mitigate the infestation until maize hybrids with more effective resistance are developed and deployed.

The new generation of *Bt* maize technologies with multiple modes of action, together with the implementation of IRM strategies that are more dependent upon manufacturing and less dependent upon grower behavior, can mitigate the risk of resistance. Seed blends (with *Bt* and non-*Bt* seeds mixed in the seed bag), sometimes referred to as refuge-in-a-bag (RIB), offer one such solution to enhance IRM in *Bt* crops. Seed blends are a widely adopted refuge deployment strategy for dual-gene *Bt* maize products registered for use against FAW, such as MON 89034 and TC1507 × MON 810 in the Philippines and Vietnam. In contrast, the current requirement for single-gene products in these countries is a 10% structured refuge. RIB may not be without risk, as some entomologists are concerned that the RIB approach may lead to resistance development in some above-ground pests, such as FAW. The Insecticide Resistance Action Committee (IRAC) published detailed guidelines on IPM and IRM for FAW control based on South African maize conditions (https://irac-online.org/documents/ipm-irm-for-fall-armyworm-in-s-african-maize/?ext=pdf).

Although products with two or more distinct modes of action, effective dose of *Bt* protein expression, refuge compliance, and scouting/surveillance are key components of an IRM strategy (Head and Greenplate 2012; Storer *et al.* 2012b), there are other components that influence the overall success of IRM. These include:

a. Resistance monitoring programs, which can be laboratory-based (pure protein or plant tissue-based) or field-based, that help us understand resistance development.
b. Farmer surveillance reporting systems that allow technology providers to receive feedback on performance-related issues.
c. Education and training programs on the importance of IRM and other measures for farmers and relevant stakeholders.
d. Remedial measures to address any unexpected damage caused by target pest(s).
e. Pest management plans for secondary pest management.

4. Host Plant Resistance for FAW Management in Africa and Asia: Critical Gaps

- An array of FAW-tolerant/resistant germplasm in diverse genetic backgrounds needs to be developed and deployed for 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. This needs to be urgently addressed.
- Another important gap that needs urgent attention is the stacking of transgenic insect-resistant traits with native genetic resistance. This could generate significant synergistic value, ensuring sustainable yield protection from pests such as FAW.
- Deploying improved maize varieties with genetic resistance to FAW (native or transgenic) has great potential to reduce the use of pesticides by farmers. Studies should be done to empirically quantify the reduction of pesticide use together with the increase in resilience and productivity that comes with deployment of host plant resistance.

5. Priorities/Next Steps

1. In terms of native genetic resistance to FAW, the proposed priorities are:
    a) 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.
    b) 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.
    c) 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/resistant maize varieties.
    d) Strengthening the capacity of NARS institutions in Africa and Asia in breeding for resistance to FAW along with other important adaptive and agronomic traits relevant for the smallholders.
2. Regarding transgenic resistance to FAW, the priorities are:
    a) Accelerated testing and deployment of *Bt* maize with proven efficacy, biosafety, and environmental safety with appropriate support from policy makers and regulatory authorities.
    b) Pyramiding transgenes with different modes of action (*e.g.*, *cry* + *vip* genes), instead of single-gene deployment, as a part of IRM strategy.
    c) Implementing IRM and proper stewardship wherever *Bt* maize varieties have been deployed in Africa and Asia, to ensure sustainable protection against the pest.

6. Conclusions

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 safer-use 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 agroecologies and market segments. Such products must combine FAW resistance with other desirable and relevant traits for resource-constrained smallholder farmers in the target geographies.

Bt maize varieties carrying lepidopteran-specific transgene(s), wherever released in Africa and 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 the current regulatory, political, and consumer acceptance hurdles. In countries where *Bt* maize is already being commercialized, it is important to devise and implement a well-coordinated regional IRM strategy. Synergies also need to be explored between native genetic resistance and *Bt* maize for offering better and sustainable host plant resistance options to the farming communities.

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