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BREEDING FOR RESISTANCE TO FALL ARMYWORM (*Spodoptera frugiperda* J.E. Smith) IN MAIZE

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SUMMARY

Incursion of the fall armyworm (FAW) in Africa and some other part of the world since 2016 has posed serious threat to food security. Conventional breeding has been extensively used to develop resistant genotypes through artificial and natural screening. Studies have been carried out on diet combinations for mass rearing of the insect for effective screening. However, due to the length of time involved and problem of genotype by environment, a faster approach through use of transgenes have been employed. In the Americas, *Bt* maize has successfully controlled FAW, however it has been discovered that the FAW is resistant to some of these *Bt* genes. *Bt* maize has also been released in Nigeria and few other parts of Africa. Molecular markers have also been used to fast-track progress in breeding for resistance to FAW. Simple Sequence Repeat (SSR) and Single Nucleotide Polymorphism (SNP) markers have been used to determine FAW identity, validate the origin of the African FAW population, and identify the main QTL for FAW resistance in maize. One of the most sophisticated methods for mapping the regions of the genome is the use of Genome-Wide Association Studies (GWAS), which is currently being used to investigate loci associated with resistance against FAW among maize genotypes. Some FAW resistant maize genotypes have been released for commercialization and some are still in the pipeline.

Keywords: Fall armyworm; genome-wide association studies (GWAS); host plant resistance; maize (*Zea mays* L); molecular markers; transgenes

Maize (*Zea mays* L.) is one of the most important crops in the world on which more than 4.5 billion people in 100 nations are fed. Having made a significant contribution to the production of cereals generally worldwide, maize is renowned for its variety of applications in feed, food, fuel, and fiber (12; 72). The crop is regarded as the queen of cereals and has the highest genetic production potential. However, maize yield is limited by several biotic and abiotic factors. Insect pests are one of the major biotic factors that contribute to yield losses in the field with high socio-economic impact and health hazards. They attack the crop singly or in groups of different species. Stem borers used to be the major insect pest of maize in southern ecology of Nigeria causing between 24-30 % yield loss (51), until the invasion of fall armyworm (FAW) in 2016.

The FAW [*Spodoptera frugiperda* (J.E. Smith)] is a polyphagous insect and is indigenous to the Americas (65). Although the insect arrived on the African continent in January 2016, it has been reported in America since the late 17th, early 18th, and early 19th centuries (67). Presently, the pest is confirmed in 46 of Africa's 54 countries and it is likely to establish itself as a multi-generational pest of economic importance in Africa due to its natural distribution capacity, high fecundity level, favorable sub-tropical climates, wide host range, voracious appetite, and migratory activities (61;20). FAW is adjudged as one of the most damaging crop pests in the Americas, and findings have shown that FAW feeds on more than 80 crops, including sorghum, maize, rice, beet, groundnut, millet, tomato, potato (25). It has also been reported that FAW has a long history of resistance to conventional insecticides and GM toxins (29). According to a report by (3) the FAW has the ability to reduce maize yields in Africa by 8.3 - 20.6 million tonnes annually, in 12 countries that produce maize, when control measures are not put in place. In sub-Saharan Africa (SSA), annual losses of up to US$ 13 billion have been estimated in crops such as maize, rice, sorghum, and sugarcane (53;19).

The mode of action of FAW and that of stem borers are very similar, and significant correlations have been reported between the resistance indices of both pests (2; 61). The eggs of FAW are usually laid in batches (between 100 and 200 eggs), just as in stem borers, and when temperatures are ideal, they hatch in two to four days. Most adult moths have a two- to three-week lifespan. During this phase, females will mate numerous times and lay numerous egg masses, with a maximum fecundity of 1,000 eggs per female (11). Temperature (between 11°C and 30°C) and food have an impact on how quickly larvae develop in their natural habitat (11). The conducive condition of the tropics which aids survival, as well as the life-span of the adult, makes the control of FAW difficult. The sixth instars larval causes the most damage by consuming about 77 % of the plant material. It feeds on the whorls of immature maize plants, causing the leaf margins to develop tiny holes and crooked notches as a result. For instance, (48) reported negative relationship between plant age and damage severity. Larger larvae engage in cannibalism and feed on other *S. frugiperda* larvae, particularly smaller ones. FAW feeding on maize plants causes chlorophyll degradation, excessive and uncontrolled water loss, disruption of photosynthetic processes, nutrient deficiency and an increased rate of respiration (4). The infested plant responds by converting the primary metabolites into secondary metabolites for plant defense. This further reduces crop yield because the secondary metabolites are food for herbivorous insects like the fall armyworm (4). Hence, there is urgent need to study the nature and behaviour of the insect to know the most appropriate time to initiate control measures.

Different strategies have been used to lessen the threat of FAW *vis* chemical, cultural and biological control, but each is not without its limitations. Breeding for host plant resistance has been identified as a holistic approach towards solving the menace of FAW. Significant efforts have been made in breeding elite maize lines and hybrids with native genetic resistance to FAW in Africa by the International Maize and Wheat Improvement Center (CIMMYT), Mexico. These elite maize cultivars with native FAW tolerance/resistance and farmer-preferred traits have been deployed to diverse agro-ecologies in Africa and Asia (60). 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 (60). Different approaches and progress in breeding for resistance to FAW in maize is discussed in this review.

APPROACHES IN BREEDING FOR HOST PLANT RESISTANCE TO FAW

Conventional Approach

Developing resistant genotypes is an effective way to combat the threat of FAW. The release of resistant genotypes to farmers in Africa, majority of whom are smallholders with limited resources, will go a long way to improve their productivity. To successfully develop resistant cultivars, factors such as diverse germplasm base, efficient breeding techniques, effective screening procedures, and good understanding of resistance mechanism and mode of inheritance of resistance are important. Different crops have varying levels of tolerance or resistance to pests. Traditional plant breeding aims to create lines with these qualities, along with high yield. Conventional breeding procedures require time, but they do not considerably raise seed prices. Even though African farmers save their seeds against the next planting, they are likely to adopt and invest in FAW-resistant cultivars with other desirable features if they can be developed (3).

Host plant resistance (HPR) comprises of native genetic resistance (developing germplasm with resistance) and transgenic resistance (using a gene or combination of genes from an external sources), to make the host plant resistant to FAW (60). CIMMYT and its partners examined and tagged germplasms known to have resistance to FAW as potential sources of resistance genes. They later concluded that there was enough diversity and that conventional breeding could support effective FAW-resistance breeding in SSA (61). In the Americas, genetically-engineered crops with *Bt* proteins have reduced the demand for pest-resistant crops produced through traditional methods. However, there is evidence of variation in susceptibility to FAW among these maize genotypes and other crops, suggesting further exploration of opportunities in conventional breeding.

Mechanisms of Resistance

Three major mechanism of insect pest resistance are antibiosis, antixenosis (preference or non-preference) and tolerance. Preference or non-preference is a mechanism employed by the plant to prevent itself from being used for oviposition, shelter or food by the insect. Antibiosis refers to those antagonistic effects on the life of the FAW insect as a result of using resistant plants as food. Antibiosis results in lower levels of survival, rate of feeding, size, and fitness, as well as lower levels of plant attractiveness, which lowers levels of oviposition. The capability of the host-plant to survive insect damage is tolerance, which is an innate genetic strength.

Resistance to FAW can manifest itself in a variety of ways, including lower survival and feeding rate, as well as decreased attractiveness for oviposition (3). Viana and Potenza (2000) identified the resistance of popcorn genotypes to FAW as a non-preference type, while (50) identified antibiosis as the main mode of resistance.

According to (62), how much of a leaf an insect consumes depends on the chemical (allelochemical) and nutritional characteristics of the leaves as well as their thickness, hardness, texture, epicuticular wax content, and surface hairiness. The Honduran landrace accessions of sorghum (San Bernardo III, Hilate179, Piña-61, and Lerdo-104) also had antibiosis against FAW (40). Ferreira *et al.* (2003) investigated several maize varieties and discovered that taller cultivars with higher ear insertion height were less likely to be injured. Williams *et al.* (69) observed that FAW-resistant maize had reduced leaf damage and larvae that grew at a slower rate. Both resistant and susceptible types suffered less harm as they aged, although resistant versions matured sooner and experienced less harm (56).

Biochemical Basis for FAW Resistance

The biochemical basis for resistance to fall armyworm (FAW) in plants involves a complex interplay of various pathways and compounds. Plants respond to FAW infestation by initiating biochemical responses to deter feeding and minimize damage. Chemical defense compounds, such as alkaloids, terpenoids, phenolics, and glucosinolates, act as deterrents or have toxic effects on FAW (13). Inducible defense mechanisms activated in response to herbivores attack involve the signaling molecule jasmonic acid, leading to the production of defense compounds. The nutritional levels and allelochemical composition of plants play a vital role in determining their suitability and resistance to insect herbivores (13). Insects that consume plants rich in nitrogen demonstrate higher growth rates, increased food conversion efficiency, and shorter developmental times compared to those feeding on low-nitrogen plants (14). Some nutritional and biochemical factors have been identified to confer resistance to FAW in maize genotypes. For instance, Mp708 and FAW7050 maize genotypes were identified as FAW resistant due to increased translation of photosynthates to protective proteins, while genotype Ab24E was susceptible to FAW as a result of a high protein-to-carbohydrate proportion as well as a low level of induced-defensive compounds (13). According to (63) a maize variety that resists insect herbivory releases (E)-B-Caryophyllene. Reports have shown that the terpenoid (E) caryophyllene, which is produced in Mp708, is connected to resistance. Terpenoids, including volatile terpenes, and phenolic compounds, such as flavonoids and tannins, contribute to plant defense by acting as feeding deterrents or interfering with insect physiology. Mp708 (resistant) and Tx601 (susceptible) FAW-fed samples both displayed a high tps23 transcript number (59).

One of a latent group of proteins that can protect maize against herbivorous animals that chew the plants is the hazardous protein RIP2, which is activated by caterpillar feeding (15). Malook *et al*. (39) identified a Chinese maize inbred line Xi502 that was able to mount effective defense in response to FAW attack. The study showed that Xi502 accumulates higher levels of benzoxazinoids, effective against FAW than susceptible B73. Leaf feeding by FAW was also reported to be dependent on composition of the cell wall of the plant. Hence, hemicellulose, a constituent of cell wall is a vital factor conferring resistance of maize to leaf feeding by FAW. Hemicellulose level was reported to be greater in resistant maize genotypes than in susceptible genotypes (26). A study by (46) opined that at the seedling stage, promising earworm-resistant maize inbred lines could give cross resistance to foliage eating FAW. Efforts focus on enhancing systemic acquired resistance (SAR), allowing plants to induce resistance throughout the entire plant in response to localized infection or herbivores attack (27). By manipulating these biochemical pathways, scientists aim to optimize the plant's defense response, developing more resilient and sustainable crop varieties with improved resistance to FAW.

Genetics and Breeding Techniques for FAW Resistance in Host Plants

Several breeding techniques have been used to create crop plants that are resistant to insects (17). Through mass selection, pure line selection, backcross breeding, bulk breeding, and recurrent selection, arthropod resistance genes are frequently inserted into crop plants. A study on insect genetic research conducted by (9, 10) showed that maize FAW resistance is largely polygenic in nature, with both dominant and additive gene action controlling it. Combining ability studies can also help to better understand the nature of gene action and the underlying mechanisms of inheritance of FAW resistance. Prasanna *et al.* (58) reported that some breeding methods *viz-a-viz* diallel, line-tester analysis, and North Carolina Designs were efficient in understanding general and specific combining ability (GCA, SCA) effects for FAW resistance. It was reported that both GCA and SCA effects were important in the genetic control of FAW resistance, with GCA effects predominating (68). Hybrid breeding may be able to increase maize resistance to FAW because dominant gene action and epistatic gene effects exist. Long-lasting horizontal resistance to FAW is created by the practice of recurrent selection to additive genes. Also, the findings of (2) on the polygenic genetic control of FAW resistance further supports the idea that additive genes have been accumulated through repeated selection. Kamweru *et al.* (32) reported moderately high heritability estimates for FAW leaf damage. Their study revealed that native genetic resistance to FAW is quantitative in nature and is controlled by many minor genes.

Screening For Resistance to FAW

Screening for resistance to FAW in various parts of the world especially in Africa, have been going on since the invasion in 2016. For effective screening, proper mass rearing of the insect is essential. Research centres such as IITA, CIMMYT and KALRO in Kenya have studied appropriate artificial diet for FAW and have been able to mass-rear FAW for artificial infestation. Kasoma *et al.* (34) studied the developmental stages of the insect, the distinct features and also compared use of natural and artificial diet in rearing of FAW. They found out that the egg, larva, pupa and adult stages had mean durations of 2, 24, 20 and 12 days, respectively. They also recorded higher mean larva survival rate of 80% for the natural (maize leaves and stalks) than the artificial diet (40%) at 27 ± 1 ◦C temperature, 60 ± 5% relative humidity and 12 h day length.

Since February 2018, over 250,000 neonate larvae and about 40,000 neonates per net-house have been generated and used by KALRO in Kiboko, Kenya, for the purpose of screening germplasm. Kiboko's screening capacity were later extended to 14 net houses (300 entries per net house) and Harare's capability to 8 net houses (58). Some outstanding CIMMYT maize inbred lines identified and validated in Kiboko, Kenya were CML70, CML71, CML333, CKSBL10027, CKSBL10008, CKSBL10002, CKSBL10025, CKSBL10060, CKSBL10039 and MBR C6Bc F234-1. Leaf damage scores varied from 2.0 to 6.0 for these inbreds, and ear damage ratings were below 3.0, while susceptibility rating was 7.0 or above. Some outstanding CIMMYT maize inbreds authenticated by USDA-Mississippi team were CML70, CML71, CML453, CML404, CML15, CML122, CML484, CML67, CML332, CML432, CML333, CML338, CML322, CML286 (58). CKIR06007, CKIR06001, and CKDHL164288/CLRCY039 were a few of the outstanding F_1 CIMMYT's maize hybrids with FAW resistance that were artificially infested in Kiboko, KALRO, Kenya. More promising maize hybrids with tolerance to the FAW have also been developed by CIMMYT through conventional approach (59).

Since 2018, FAW-tolerant/FAW-resistant CMLs (CIMMYT maize lines) 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 (60). CIMMYT lines CML 338, CML 67 and CML 139 have been reported to be among the FAW-tolerant donor lines used for conferring FAW genes into locally adapted genotypes (41). Some of these lines are being used in recent screenings for FAW resistance. The Davis scale, which rates the severity and extent of damage to foliage or ears on a scale from 1 (most resistance) to 9 (most susceptible), is used to determine level of FAW resistance (18, 28). However, according to (68), foliar damage to maize may not result in a significant loss in grain yield.

USDA-ARS (Mississippi) used FAW-resistant tropical maize genotypes from CIMMYT along with temperate maize genotypes, to create and register some temperate maize inbred lines, including Mp704, Mp708, Mp713, Mp714 and Mp716 (57). Additionally, some of the temperate-tropical introgression lines from the CIMMYT have proved promising for FAW resistance, for instance CKLTI0348. The 'CRW3(S1) C6' western corn rootworm showed resistance to S. *frugiperda* feeding. Investigations of the genetic diversity and quantity of FAW predator showed that 'CRW3(S1)C6' and 'Ab24E' had the maximum and minimum predator abundance, respectively. However, there was no association between predator abundance and injury ratings of FAW (47).

Over 500 hybrids including single- and three-way crosses, were tested across different management conditions, including screening against FAW under artificial infestation in Kiboko, Kenya between 2019-2020 (60). Diverse genotypes responded in varying degrees to FAW infestation in Zimbabwe as well as in Zambia (33).

Twenty (20) OPV maize were screened for FAW resistance at the Institute of Agricultural Research and Training (IAR&T), Nigeria, in both natural and artificially-infested conditions across five environments in 2018. The genotypes comprised of IAR&T maize genotypes and stem borer resistant maize genotypes from the International Institute of Tropical Agriculture (IITA), Nigeria. Some promising genotypes have been identified with leaf damage rating ≥ 3 on Davis scale of 1-9 (52) These genotypes are currently undergoing cycles of mass selection to develop FAW resistance maize and extract lines. Scientists at IITA have also screened some maize genotypes for resistance to FAW using natural and artificial infestation. The selected genotypes have been used to develop white and yellow FAW-resistant varieties which are now released for commercial use.

Kasoma *et al*. (34) examined two different collections of maize germplasm comprising inbred lines, OPVs, hybrids and landraces in order to study the genetic heterogeneity of the germplasm as a source of FAW resistance. Highly significant differences were detected among the test genotypes for leaf damage, cob damage and agronomic traits. Grain yield was negatively correlated leaf and cob damage. According to their study, in order to lessen the confounding season effect and temperature on the crops during their developmental stage, leaf-damage should be rated within 16 to 30 days after the preliminary infestation, and it should be recorded at least four times. This is in conformity with (30), who reported that the greatest yield loss to FAW occurs when the pest is not controlled within 30 days of infestation. Kasoma *et al*. (34) screened 63 selected tropical maize genotypes comprising 57 elite CIMMYT inbred lines, four OPVs and two single-cross commercial hybrids as controls. They also reported significant differences among test genotypes for second, third, fourth and fifth FAW leaf damage score. (32) screened 424 maize lines under artificial FAW infestation and reported that all FAW parameters had significant positive correlations with themselves, but negative correlations with grain yield.

(42) screened 23 maize genotypes with varying levels of SB resistance under artificial FAW-infested and FAW-protected conditions. Significant genotypic differences were reported for all the traits under both conditions. Mean grain yield was 4.61 t ha-^{1} under FAW-infested condition, and 4.86 t ha-^{1} under FAW-protected condition. Across genotypes, FAW infestation reduced grain yield by 5.1%, suggesting that stem borer resistance could confer tolerance to FAW. They also reported significant negative correlations between grain yield under FAW-infested condition with FAW leaf damage and ear damage. Asare *et al*. (5) in Ghana evaluated 35 maize inbred lines together with 60 single-cross hybrids and 20 double-crosses developed from 17 desirable inbred lines, for resistance to fall armyworm under artificial and natural infestations in 2020 and 2021. Significant differences were recorded among the inbred lines, F_1 hybrids, and the double crosses. Promising hybrids have been recommended for commercialization in SSA.

Due to inbreeding depression, inbred lines grow more slowly, allowing FAW larvae to feed on whorl tissues for a longer period prior to whorl stage of the plant, which is their ideal eating stage. As opposed to inbred lines, landraces, hybrids, and OPVs have greater vigor (23) and develop more quickly to complete the FAW larvae preferred feeding stage (61). Despite the fact that maize genotypes may withstand small to large amounts of leaf defoliation without experiencing a major loss in yield, the direct attack on the sensitive parts of the plant, may cause a significant yield loss (61). Leaf damage, though has the potential to lower yield, it cannot be considered as the primary predictor of maize yield loss. This is because the insect cannot significantly reduce yield without completely destroying the leaf whorl (38). The type of tested germplasm and crop growth stage are critical factors in determining the FAW ratings.

Some possible sources of FAW-resistance for breeding include wild-relatives, extinct cultivars, landraces, elite cultivars, mutant genotypes and breeding populations (44). For example, Mexican landraces, according to (64) contain FAW-resistance genes that could be used to develop disease-resistant genotypes. FAW resistance has also been linked to Balsas Teosinte, an ancestor of maize cultivars that has previously been utilized to improve morpho-agronomic traits (64).

Modern Approach

Marker-Assisted Selection (MAS)

Plant breeders need to continuously introduce new crop types with high production potential, excellent quality, resistance or tolerance to biotic and abiotic factors, and high nutrient-use efficiency, for sustainable crop productivity (36). Although few plant breeders have access to insect rearing facilities, which are required to improve selection effectiveness, negative traits frequently conceal genetic gains in resistance during the early generations of backcrossing, and resistance levels are typically moderate. Thus, genetic resistance can be manipulated, and some of these problems can be addressed through quantitative trait locus (QTL) mapping (10). A QTL is a genetic region linked to a specific phenotypic trait. The primary aims of QTL mapping in plants are to (i) advance biological understanding of the genetic architecture and inheritance of quantitative traits, and (ii) identify markers that can be used as indirect selection tools in breeding (7).

Genomics is a field of paramount importance for understanding the genetic architecture of complex quantitative traits and characterizing germplasm collections to achieve accurate and precise manipulation of desirable alleles/genes (24). Different markers have been used to study FAW resistance in crops. Restriction Fragment length Polymorphism (RFLP) has been used to differentiate FAW from other pests in maize (Lewter *et al.,* 2006). Amplified Fragment Length Polymorphism (AFLP) and Simple Sequence Repeat (SSR) were used to develop linkage map for FAW resistant genes in buffel grass (31). SSR was used to ascertain FAW identity and detect FAW candidate migrant in maize (55). Single Nucleotide Polymorphism (SNP) markers were utilized to identify foremost QTL for FAW resistance in maize, identify FAW types existing in Africa, determine a potential route of FAW entry into Africa (16) and validate the source of the FAW populations in maize and sorghum in Africa (45). The QTL validation serves as the basis for the inclusion of MAS in FAW resistance breeding. There are some known QTL linked to resistance to FAW in maize (10, 9). Womack *et al.* (71) suggested that the use of molecular markers would make phenotypic selection for FAW resistance easier. This implies that the only purpose of selection pressure is to confirm the choices made through MAS. One of the most sophisticated methods for mapping the regions of the genome is the use of genome-wide association studies (GWAS), which is currently being used to investigate loci associated with resistance against FAW among maize genotypes. The first report on GWAS studies was carried out by (6) to identify loci responsible for FAW and maize weevil resistance in African maize genotypes. The study made use of a large association mapping panel of inbred lines and doubled-haploid maize lines grown in a diverse agro-ecologies in Africa. They discovered that 6 of the 62 quantitative trait nucleotides (QTNs), associated with both FAW and maize weevil resistance were found on ten maize chromosomes, indicating pleiotropic genetic control of these pests resistance. A GWAS study by Kamweru *et al*. (2022) revealed 56 significant marker–trait associations. Chromosome 4 accounted for the highest number (15 %) of the SNP markers associated with foliar damage. Grain yield under artificial FAW infestation exhibited peaks of association signals on chromosomes 4 and 10. Chromosomes 4 and 9 have been reported to harbor SNP markers associated with resistance to major lepidopteran pests in maize (43).

Use of Transgenes

*Pesticides were the primary means of controlling FAW in Brazil until an issue with insecticide resistance forced the introduction of Bt maize (21). F*ollowing the introduction of *Bt* maize in the US in the 1990s, traditional FAW resistance breeding for FAW took a backseat. In the Americas, *Bt* maize has been used to effectively control FAW (71) but with constant resistance breakdown within a 3–4-year cycle (21). It has been discovered that FAW is resistant to maize harboring the Cry1F gene, with minor cross resistance to the Cry1Ab gene (57). There is also evidence of FAW resistance to *Bt* cotton. Pyramiding numerous *Bt* genes in the same crop variety is now being utilized. A section of maize in an area should have specific non-*Bt* genotypes in order to serve as a "refuge or safe zone" where *Bt* susceptible insects can reproduce in order to prevent the development of resistance. The findings of (8) showed high levels of FAW mortality (> 99%) in South Africa due to the pyramid toxic event Cry1A.105 + Cry2Ab2 in genotypes that are tolerant and resistant.

The results of the water-use efficient maize for Africa (WEMA) project, which began in 2012 in Mozambique, Uganda, and, Kenya showed that the introduction of MON810 into cultivars of maize that are appropriate for the region confers high stem borer resistance and partial control of FAW in maize (61). Farmers in nations where GM maize can be grown have a good alternative for managing FAW by using these *Bt* events. Botha *et al.* (8) suggested that the majority of African countries where FAW was first introduced may harbor resistance alleles to Cry1Ab, necessitating the use of gene stacking for efficient FAW control in Cry1Ab *Bt* maize events like MON810. The evaluation of *Bt* maize in Vietnam began in 2010 and since then three *Bt* maize events (MON 89034, *Bt*11 and TC1507) have been approved for environmental release (60).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 (1). The genetic engineering process of TELA maize involved using hybrid parent materials of select well-adapted DroughtTEGO that had been introgressed with *Bt* or *Bt* and *DT* genes in crosses to form single-cross or three-way hybrids which are known as TELA (derived from the Latin word, TUTELA, meaning 'protection') (49). From the confined field trials (CFTs) conducted to demonstrate the efficacy of the TELA traits (*Bt* MON810; *Bt* MON89034; *DT* MON87460), under natural FAW and artificial stem borer infestation, TELA hybrids with *Bt* MON810 trait gave an average of 43 % yield advantage compared with the isogenic hybrids from 12 CFTs across six locations in five countries from 2016–2020 (49). Similar trials on *Bt* MON89034 conducted in Nigeria for two years showed that the TELA hybrids gave 19 % higher yield than their non-transformed isogenic versions, and 40 % higher yield than the commercial checks under the target pests' infestation (54). TELA maize is now released in Nigeria for commercialization.

CONCLUSION

The challenges posed by insect pests, particularly the fall armyworm (FAW) in maize production require a comprehensive and multi-facet approach. Breeding for host plant resistance includes conventional approach where resistant genotypes are developed through a combination of diverse germplasms, effective screening procedures followed by selection of promising lines. Knowledge of mechanisms of resistance, biochemical basis for resistance and appropriate feeding techniques for mass-rearing of the FAW for screening, are essential for effective traditional breeding.

Modern approach such as Marker-Assisted Selection (MAS) and use of transgenes, offer promising avenues for enhancing FAW resistance in maize. MAS allows for the identification of quantitative trait loci (QTL) linked to resistance, enabling more efficient and precise selection of resistant genotypes. The introduction of transgenes, particularly Bacillus thuringiensis (*Bt*) toxins, has proven effective in controlling FAW, with the possibility of stacking multiple *Bt* genes to address resistance challenges.

The challenges posed by FAW necessitate a collaborative and interdisciplinary approach, involving plant breeders, entomologists, geneticists, and biotechnologists. Sustainable solutions will likely emerge from a combination of traditional breeding practices and cutting-edge technologies. There should be increased application of modern genetic tools such as MAS and GWAS in accelerating breeding for FAW resistance to improve Africa-adapted maize genotypes. This will improve farmers' livelihood and solve the problem of food insecurity.

LITERATURE CITED

1. **AATF 2021.** *Study report on evaluation and impact assessment of the WEMA project in Kenya, Tanzania, and Uganda*. Technical Report, July 2021, AATF, Nairobi, Kenya. 65pp.
2. **Abel, C.A., Wilson, R.L., Wiseman, B.R., White, W.H. and Davis, F.M. 2000.** Conventional Resistance of Experimental Maize Lines to Corn Earworm (Lepidoptera: Noctuidae), Fall Armyworm (*Lepidoptera: Noctuidae*), Southwestern Corn Borer (Lepidoptera: Crambidae), and Sugarcane Borer (Lepidoptera: Crambidae). *Journal of Economic Entomology, 93*(3): 982–988. doi:10.1603/+0022-0493-93.3.982.
3. **Abrahams, P., Bateman, M., Beale, T., Clottey, V., Cock, M., Colmenarez, Y. and Witt, A. 2017**. *Fall armyworm: Impacts and Implications for Africa*. Department of Biosciences, University of Exeter, CABI, UK.
4. **Anjorin, F.B., Odeyemi, O.O., Akinbode, O.A. and Kareem, K.T. 2022.** Fall armyworm (*Spodoptera frugiperda* J.E. Smith) (Lepidoptera: Noctuidae) infestation: maize yield depression and physiological basis of tolerance. *Journal of Plant*

Protection Research, 62(1): 12–21, doi: 10.24425/jppr.2022.140294

5. **Asare, S., Kena, A., Amoah, S., Annor, B., Osekre, E.A. and Akromah, R. 2023.** Screening of maize inbred lines and evaluation of hybrids for their resistance to fall armyworm. *Plant Stress, 8*. https://doi.org/10.1016/j.stress.2023.100148.
6. **Badji, A., Kwemoi, D. B., Machida, L., Okii, D., Mwila, N., Symphorien, A. and Rubaihayo, P. 2020.** Genetic basis of maize resistance to multiple insect pests: integrated genome-wide comparative mapping and candidate gene prioritization. *Genes, 11*. 689. https://doi.org/10.3390/genes11060689.
7. **Bernardo, R. 2008.** Molecular markers and selection for complex traits: Learning from the last 20 years. *Crop Science, 48*: 1649-1664.
8. **Botha, A. S., Erasmus, A., Plessis, H. and Van den Berg, J. 2019.** Efficacy of *Bt* maize for control of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in South Africa. *Journal of Economic Entomology,* 112: 1260-1266. https://doi.org/10.1093/jee/toz048
9. **Brooks, T. D., Bushman, B. S., Williams, W. P., McMullen, M. D. and Buckely, M. P. 2007**. Genetic basis of resistance to fall armyworm (Lepidoptera: Noctuidae) and southwestern corn borer (Lepidoptera: Crambridae) leaf feeding damage in maize. *Journal of Economic Entomology, 100*(4):1470–1475. doi: 10.1603/0022-0493(2007)100[1470:gbortf]2.0.co;2.
10. **Brooks, T.D., Wilcox, M.C., Williams, W.P. and Buckely, P.M. 2005.** Quantitative Trait Loci conferring resistance to fall armyworm and southwestern corn borer leaf feeding damage. *Crop Science, 45*(6): 2430–2434. doi:10.2135/cropsci2004.0656.
11. **CABI 2017.** Datasheet *Spodoptera frugiperda* (fall armyworm). *Invasive Species Compendium*. http://www.cabi.org/isc/datasheet/29810 [Accessed August 2017].
12. **Cairns, J. E., Hellin, J., Sonder, K., Crossa, J., Araus, J.L., MacRobert, J.F. and Prasanna, B. M. 2013.** Adapting maize production to climate change in sub-Saharan Africa. *Food Security, 5*: 345–360.
13. **Chen, Y., Ni, X. and Buntin, G. 2009.** Physiological, Nutritional, and Biochemical Bases of Corn Resistance to Foliage-Feeding Fall Armyworm. *Journal of Chemical Ecology, 35*: 297–306.
14. **Chen, Y., Ruberson, J.R. and Olson, D.M. 2008.** Nitrogen fertilization rate affects feeding, larval performance, and oviposition preference of the beet armyworm, *Spodoptera exigua*, on cotton. *Entomologia Experimentalis et Applicata, 126*:244–255.

15. **Chuang, W. P., Herde, M., Ray, S., Castano-Duque, L., Howe, G. A, and Luthe, D. S. 2014.** Caterpillar attack triggers accumulation of the toxic maize protein RIP2. *New Phytologist, 201*: 928-939.

16. **Cock, M. J. W., Beseh, P. K., Buddie, A. G., Cafá, G. and Crozier, J. 2017.** Molecular methods to detect *Spodoptera frugiperda* in Ghana, and implications for monitoring the spread of invasive species in developing countries. *Scientific Reports, 7*. doi: 10.1038/s41598-017-04238-y.

17. **Dahms, R.G. 1972.** Techniques in the evaluation and development of host-plant resistance. *Journal of Environmental Quality, 1*: 254-258.

18. **Davis, F. M., Ng, S. S. and Williams, W. P. 1992.** *Visual rating scales for screening whorl stage corn for resistance to fall armyworm.* Technical bulletin - Mississippi Agricultural and Forestry Experimental Station, 186: 1-9. http://agris.fao.org/agrissearch/search.do◦recordID=US9406363

19. **Day, R., Abrahams, P., Bateman, M., Beale, T., Clottey, V., Cock, M., Colmenarez, Y., Corniani, N., Early, R., Godwin, J., et al. 2017.** Fall armyworm: Impacts and implications for Africa. *Outlooks on Pest Management, 28*: 196–201.

20. **De Groote, H., Kimenju, S.C., Munyua, B., Palmas, S., Kassie, M. and Bruce, A. 2020.** Spread and impact of fall armyworm (*Spodoptera frugiperda* J.E. Smith) in maize production areas of Kenya. *Agriculture, Ecosystems & Environment, 292*. 106804.

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

22. **Ferreira A., Neto, J., Viera, F.V., Alves, J.F. and Almeida, F. C. G. 1993.** Sources of resistance to *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera, Noctuidae) in genotypes of maize. *Revista de la Facultad de Agronomía, Universidad Central de Venezuela, 19* (2): 185-203

23. **Fu, D., Xiao, M., Hayward, A., Fu, Y., Liu, G., Jiang, G. and Zhang, H. 2014.** Utilization of crop heterosis: A review. *Euphytica. 197*: 161-173.

24. **Gedil, M. and Menkir, A. 2019.** An integrated molecular and conventional breeding scheme for enhancing genetic gain in maize in Africa. *Frontiers in Plant Science, 10*: 1-17. doi: 10.3389/fpls.2019.01430.

25. **Goergen, G., Kumar, P. L., Sankung, S. B., Togola, A. and 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." *PLoSOne,* https://doi.org/10.1371/journal.pone.0165632 (accessed 23 Jan. 2018).

26. **Hedin, P.A., Davis, F.M. and Fisher, T.H. 1996.** Hemicellulose is an important leaf feeding resistance factor in corn to fall armyworm. *Journal of Chemical Ecology, 22*: 1655-1668.

27. **Heil, M. and Bostock, R.M. 2002.** Induced systemic resistance (ISR) against pathogens in the context of induced plant defences. *Annals of Botany, 89*(5):503-512. doi: 10.1093/aob/mcf076.

28. **Huang, F., Qureshi, J. A., Meagher, R. L., Reisig, D. D., Head, G. P., Andow, D. A., Ni, X., Kens, D., Buntin, D., Niu, Y. and Yang, F. 2014.** Cry1F resistance in fall armyworm, *Spodoptera frugiperda*: Single gene versus pyramided *Bt* maize. *PLoSONE*, 9: e112958. https://doi.org/10.1371/journal.pone.0112958.

29. **Huesing J. 2017.** Fall Armyworm in Africa: *A Guide for integrated pest management.*

30. **SDSN** carbon-free e-conference 'Responding to Fall Armyworm in Africa', 22-26 October 2017. USAID Washington DC, USA.

31. **Ibraheem, F. and El-Ghareeb, E.M. 2019.** Assessment of natural variability in leaf morphological and physiological traits in maize inbreds and their related hybrids during early vegetative growth. *Egyptian Journal of Basic and Applied Science, 6*(1): 22-45.

32. **Jessup, R. W., Renganayaki, K., Reinert, J. A., Genovesi, A. D., Engelke, M. C., Paterson, A. H. and Burson, B. L. 2011.** Genetic mapping of fall armyworm resistance in Zoysia grass. *Crop Science, 51*: 1774-1783.

33. **Kamweru, I., Anani, B.Y., Beyene, Y., Makumbi, D., Adetimirin, V.O., Prasanna, B.M. and Gowda, M. 2022.** Genomic Analysis of Resistance to Fall Armyworm (*Spodoptera frugiperda*) in CIMMYT Maize Lines. *Genes, 13*. https://doi.org/10.3390/genes13020251.

34. **Kansiime, M. K., Mugambi, I., Rwomushana, I., Nunda, W., Lamontagne-Godwin, J., Rware, H. and Day, R. 2019.** Farmer perception of fall armyworm (*Spodoptera frugiderda* J.E. Smith) and farm-level management practices in Zambia. *Pest Management Science,* 75: 2840-2850. https://doi.org/10.1002/ps.5504

35. **Kasoma, C. Shimelis, H.; Laing, M.D. and Mekonnen, B. 2022.** Fall Armyworm Infestation and Development: Screening Tropical Maize Genotypes for Resistance in Zambia. *Insects, 13*. https://doi.org/10.3390/insects13111020

36. **Kasoma, C., Shimelis, H., Laing, M., Shayanowako, A. I. T. and**

Mathew, I. 2020. Screening of inbred lines of tropical maize for resistance to fall armyworm, and for yield and yield-related traits. *Crop Protection. 136*: https://doi.org/10.1016/j.cropro.2020.105218

37. **Leng, P., Lubberstedt, T. and Xu, M. 2017.** Genomics-assisted breeding- A revolutionary strategy for crop improvement. *Journal of Integrative Agriculture, 16*(12): 2674–2685.

38. **Lewter, J.A., Szalanski, A.L., Nagoshi, R.N., Meagher, R.L., Owens, C.B. and Luttrell, R.G. 2006.** Genetic variation within and between strains of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Florida Entomologist, 89*(1): 63–68.

39. **Lima, M.S., Silva, P.L.S., Oliviera, O.F., Silva, K.M.B. and Freitas, F.C.L. 2010.** Corn yield response to weed and fall armyworm controls. *Planta Daninha, 28*: 103-111.

40. **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 infuences insect oral secretion elicitation activity and nullifies herbivores' suppression of plant defense. *BioRxiv*. https://doi.org/10.1101/2021.05.17.444416

41. **Meckenstock, D.H., Castro, M.T., Pitre, H.N. and Gomez, F. 1991.** Antibiosis to fall armyworm in Honduran landrace sorghum. *Environmental Entomology, 20*(5): 1259 - 1266.

42. **Mihm, J.A., Smith, M.E. and Deutsch, J.A. 1988.** Development of open-pollinated genotypes, non-conventional hybrids and inbred lines of tropical maize with resistance to fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), at CIMMYT. *Florida Entomologist, 71*: 262. https://doi.org/10.2307/3495430.

43. **Moussa, N.A.Z, Abe, A., Job, A.O., Kolawole, Y.O. and Olaniyan, A.B. 2023.** Evaluation of stem borer resistant maize genotypes for resistance to fall armyworm (*Spodoptera frugiperda* J.E. Smith) infestation. *Journal of Plant Breeding and Crop Science, 15*(3): 99-109. doi: 10.5897/JPBCS2023.1023.

44. **Munyiri, S.W. and Mugo, S.N. 2017.** Quantitative Trait Loci for Resistance to Spotted and African Maize Stem Borers (*Chilo partellus* and *Busseola fusca*) in a Tropical Maize (Zea mays L.) Population. *African Journal of Biotechnology, 16*: 1579–1589.

45. **Mwadzingeni, L., Figlan, S., Shimelis, H., Mondal, S. and Tsilo, T. J. 2017.** Genetic resources and breeding methodologies for improving drought tolerance in wheat. *Journal of Crop Improvement, 31*(5): 648–672. doi:10.1080/15427528.2017.1345816.

46. **Nagoshi, R.N., Goergen, G.,**

Tounou, K.A., Agboka, K., Koffi, D. and Meagher, R.L. 2018. Analysis of Strain Distribution, Migratory Potential, and Invasion History of Fall Armyworm Populations in Northern sub-Saharan Africa. *Scientific Reports, 8*: 3710. doi:10.1038/s41598018-21954-1.

47. **Ni, X., Da, K., Buntin, G. D. and Brown, S. L. 2008.** Physiological basis of fall armyworm (Lepidoptera: Noctuidae) resistance in seedlings of maize inbred lines with varying levels of silk maysin. *Florida Entomologist, 91*: 537-545. https://doi.org/10.1653/0015-4040-91.4.537.

48. **Ni, X. Z., Chen, Y. G., Hibbard, B. E., Wilson, J. P., Williams, W. P., Buntin, G. D., and Li, X. 2011.** Foliar resistance to fall armyworm in corn germplasm lines that confer resistance to root- and ear-feeding insects. *Florida Entomologist, 94*(4): 971-981.

49. **Odeyemi, O.O., Lawal, B.O., Owolade, O.F., Olasoji, J.O., Egbetokun, O. A., Oloyede-Kamiyo, Q.O., and Anjorin, F.B. 2020.** Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae): Threat to maize production in Nigeria. *Nigerian Agricultural Journal, 51*(1): 101-108.

50. **Oikeh, S.O. 2023.** Progress in developing and deploying drought-tolerant and insect- pest resistant climate-resilient DroughtTego® and TELA® maize varieties. *African Journal of Food, Agriculture, Nutrition and Development, 23*(10): 1- 14.

51. **Oliveira, N.C., Suzukawa, A.K., Pereira, C.B., Santos, H.V., Hanel, A., de Albuquerque, F.A. and Scapim. 2018.** Popcorn genotypes resistance to fall armyworm. Ciência Rural. *Santa Maria, 48*(2): 1-6.

52. **Oloyede-Kamiyo, Q.O., Ajala, S.O. and Akoroda, M.O. 2011.** Variability for resistance to the pink stem borer (*Sesamia calamistis* Hampson) and the sugarcane borer (*Eldana saccharina* Walker) in two tropical maize populations. *Maydica. 56*: 257-263.

53. **Oloyede-Kamiyo, Q.O. and Odeyemi, O.O. 2020.** Early detection of fall armyworm resistant source in some tropically-adapted maize genotypes in southern Nigeria. *Acta Agriculturae Slovenica, 117(*2): 1-8. doi:10.14720/aas.2021.117.2.1944.

54. **Overton, K., Maino, J.L., Day, R., Umina, P.A., Bett, B., Carnovale, D., Ekesi, S., Meagher, R. and Reynolds, O.L. 2021.** Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): A review. *Crop Protection, 145*. 105641.

55. **Oyekunle, M., Adamu, R.S., Ndou, E., Beyene, Y., Abdulmalik, M.M. and Oikeh, S.O. 2023.** Efficacy of Drought-

tolerant and Insect-protected Transgenic TELA® Maize Traits in Nigeria. *Transgenic Research*. https://doi.org/10.1007/s11248-023-00345-x

56. **Pavinato, V.A., Martinelli, S., Zucchi, M.I. and Omoto, C. 2013.** Microsatellite markers for genetic studies of the fall armyworm, *Spodoptera frugiperda*. *Genetics and Molecular Research, 12*(1): 370–380.

57. **Pitre, H. N., Portillo, H. E., Meckenstock, D.H., Castro, M.T., Lopez, J.I., Andrews, K. L., Gomez, F., Vergara, O.R. and Trabanino, R. 1997.** A complex of lepidopterous defoliators on sorghum and maize in Honduras: some management tactics. *CEIBA, 38* (2): 109-119.

58. **Prasanna, B.M. 2017.** *Host plant resistance to fall armyworm*. CIMMYT.

59. **Prasanna, B.M. 2018.** *Breeding for native genetic resistance to fall armyworm*. CIMMYT. Hohenheim.

60. **Prasanna, B.M. 2019.** Host Plant resistance to fall armyworm: Status and prospects. WTO Meeting, CIMMYT, March 19, 25pp. SDSN carbon-free e-conference 'Responding to fall armyworm in Africa', 22-26 October 2017. USAID Washington DC, USA.

61. **Prasanna, B.M., Bruce, A., Beyene, Y., Makumbi, D., Gowda, M., Asim, M., Martinelli, S., Head, G.P. and Parimi, S. 2022.** Host plant resistance for fall armyworm management in maize: relevance, status and prospects in Africa and Asia. *Theoretical and Applied Genetics, 135*:3897–3916. https://doi.org/10.1007/s00122-022-04073-4.

62. **Prasanna, B.M., Huesing, J.E., Eddy, R., Peschke, V.M., Regina, E. and Virginia, M.P. 2018.** *Fall Armyworm in Africa: A Guide for Integrated Pest Management,* 1st Edition. Prasanna, B.M., Regina, E., Virginia, M.P., Eds.; CIMMYT: Queretaro, Mexico.

63. **Smith, C.M. 2005.** *Plant resistance to arthropods: Molecular and conventional approaches*. Springer. Dordrecht, The Netherlands. xi+423pp

64. **Smith, W. E. C., Shiwaji, R., Williams, W. P., Luthe, D. S., Sandoya, G. V., Smith, C. L. and Brown, A. 2012.** A maize line resistant to herbivory constitutively releases (E)-β-Caryophyllene. *Journal of Economic Entomology, 105*(1): 120-128.

65. **Takahashi, C. G., Kalns, L. L. and Bernal, J. S. 2012.** Plant defense against fall armyworm in micro-sympatric maize (*Zea mays* ssp. *Mays*) and Balsas Teosinte (*Zea mays* ssp. *Parviglumis*). *Entomologia Experimentalis et Applicata,145*(3): 191–200. doi:10.1111/eea.12004

66. **Todd, E. L. and Poole, R. W. 1980.** Keys and illustrations for the armyworm moths of the noctuid genus *Spodoptera Guenée* from the

Western Hemisphere. *Annals of Entomological Society of America, 73*(6): 722–738. Doi:10.1093/aesa/73.6.722.

67. **Viana, P.A. and Potenza, M.R. 2000.** Evaluation of antibiosis and non-preference of maize cultivars selected for resistance to fall armyworm. *Bragantia. 59*(1): 27-33.

68. **Vickery, R. A. 1929.** *Studies of the fall armyworm in the Gulf Coast district of Texas.* USDA Technical Bulletin, No. 138. 64 p.

69. **Wightman, J. A. 2018.** Can lessons learned 30 years ago contribute to reducing the impact of the fall army worm, *Spodoptera frugiperda,* in Africa and India*? Outlook on Agriculture, 47*: 259-269. https://doi.org/10.1177/0030727018814849.

70. **Williams, P.W., Davis, F. M., Buckley, P. M., Hedin, P. A., Baker, G. T. and Luthe, D. S. 1998.** Factors associated with resistance to fall armyworm (Lepidoptera: Noctuidae) and southwestern corn borer (Lepidoptera: Crambidae) in corn at different vegetative stages. *Journal of Economic Entomology, 91*(6): 1471-1480.

71. **Williams, P. W., Windham, G. L., Matthews, G. A. and Buckley, P. M. 2018.** Diallel analysis for Aflatoxin accumulation and fall armyworm leaf-feeding damage in maize. *Journal of Crop Improvement, 32*(2): 254-263. doi:10.1080/15427528.2017.1408732.

73. **Womack, E.D., Warburton, M. and Williams, W.P. 2018.** Mapping of Quantitative Trait Loci for resistance to fall armyworm and southwestern corn borer leaf-feeding damage in maize. *Crop Science, 58*(2): 529-539. doi:10.2135/cropsci2017.03.0155.

74. **Yadav, G. S., Datta, M., Babu, S., Das, A., Bhowmik, S. N., Yadav, O. P. and Yadava, P. 2015.** Effect of tillage and crop establishment techniques on productivity, profitability and soil health under maize (*Zea mays*)-maize-field pea (*Pisum sativum*) cropping system. *Indian Journal of Agronomy, 60*(3): 360-364.