




Maize diversity for fall armyworm resistance in a warming world

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Abstract

Currently, maize (*Zea mays* L.) production is under threat from climate change, drought, and pests such as fall armyworm (FAW) [*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)]. Since its first detection outside of its native range in 2016, FAW has spread into 76 nations across Africa and Asia adversely affecting maize production and, in turn, the livelihoods of millions of smallholder farmers. Thus, there is a strong need for the development of cost-effective and biologically based integrated pest management (IPM) practices including host-plant resistance (HPR). However, most of the commercial maize cultivars have lost some defensive traits through selective breeding for yield during domestication. The majority of the commercially cultivated hybrids and cultivars in Asia and Africa are highly susceptible to FAW. Therefore, this review summarizes information about various maize landraces, native germplasm, and crop wild relatives (CWRs) possessing FAW resistance traits and about their potential resistance mechanisms, namely antibiosis, antixenosis, and tolerance. There is clear evidence of FAW resistance acting through diverse mechanisms in several maize landraces, germplasm lines, native populations, and CWRs such as Antigua race, FAW Tuxpeno, Zapalote Chico 2451F, Doce Flor da Serra, FAWCC (C5), CMS 14C, PopG (C2), MpSWCB-4, Mp708, Mp 704, CML 67, and FAW 7050, as well as a few species of teosinte and *Tripsacum* L. Further, a scheme that outlines strategies and approaches for prebreeding and their introgression into elite cultivars for developing FAW-resistant maize is proposed as a possible way forward.

1 | INTRODUCTION

Maize (*Zea mays* L.) is one of the most productive staple cereals known for its broad phenotypic and genotypic elas-

ticity (Liu et al., 2020). Originating in Mexico (Mesoamerica), maize has expanded from 142 countries in 1961 to 168 countries at present, with an 83.5% increase in cultivation area worldwide (<https://www.fao.org/faostat/en/#data>). In spite of its high productivity, maize yields are below their potential because of many abiotic and biotic stresses (Assefa & Ayalew, 2019). Global models of climate change have projected that

Abbreviations: EBV, estimated breeding value; FAW, fall armyworm; HPR, host-plant resistance; IPM, integrated pest management; JA, jasmonic acid.

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in major cropping areas of wheat (*Triticum aestivum* L.) and maize, drought would intensify and become more persistent in future decades (Dai, 2013; Seneviratne et al., 2012; Trenberth et al., 2014). The final yield of maize was claimed to be decreased by 1 and 1.7% under favorable and drought-stressed conditions, respectively, for every degree increase in temperature on days when the temperature surpasses 30 °C (Tesfaye et al., 2017), whereas under combined drought and heat, yield may be reduced by up to 40% (Lobell et al., 2011). Maize production in Africa is expected to be affected, and about 40% of the maize-growing area in Africa is already experiencing periodic drought stress (Fisher et al., 2015). Furthermore, climate change might not only cause frequent droughts and heat waves but also increase pest and disease incidence in both livestock and crops (IPCC, 2013). As temperature increases within optimal range of development, insect metabolism and consumption rates increase. This makes them develop faster and larger, reproduce faster, and suffer less mortality (Bentz et al., 2019; Ngumbi, 2020). For example, the optimal temperature for egg-to-adult development for fall armyworm (FAW) [*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)] was in the range of 26–30 °C, and the larval development was fastest at 30 °C (Du Plessis et al., 2020). Similarly, the egg, larval, and pupal development time of FAW decreased remarkably as the temperature increased from 19 to 31 °C (Huang et al., 2021). A model predicts that a 2 °C rise in average global surface temperature would increase maize yield losses by 31%, on average, owing to pest pressure, which would mean an annual loss of 62 Tg (Deutsch et al., 2018).

Currently, maize production in Africa, Asia, and the Near East is facing a serious menace from this invasive insect pest, FAW. With a reported host range of 353 plant species, FAW is a polyphagous pest native to the tropical and subtropical Americas, wreaking havoc on major staple and cash crops including maize, rice (*Oryza sativa* L.), sorghum [*Sorghum bicolor* (L.) Moench], sugarcane (*Saccharum officinarum* L.), upland cotton (*Gossypium hirsutum* L.), soybean [*Glycine max* (L.) Merr.], and peanut (*Arachis hypogaea* L.) (Day et al., 2017; Johnson, 1987; Montezano et al., 2018; Sparks, 1979). FAW attacks maize at virtually every developmental stage. Damage caused by FAW to ears also increases aflatoxin contamination of the grains by exposing the ear to mycotoxin-producing fungi and making it unusable (FAO, 2020; Williams et al., 2018). FAW has been documented to inflict significant maize damage in the Americas, with yield losses of up to 34% in Brazil (Lima et al., 2010), 40% in Honduras (Wyckhuys & O'Neil, 2006), and 72% in Argentina (Murúa et al., 2006). Outside of its native range, FAW was first detected in central and western Africa in 2016 (Goergen et al., 2016), thereafter, within 2 yr, it spread rapidly in sub-Saharan Africa (Early et al., 2018). Subsequently, it invaded the Asian continent: India in 2018, followed by Bangladesh, Sri Lanka, and Thailand (FAO, 2020; Ganiger et al., 2018; Sharanabas-

Core Ideas

- Current maize production in Africa and Asia is under serious threat from fall armyworm (FAW).
- There is a strong need for deploying host-plant resistance traits against FAW in maize.
- Maize diversity with reported resistance to FAW and their underlying mechanisms are summarized.
- An empirical prebreeding scheme for facilitating the development of FAW resistance maize is proposed.

appa et al., 2018). As of October 2021, FAW has invaded 76 countries (Africa, 47; Asia, 23; Oceania, 6) outside its native range (CABI, 2021). According to a model based on bioclimatic variables, there is a tremendous climatic potential for further spread of FAW, with a possible increase of 12–44% in the future, primarily around the United States–Canada border, in sub-Saharan Africa, and in central Europe (Zacarias, 2020). Food insecurity and rural poverty may worsen as a result of FAW's rapid spread and capacity to cause crop damage (FAO, 2020). Day et al. (2017) estimated that in just 12 of Africa's maize-cultivating countries, FAW can cause 8.3–20.6 Tg maize yield losses per year (worth US\$2.5–6.2 billion) in the absence of any control measures, which is sufficient to feed 40–100 million people (FAO, 2020). In addition, Eschen et al. (2021) reported that the total predicted yearly cost of FAW to agriculture in Africa might reach US\$9.4 billion. In the Rangareddy district of Telangana, India, maize yield losses attributable to FAW were estimated to be 33% (Balla et al., 2019), whereas in Dehong prefecture of China, the economic loss caused by FAW to maize production in 2019 was around 18.5 million Yuan based on a householder survey (Wan et al., in press).

As FAW is now well established in much of Africa and Asia, there is a strong call for the development and adoption of cost-effective, eco-friendly, and sustainable control strategies such as integrated pest management (IPM). The IPM strategy for FAW control would include a variety of measures like host-plant resistance (HPR), biological control, agroecological methods, and eco-friendly pesticides (Harrison et al., 2019; Kasoma et al., 2021; Matova et al., 2020; Njuguna et al., 2021; Prasanna et al., 2018). However, despite harm to the environment and health of the growers and consumers, synthetic insecticides have been broadly used by growers to control FAW in conventional farming systems in southwestern China (Wan et al., in press; Yang et al., 2021). Kumela et al. (2019) reported that in Ethiopia and Kenya, farmers use synthetic insecticides, plant extracts, handpicking of larvae, and putting soil in corn whorls as control methods for FAW. Similarly, Tambo et al. (2020) found that pesticide

spraying and handpicking of larvae were the most common control methods adopted by farmers in Zambia and Ghana. These findings showed there was an increasing trend of pesticide usage against FAW, but before the arrival of FAW most of the smallholding maize farmers in Africa used few or no chemical insecticides and majority used cultural control methods to manage insect pests (Hruska, 2019). In addition, most of the cheapest and broadly used pesticides in Africa (e.g. organophosphates and pyrethroids-pyrethrins) are categorized as broad-spectrum chemical insecticides to which FAW has developed resistance in the Americas (Day et al., 2017), and their use would suppress natural enemies of FAW and their action on FAW populations (Harrison et al., 2019).

Hence, there is a strong incentive to develop and introduce locally adapted IPM programs with greater emphasis on biological alternatives in the newly invaded areas (Guo et al., 2020). Moreover, most farmers in America affected by FAW have large-scale farm operations, whereas in Africa and Asia most of the maize farmers are smallholders; therefore, local contexts with social, economic, and cultural components should be considered when developing locally customized IPM interventions (Hruska, 2019; Njuguna et al., 2021). For example, pest-resistant transgenic crops are the dominating strategy against FAW in Brazil (Burtet et al., 2017), but its application, at least in the near term, will be limited in Africa, as few countries have approved the use of transgenic crops there. The price of transgenic maize seeds, inadequate suitable supply chain, and lack of financial incentive for smallholders to cultivate such maize (owing to low and fluctuating prices) (FAO, 2018) may also slow the uptake of transgenic maize (Baudron et al., 2019). A study in Brazil revealed that most of the Bt maize hybrids had lost resistance to FAW in just 3 yr after their release (Fatoretto et al., 2017), except Bt maize having Vip3Aa20 (VIP: vegetative insecticidal protein), which remains effective (Burtet et al., 2017). Continuous expression of Bt proteins (generally governed by mono or oligo genes) in maize could impose strong selection pressure on targeted pest populations, facilitating the development of resistance (Cruz et al., 2012; Matova et al., 2020; Pogue, 2002). Therefore, deploying HPR, an important and critical pillar of IPM, may be sustainably effective against FAW particularly in Africa where the majority of farmers have smallholdings and limited access to safe and cost-effective FAW management solutions (Matova et al., 2020; Prasanna et al., 2018), but it should also be applicable in Asia.

So far, no commercial maize cultivars in sub-Saharan Africa have been reported as resistant to FAW, and FAW-resistance breeding is very limited there (Kasoma et al., 2021; Matova et al., 2020). However, many naturally occurring maize populations and germplasm showing resistance to FAW were identified in the Americas (Prasanna et al., 2018). This is partly because of the fact that many crops, including maize, have lost some of their defensive traits because of a trade-

off for yield during selective breeding (Bellota et al., 2013; de Lange et al., 2014; Rosenthal & Dirzo, 1997). A genetic bottleneck has resulted from the extensive usage of modern and improved cultivars, resulting in the reduction of crop and allelic diversity (Peroni & Hanazaki, 2002; Tsegaye & Berg, 2007). As far as HPR is concerned, exploring crop genetic resources is vital, as they are the usual sources of novel alleles for various stress-tolerance traits (FAO, 2015). Crop wild relatives (CWRs), in general, are a potential source of novel alleles for crop improvement, such as abiotic and biotic tolerance, thus increasing yield stability (Maxted et al., 2012). Therefore, Matova et al. (2020) proposed to evaluate new and old commercial cultivars, breeding populations, and lines for FAW resistance. Furthermore, Kasoma et al. (2021) suggested that combination of participatory rural appraisal based prebreeding and hybrid breeding activities using conventional and next-generation sequencing techniques would be pivotal for sustainable management of FAW in maize in Africa. Based on the previous reviews on FAW resistance maize breeding made by Kasoma et al. (2021) and Matova et al. (2020), we have further summarized the natural resistance in landraces, native populations, germplasm lines, and CWRs of maize against FAW as well as the related mechanisms of resistance. The purpose of this review was to provide detailed information on the availability and use of diverse maize landraces, native germplasm, and CWRs to develop next-generation FAW-resistant commercial maize cultivars in the context of global warming. A conceptual framework of prebreeding for FAW resistance traits and their introgression into commercial cultivars is also illustrated.

2 | FAW RESISTANCE IN MAIZE LANDRACES AND OTHER NATIVE GERMPLASM

Landraces are dynamic populations with prehistoric origins, known to be genetically diverse and lacking formal crop improvement. They are locally adapted to various climatic conditions, preserved and selected by traditional farmers to meet domestic needs, and mostly produced on marginal lands with limited inputs. Hence, they may serve as genetic resources for various adaptation traits (Ficiciyan et al., 2018; Teshome et al., 1997; Villa et al., 2005). Maize landraces display extraordinary diversity and environmental tolerance in the region of their origin and thrive in a wide range of climatic conditions. In Mexico, 59 genetically distinct maize races have been described and well characterized (Sanchez et al., 2000; Ureta et al., 2012) and a large number of cultivars also are maintained by farmers (Hellin et al., 2014). Previous studies have already found many maize landraces, natives, and other germplasm with considerable resistance to FAW (Table 1).

TABLE 1 Maize landraces, native, and other population germplasm resistant or partially resistant to fall armyworm (FAW) damage

| Maize germplasm | Resistance traits or mechanisms | References |
|---|--|--|
| Antigua Gpo2 | <i>mir-1</i> CP, antibiosis, etc. | Welcker et al. (1997) |
| Antigua 2D-118 | Nonpreference | Wiseman et al. (1981) |
| CMS 14C | Antibiosis & nonpreference | Viana and Guimaraes (1997) |
| CMS 23 | – | Viana & Guimaraes (1997) |
| CMS 24 | – | Viana & Guimaraes (1997) |
| Cuba Honduras 46-J | Least leaf sheath damage | Wiseman et al. (1967) |
| Eto Amarillo | Least leaf sheath damage | Wiseman et al. (1967) |
| FAW #1 selection | Seedling resistance | Wiseman et al. (1966) |
| FAW GCA | – | CIMMYT (1998) |
| FAW Tuxpeno | – | CIMMYT (1998) |
| FAW Non-Tuxpeno | – | CIMMYT (1998) |
| GT-FAWCC (C5) | Nonpreference & antibiosis | Wiseman et al. (1996) Widstrom et al. (1993) |
| MpSWCB-4 | Antibiosis & nonpreference | Scott and Davis (1981b), Wiseman et al. (1981) |
| Pool 16 | – | Kasoma et al. (2020a) |
| Perola (Brazilian landrace) | Oviposition, nonpreference & antibiosis | Nogueira et al. (2019) |
| PopG (C2) | Intermediate resistance | Welcker et al. (1997) |
| Population 590 (multiple borer resistant) | – | Benson (1986) Mihm et al. (1988) |
| Population 390 (multiple insect-resistant tropical) | – | Mihm (1985) Mihm et al. (1988) |
| Pool 26 sequia | Tolerant to drought & FAW | CIMMYT (1998) |
| PR030-Doce Flor da Serra & MG 161-Branco Doce (sweet corn landraces) | Antibiosis & impaired insect development | Crubelati-Mulati et al. (2019) |
| Zapalote Chico 2451F (derived from Zapalote Chico Oaxaca Gpo. 35 landrace) | Maysin | Byrne et al. (1996), Widstrom et al. (2003), Waiss et al. (1979) |
| Zapalote Chico sh2 | Maysin and isoorientin | Widstrom et al. (2003), Nuessly et al. (2007) |
| ZM 4236 | – | Kasoma et al. (2020a) |
| ZM 7114 | – | Kasoma et al. (2020a) |

Generally, HPR operates by three mechanisms: antibiosis, antixenosis, and tolerance. Antibiosis is characterized by host plants adversely affecting the insect, usually reducing survival, development, and fecundity. Antixenosis describes the nonpreference or avoidance of a host by the pest when a plant lacks the usual attractive elements or traits for oviposition, feeding, and shelter. Tolerance refers to a host plant's or cultivar's ability to yield well despite pest infestations that severely harm and lower the yield of susceptible host plants (Painter, 1951). Fall armyworm damage to maize germplasm is usually scored according to the Davis scale (Davis et al., 1992), which ranges from 0 (no visible damage) to 9 (whorl and furl leaves almost totally destroyed) based on leaf and whorl damage (Toepfer et al., 2021). According to Prasanna et al. (2018), most native or naturally occurring resistance is polygenic, exhibits partial resistance, and scores around 3–5

on the Davis scale, whereas transgenic lines exhibit scores of 1–2 (Figure 1). Peairs (1977) found FAW resistance in tropical Mexican maize populations, whereas Smith (1982) identified FAW resistance related to antibiosis and antixenosis in some Caribbean maize germplasm and a moderate level of resistance in selected Tuxpeño germplasm lines. The genetic basis for FAW resistance in Caribbean germplasm and Tuxpeño was found to be polygenic, and variation was primarily attributable to additive gene action (Widstrom et al., 1972; William et al., 1978; Smith, 1982); however, both additive and nonadditive gene action were also found in some populations (Ramírez et al., 2018; del Pilar Alvarez & de Miranda Filho, 2002). Furthermore, Williams and Davis (1997) found that resistant genotypes had thicker cuticles and epidermal cell walls as well as high fiber and low total protein content in their leaves. Tamiru et al. (2011) observed that maize

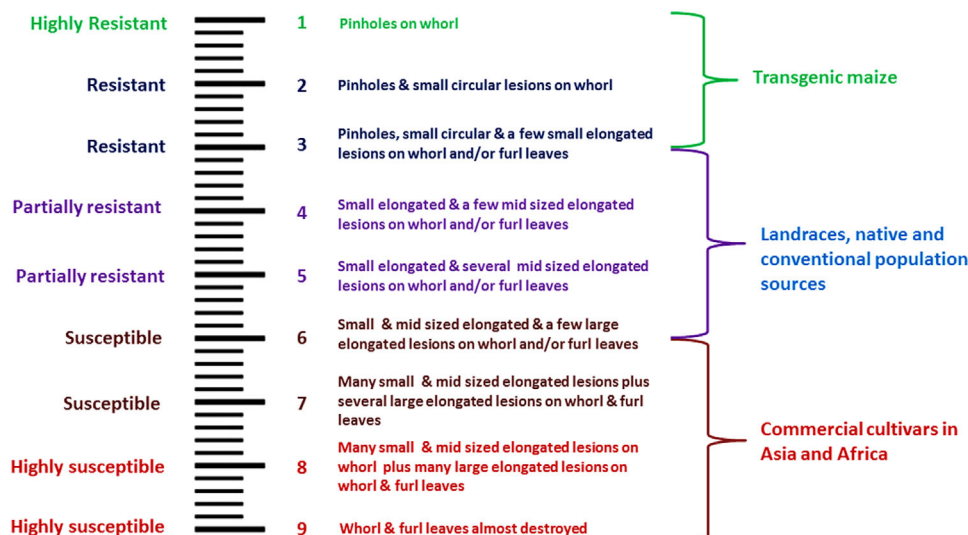


FIGURE 1 Resistance levels of maize germplasm according to the modified Davis scale [adapted and modified from Prasanna et al. (2018), Prasanna (2019), and Toepfer et al. (2021)]

landraces released herbivore-induced plant volatiles against egg deposition of *Chilo partellus* that attracted parasitic wasps, but this phenomenon was completely absent in commercial maize hybrids.

Further, in close alternative hosts of FAW like sorghum, many landraces of the Maicillo group (San Bernardo III, Pina-61, Hilate-179, and Lerdo-104) from Honduras were found to possess antibiosis against FAW, which was thought to have developed as a result of increased selection pressure on the Maicillo landraces as a result of intercropping with maize (Meckenstock et al., 1991). Therefore, native genetic resources could be a potential nontransgenic source of FAW resistance in maize. Initially, the resistance of maize to FAW was found in an Antigua race (Wiseman et al., 1966, 1967). Wiseman et al. (1966) reported that FAW #1, a selection from the Antigua 2D × (B10 × B14) showed good resistance to FAW at seedling stages. Latin American lines Cuba Honduras 46-J and Eto Amarillo were reportedly less damaged among 81 lines screened for FAW damage (Wiseman et al., 1967). A bulked native population named PopG, collected from Guadeloupe Archipelago, showed substantial genetic variation for resistance to FAW feeding after two cycles of selection [PopG (C2)] and showed an intermediate level of resistance against FAW feeding (Welcker et al., 1997). An open-pollinated cultivar population named ‘CMS 14C’ developed by 4–5 cycles of selection at the Brazilian Agricultural Research Corporation Maize-Improvement Program at the National Center for Maize and Sorghum Research, Brazil, was shown to possess antibiosis type of resistance to FAW (FAW took longer to develop into pupa and adult and had low larval and pupal weights) and nonpreference, whereas two other populations, CMS 23 and CMS 24, were also found to be resistant based on leaf damage screening at the Brazil-

ian Agricultural Research Corporation (Viana & Guimaraes, 1997).

Zapalote Chico 2451F (ZC-2451F) is an another improved source of resistance to FAW with less ear damage (Nuessly et al., 2007; Widstrom et al., 2003; Wiseman & Widstrom, 1986) that was derived from Zapalote Chico landrace Oaxaca Gpo. 35 through three cycles of recurrent mass selection and was found to be resistant to FAW and silk fly (*Euxesta stigmatias* Loew). Its resistance was comparable to the level of GSS 0966, a Cry 1A(b) construct Bt test hybrid (Widstrom et al., 2003). Waiss et al. (1979) reported that part of the Zapalote Chico silk's resistance is linked to a flavonol-C-glycoside compound known as maysin. Maysin, which is generated in flavonoid biosynthetic pathways, confers antibiosis-based resistance to silk feeding (Byrne et al., 1996). Meyer et al. (2007) reported that candidate genes *p* (pericarp color), *c2* (colorless2), and *whp1* (white pollen1) control maysin synthesis in maize. Another line named shrunken Zapalote Chico (ZC-sh2), derived from Zapalote Chico 2451, was also found to be resistant to FAW damage (Widstrom et al., 2003). The maysin and isoorientin (an analog of maysin) concentrations in nonpollinated corn silks were found to be higher in ZC-sh2 than in Zapalote Chico 2451, GSS-0996, and Primetime (susceptible sweet corn to FAW) (Nuessly et al., 2007).

Both Zapalote Chico 2451 and ZC-sh2 genotypes performed as well as Bt-GSS-0966 hybrid did against FAW and better than Bt-GSS-0966 hybrid against silk fly (Nuessly et al., 2007). Furthermore, landrace Doce Flor da Serra (sweet corn) was observed to exhibit antibiosis to FAW, showed reduced leaf area consumption, and impeded insect development (Crubelati-Mulati et al., 2019). Nogueira et al. (2019) observed that a Brazilian landrace named perola was least

preferred by FAW for oviposition, whereas larvae fed with perola consumed a lesser amount of leaves, took longer to develop, and had reduced survival rates until the end of the pupal stage. Compared with other Brazilian germplasm, this landrace was also found to be resistant under field conditions with less leaf injury and fewer larvae in infested plants (Costa et al., 2020). Interestingly, two landraces (ZM 4236 and ZM 7114) and one open-pollinated cultivar (Pool 16) collected from Zambia were selected for their desirable agromorphological traits and FAW resistance for developing maize cultivars suitable for local conditions (Kasoma et al., 2020a).

In 1984, the CIMMYT began developing a new maize population and improved its resistance to major pests of maize, which resulted in 'multiple borer resistance population 590' formed predominantly from subtropical and temperate germplasm that was reported to have high or moderate resistance to FAW, European corn borer (*Ostrinia nubilalis*), southwestern corn borer (*Diatraea grandiosella*), sugarcane borer (*D. saccharalis* Fabricius), and spotted stem borer (*Chilo partellus*) (Benson, 1986; Mihm et al., 1988). Similarly, another population named 'multiple insect-resistant tropical (MIRT) population 390' was also developed by CIMMYT for lowland humid tropics, which had a high level of resistance to major borers, armyworms (resistance mostly derived from Antigua collections), and maize streak virus (Mihm, 1985; Mihm et al., 1988). Many other populations, including FAW GCA, FAW Tuxpeno, FAW Non-Tuxpeno, and Pool 26 sequia, were improved for FAW resistance, within which pool 26 sequia was reported to be tolerant to both drought and FAW (CIMMYT, 1998).

A number of FAW-resistant lines derived from various native and other germplasm were developed by Mississippi State Agricultural and Forestry Experiment Station, USDA-ARS, CIMMYT, Mexico, and at other centers (Table 2), and some of them were used as resistant checks in FAW damage scoring. Two experimental lines, 100-R-3 and 116-B-10, derived from Peruvian landrace populations PI 503849 and PI 503720 (both resistant to European corn borer), respectively, in combination with B94 inbred line, were resistant to FAW leaf feeding (Abel et al., 2000). In a study using USDA-ARS germplasm enhancement of maize germplasm, three lines, two (GEMS-0100 and entry 15) of which derived from Dente Branco and mixed creole races, respectively, were found to be resistant to FAW based on leaf injury and predatory survey (Ni et al., 2014).

Two inbred lines, Mp708 and Mp704, derived from Antiguan germplasm, were resistant to FAW (Williams & Davis, 1982; Williams et al., 1990), and in these inbreds, a distinct 33-kD cysteine proteinase, which is encoded by the *mir1* gene (Pechan et al., 1999), accumulates in reaction to FAW larval feeding in the whorls (Jiang et al., 1995; Pechan et al., 2000). Lower levels of *mir1-cp* transcripts were also detected before herbivory in Mp 708 (Shivaji et al., 2010).

In addition, Mp708 and Mp704 had more crude fiber in the whorls as well as more hemicellulose (with high cross-linking) and more cellulose than susceptible lines Ab24E and SC229 (Hedin et al., 1996). A significantly thicker leaf with thicker lower and upper cell wall complexes was observed in Mp708 compared with FAW-susceptible lines (Davis et al., 1995). In a few FAW-resistant maize cultivars, antixenosis traits, including dense surface wax (Yang et al., 1991, 1993) and dense vascular bundles (Davis et al., 1995), were also observed. Mp708, a promising FAW-resistant line, primarily derived from Mp704 × Tx601, is used as a resistant check in many breeding programs (Williams et al., 1990). Various traits operating in Mp708 for FAW resistance have been explored and used. Additionally, in Mp708, *mir1-CP* (*mir1*-Cysteine proteinase) rapidly accumulates in vascular tissues (Lopez et al., 2007) in response to FAW herbivory, which attacks and permeates the peritrophic matrix (structure surrounding the food bolus) of insect and inhibits caterpillar growth (Mohan et al., 2008). Further, Mp708 was found to have approximately 3× higher levels of jasmonic acid (JA) before FAW herbivory as well as high constitutive levels of JA precursor, 12-oxo-phytodienoic acid, and increased constitutive expression of JA signaling and biosynthetic genes (*PLD*, *ZmLOX 1*, *ZmLOX 3*, *AOS*, and *OPR 2*) compared with susceptible inbred Tx601, implying that Mp708 might be on constant defense against FAW (Shivaji et al., 2010).

Furthermore, Chen et al. (2009) explained that susceptibility of Ab24E to FAW was due to increased protein/total non-structural carbohydrates ratio, reduced production of induced defensive compounds in response to FAW herbivory, and increased amounts of constitutive nondefensive proteins. Resistance in Mp 708 was due to increased defensive proteins against FAW herbivory in addition to reduced protein/total nonstructural carbohydrates ratio, whereas, in FAW 7050 line [a partial inbred derived from FAWCC(C5)] resistance was due to elevated defensive proteins (Chen et al., 2009). Additionally, after FAW herbivory, increased levels of glucose were detected in both Mp 708 and FAW 7050, with no changes in starch content, implying that FAW feeding could have inhibited glucose conversion to certain chemicals in these lines but not to total protein content (Chen et al., 2009). Furthermore, the terpenoid volatile (*E*)-caryophyllene associated with resistance was emitted continuously in Mp708, whereas a greater number of terpene synthase 23 (*tps23*) transcripts, which encode for (*E*)-caryophyllene, was observed in FAW-fed samples of Mp708 and Tx601 compared with unfed (control) samples (Smith et al., 2012). In addition, (*E*)-caryophyllene emission was observed to attract natural enemies of maize insect pests (Köllner et al., 2008). An increased level of hydrogen peroxide (secondary messenger in JA-mediated defense signaling) and increased number of nicotinamide adenine dinucleotide phosphate oxidase transcripts, which catalyze superoxide production, were comparatively

TABLE 2 Fall armyworm (FAW)-resistant inbreds or lines derived from native and other maize germplasm

| Inbred or line | Derived from | Resistant traits or mechanisms | References |
|----------------------|--|--|---|
| 100-R-3 | Peruvian landrace PI 503849 | Unidentified | Abel et al. (2000) |
| 116-B-10 | Peruvian landrace PI 503720 | Unidentified | Abel et al. (2000) |
| CML67 | Antigua Gpo. 2 | Resistant to Southwestern corn borer & FAW | CIMMYT (1998), Kumar (2002), López et al. (2005) |
| CML70 | Antigua Gpo. 2 | – | CIMMYT (1998) |
| CML71 | Antigua Gpo. 2 | – | CIMMYT (1998) |
| CML139 | Mp78:518 | Resistant or tolerant to Southwestern corn borer & FAW | CIMMYT (1998) |
| CML444B | – | – | Kasoma et al. (2020b) |
| CML491 | – | – | Kasoma et al. (2020b) |
| CZL1310c | – | – | Kasoma et al. (2020b) |
| CZL15220 | – | – | Kasoma et al. (2020b) |
| FAW 7061 | GT-FAWCC (C5) population | Less leaf injury | Ni et al. (2011) |
| FAW 1382 | – | Resistant to FAW and low aflatoxin | Scully et al. (2012) |
| FAW 1430 | – | Resistant to FAW and low aflatoxin | Scully et al. (2012) |
| FAW 7050 | GT-FAWCC (C5) population | Elevated defensive proteins in response to FAW herbivory | Chen et al. (2009) |
| GEMS-0100 & Entry 15 | Dente Branco and mixed creole races respectively | Less leaf injury and more predators | Ni et al. (2014) |
| Mp 496 | Antigua Gpo. 2 | – | Scott and Davis (1981) |
| Mp 701 | Antigua Gpo. 1 & Antigua Gpo. 2 | – | Scott et al. (1982) |
| Mp 702 | Antigua Gpo. 2 & Republica Dominica Gpo. 1 | – | Scott et al. (1982) |
| Mp 703 | Antigua Gpo. 1 & Antigua Gpo. 2 | – | Williams and Davis (1980) |
| Mp 704 | Mp 496 & Republica Dominica Gpo. 1 | <i>mir1</i> -Cysteine proteinase (<i>mir1</i> -CP); higher content of crude fiber, hemicellulose, and cellulose in whorls | Pechan et al. (1999), Pechan et al. (2000), Williams and Davis (1982), Williams & Davis (1982), Williams et al. (1990) |
| Mp 705, 706 & 707 | MpSWCB-4(1) | – | Williams and Davis (1984), Williams et al. (2018) |
| Mp 708 | Mp704 and Tx601 | (E)- β -caryophyllene; <i>mir1</i> -CP; Oxophytodienoic acid (OPDA); low protein/total nonstructural carbohydrates ratio; thicker leaf; higher content of crude fiber, hemicellulose, and cellulose in whorls; thicker lower and upper cell wall complexes; constitutive expression of jasmonic acid genes | Chen et al. (2009), Davis et al. (1995), Shivaji et al. (2010), Smith et al. (2012), Williams et al. (1990), Williams et al. (2018) |
| Mp 713 | Multiple borer resistant populations | – | Williams and Davis (2000), Williams et al. (2018) |
| Mp 714 | GT-DDSA (C5) population | – | Williams & Davis (2000), Williams et al. (2018) |
| Mp 716 | Mp708 & Mp78:518 | – | Williams and Davis (2002), Williams et al. (2018) |
| TL1512847 | – | – | Kasoma et al. (2020b) |
| Xi502 | – | High induced defensive transcriptomic signatures, higher sustained jasmonates accumulation, and higher levels of benzoxazinoids | Malook et al. (2021) |

higher in Mp708 before and after FAW feeding than in susceptible inbred Tx601 (Shivaji et al., 2010). Similarly, Malook et al. (2021) reported that Chinese inbred Xi502 showed resistance against FAW; and FAW feeding induced more defensive transcriptomic signatures, higher sustained jasmonates accumulation, and higher levels of benzoxazinoids in Xi502 than B73. Kasoma et al. (2020b) selected inbred lines CZL1310c, CML444-B, CZL15220, TL1512847, and CML491 with partial resistance to FAW, earliness to flowering, and high grain yield in an evaluation trial, which can be used in developing maize breeding populations with both partial resistance to FAW and yield gains for tropical and subtropical regions. As FAW feeding could expose ears to fungal infection, like *Aspergillus flavus* (produces aflatoxin), three single-cross hybrids (Mp715 × Mp707, Mp715 × Mp716, and Mp719 × Mp716) showed resistance to both FAW infestation and aflatoxin accumulation (Williams et al., 2018).

3 | CROP-WILD RELATIVES OF MAIZE AND THEIR RESISTANCE TO FAW

Crop wild relatives, which comprise crop progenitors as well as other species that are more or less closely related to them, are valuable genetic resources for plant breeders looking for specific alleles (Hajjar & Hodgkin, 2007). Present cultivars, unlike their wild relatives, have been primarily selected and bred for greater yield rather than for stress resistance, making them excellent food sources for pests (Bebber et al., 2014; Lindig-Cisneros et al., 2002; Rosenthal & Dirzo, 1997). A model proposed by Rosenthal and Dirzo (1997) regarding loss of defensive traits against herbivorous insects in four related taxa of maize states that an inverse relationship exists between investment on growth and reproduction (wild perennial teosinte < wild annual teosinte < landrace cultivars < modern cultivars) and defense against insects (wild perennial teosinte > wild annual teosinte > landrace cultivars > modern cultivars). Therefore, seeking novel alleles from CWRs and exploring FAW-defense mechanisms operating in CWRs of maize and incorporating them into modern cultivars with conventional population improvement strategies, assisted by molecular breeding methods, and with the help from robust biotechnological aids could play key roles in minimizing FAW losses. Till now, teosinte and *Tripsacum* are the most important and well-studied CWRs of maize for resistance to FAW (Table 3).

Indigenous to Mexico and Central America, including Nicaragua (Iltis & Benz, 2000), Guatemala (Wilkes, 1977), and Honduras (Standley, 1950), teosinte is known to release volatile organic compounds after herbivory (Gouinguéné et al., 2001), which attract more beneficial insects compared with maize (de Lange et al., 2014). Hence, restoring and improving such important parasitoid attraction strate-

gies in cultivated plants could improve natural pest control. Szczepaniec et al. (2012) found that expression of herbivore-resistance genes, wound-inducible protein (*wip1*), maize protease inhibitor (*mpi*) (found to interfere with gut digestive enzymes), and pathogenesis-related protein (*PR-1*) was much greater in the balsas teosinte (*Z. mays* subsp. *parviglumis* H. H. Iltis & Doebley) than in maize against FAW herbivory, whereas in diploperennial teosinte (*Z. diploperennis* H. H. Iltis et al.) plants, high levels of chitinase, *mpi*, and *PR-1* genes were expressed after exposure to FAW. Furthermore, FAW larvae on wild maize were 15–20% smaller than those on cultivated maize (Szczepaniec et al., 2012). Likewise, FAW growth was hampered by leaf extracts and residual fiber from diploperennial teosinte, which reduced the length and width of pupae and increased their cumulative mortality rate (Farias-Rivera et al., 2003).

Additionally, diploperennial teosinte was found to be resistant to several viruses to which most other *Zea* species were vulnerable (Nault, 1983), and it showed resistance to root parasite *Striga* spp. (Rich & Ejeta, 2008), which is known to have a strong impact on cereal cultivation in sub-Saharan Africa (Ejeta & Butler, 1993). When maize and balsas teosinte were compared for FAW infestation in the field, maize was infested 1.8× more frequently than balsas teosinte, whereas larval growth on maize was 1.2-fold higher than on balsas teosinte under laboratory conditions (Takahashi et al., 2012). Bernal et al. (2015) reported that in the field, superior performance of FAW larvae on maize over balsas teosinte might partly relate to the toughness of teosinte and higher parasitism and predation by natural enemies in balsas teosinte than maize. The variation in production of herbivore-induced plant volatiles (attracts natural enemies of herbivores) between maize and teosinte could be the possible reason for higher parasitism and predation in balsas teosinte than maize (Gouinguéné et al., 2001). These findings imply that crop domestication, selection, and development reduced the expression of maize *wip1* and other defense genes, thus increasing its vulnerability to FAW infestation. Identifying and defining loci responsible for improved herbivore tolerance in balsas teosinte could be important for breeding and genomic initiatives aimed at increasing the expression of insect pest-induced resistance in commercial maize (Degenhardt et al., 2009). Further, presence of more trichomes in maize CWRs reduced insect feeding and damage. As examples, perennial teosinte [*Z. perennis* (Hitchc.) Reeves & Mangelsd.] and balsas teosinte showed higher trichome density at the six-leaf stage compared with landraces, and, at the same time, significantly less FAW damage was seen in them (Moya-Raygoza, 2016). The locus promoting trichome (macrohair) initiation in the leaf blade was found to be maize *macrohairless 1* (*mhl1*) (Moose et al., 2004).

Tripsacum is another genus closely related to *Zea*, with 13 known species, extending from Massachusetts to Paraguay.

TABLE 3 Maize wild relatives showing resistance to fall armyworm

| Wild relatives | Resistance traits | References |
|----------------------------------|--|--|
| Teosinte | | |
| <i>Zea mays ssp. parviglumis</i> | <i>wip1</i> , <i>mpi</i> , <i>PR-1</i> are highly expressed, antibiosis, high leaf toughness, and trichome density | Bernal et al. (2015), Szczepaniec et al. (2012) |
| <i>Zea diploperennis</i> | <i>wip1</i> , Chitinase, and <i>PR-1</i> are highly expressed, antibiosis and leaf chemical constituents | Farias-Rivera et al. (2003), Szczepaniec et al. (2012) |
| <i>Zea perennis</i> | High trichome density on leaves | Moya-Raygoza (2016) |
| <i>Tripsacum</i> | | |
| <i>Tripsacum dactyloides</i> | Nonpreference and antibiosis | Wiseman et al. (1967), Wiseman and Davis (1979) |

One species of *Tripsacum*, eastern gamagrass [*T. dactyloides* (L.) L.], has been widely used to create intergeneric hybrids with maize (de Wet et al., 1981). In a preference study of FAW between *eastern gamagrass* and maize, *eastern gamagrass* was least preferred by FAW; it showed very little damage and FAW larvae were relatively small compared with those on antigua 2D-160-87 (Wiseman et al., 1967). In addition, Wiseman and Davis (1979) reported that no FAW egg masses or feeding occurred in various *Tripsacum* plots neither at the International Maize and Wheat Improvement Center (CIM-MYT) in Mexico nor at Tifton, GA, USA.

4 | PREBREEDING AND INTROGRESSION OF ALLELES FROM WILD RELATIVES FOR FAW RESISTANCE INTO ELITE MAIZE LINES

Genetic variability is an important prerequisite for selection and breeding. A narrow genetic base limits the possibilities to develop new cultivars for changing consumer demands and climatic conditions (Cairns et al., 2013; Pollak, 2003). For example, since the 1900s, farmers' crops have lost 75% of their genetic variation because of the use of genetically homogenous and high-yielding cultivars and hybrids (FAO, 1999). Likewise, in the United States, only six inbred lines, namely, Lancaster-type inbreds C103, Mo17, Oh43, and the Reid-type lines B37, B73, and A632, were mostly employed for hybrid development (Goodman, 2005). Similarly in China, the majority of the maize hybrids were developed from a limited number of inbreds such as Mo17, Huangzaosi, 330, E28, Dan340, and 478 (Li, 1998; Yu et al., 2007). This narrow genetic base of the commercial cultivars results in genetic vulnerability to pests and diseases (Marshall, 1977).

Therefore, broadening the genetic base of the modern cultivars through the use of CWRs and landraces would reduce genetic vulnerability. Crop-wild relatives were initially

identified as potential donors in breeding programs of major crops during the 1940s and 1950s (Plucknett et al., 1987). According to a survey by Hajjar and Hodgkin (2007) in 13 mandate crops of CGIAR institutes, >100 desired traits have been taken from CWRs, and nearly 80% of the derived traits were for pest and disease resistance. In maize, only traits for resistance to *Helminthosporium* and *Puccinia* disease were successfully transferred from *Tripsacum* species (Hajjar & Hodgkin, 2007). Nevertheless, there exists huge unexploited genetic and allelic diversity within the primary gene pool and CWRs of maize, which could be used for developing climate-resilient and stable-performing cultivars (Hellin et al., 2014).

Prebreeding is considered as an important operation between CWRs and their use (Haussmann et al., 2004; Sharma et al., 2013). According to McCouch (2013), a three-step strategy might be used for mining natural diversity: first, genotyping or fingerprinting the genetic stock conserved; second, phenotyping and evaluation for agronomic and desired traits across years; and third, creating an international database of both phenotypic and genotypic data for easy access. Though genotyping costs have reduced significantly, precision phenotyping to determine genetic potential of the landraces remains a challenge. Nevertheless, large-scale screening of underutilized and unutilized CWRs, landraces, and native populations of maize for FAW resistance, combined resistance to FAW and abiotic stresses, and agronomic traits would help to identify potential donors to tackle anticipated climate change. While screening for FAW resistance, it is important to consider not only foliar damage but also the level of ear and kernel damage (Feldmann et al., 2019). Developing a scoring scale based on combined leaf injury, ear and kernel damage can help predict the performance of lines with respect to yield. On the other hand, developing potential morphological, biochemical, and molecular markers for FAW resistance, based on extensive phenotyping (Figure 2), will further accelerate the identification of donor lines and their introgression (Sharma et al., 2008).

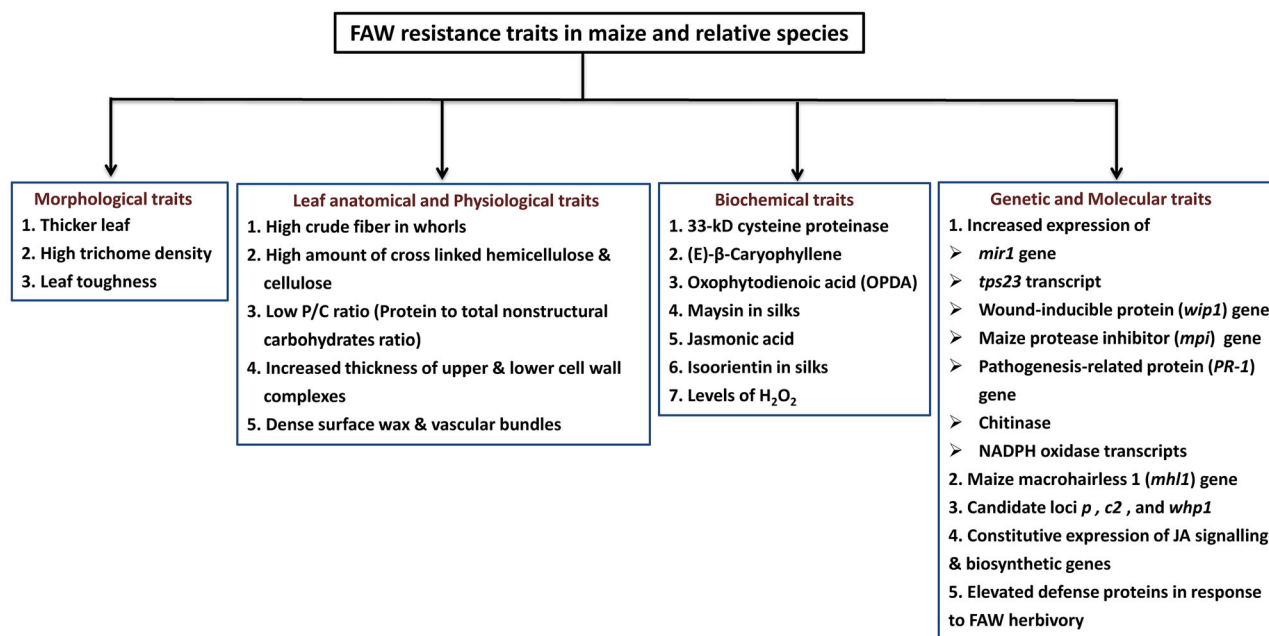


FIGURE 2 Potential morphological, physiological, biochemical and molecular traits for fall armyworm resistance in maize and relative species

Though prebreeding is a time-consuming process, its outputs could facilitate achieving short-term breeding goals (Smith & Duvick, 1989). Heterotic patterns of parental inbreds play key roles in hybrid development, and prebreeding helps to identify and categorize heterotic groups (Nass & Paterniani, 2000). Precision phenotyping of landrace stocks is a critical step that is hampered by the high genetic load of deleterious alleles (Hoisington et al., 1999). Because of high genetic load and absence of agronomically superior traits, evaluation for pest and disease resistance, and yield may incorrectly estimate the overall performance of a line. Thus, Longin and Reif (2014) suggested an approach where landraces are crossed to predefined elite lines with favorable alleles at relevant loci and their hybrids were evaluated, which can reveal the true genetic potential of the landrace in the elite genetic background. This strategy was previously used by Böhm et al. (2014) for evaluating European flint maize landraces. However, to fully utilize targeted wild diversity, an extensive evaluation of per se and test cross-performance of source germplasm for desired traits helps in the development of efficient prebreeding designs for introgression and minimizing transfer of unwanted genes (Sood et al., 2014). It should be noted that the allogamous nature of maize makes landrace populations heterozygous and heterogeneous with high intrapopulation variability, which could be efficiently harnessed by producing double haploids to rapidly stabilize variation without cumbersome recurrent selfing (Hölker et al., 2019). Furthermore, recessive lethal alleles that express in double haploids can also be eliminated at initial stages of line development (Charlesworth & Charlesworth, 1922). But this technology might not be a suitable option for large-scale

screening and breeding programs where funding is a constraint. Below, an empirical maize prebreeding and introgression scheme for FAW resistance is illustrated as a possible way forward (Figure 3).

Performing genome-wide studies using phenotypic and genotypic data should identify novel haplotypes for the trait of interest. Based on the discovery of haplotypes and nucleotide variations, nearly 70–80% of lines could be eliminated in any generation without multienvironmental evaluation (McCouch, 2013). Gorjanc et al. (2016) proposed a maize prebreeding approach for landrace populations based on genomic selection with discovery and improvement phases. The discovery phase includes producing training populations of landrace \times elite hybrids, selecting the best landraces by regressing (ridge regression) the testcross phenotypes on respective landrace genotype to predict estimated breeding value (EBV) for each seed of landrace, and choosing the best plant or seed within the selected landrace based on EBV. The improvement phase aims at further improving the selected seeds from the discovery stage by creating synthetic populations and considering EBV. Further, prebridging of germplasm can be initiated from the promising selected landraces to increase the frequency of desirable alleles, which can be later used for introgression into adapted lines. Maize has good cross-compatibility with other *Zea* species like annual teosinte but not with tetraploid perennial teosinte (Wilkes, 1977; Galinat, 1988). The natural hybridization between maize and teosintes is reported to be species dependent; for example, Mexican teosinte [*Z. mays* L. subsp. *mexicana* (Schröd.) H. H. Iltis] naturally hybridizes with maize at an extremely low rate (50%) (Ellstrand et al., 2007).

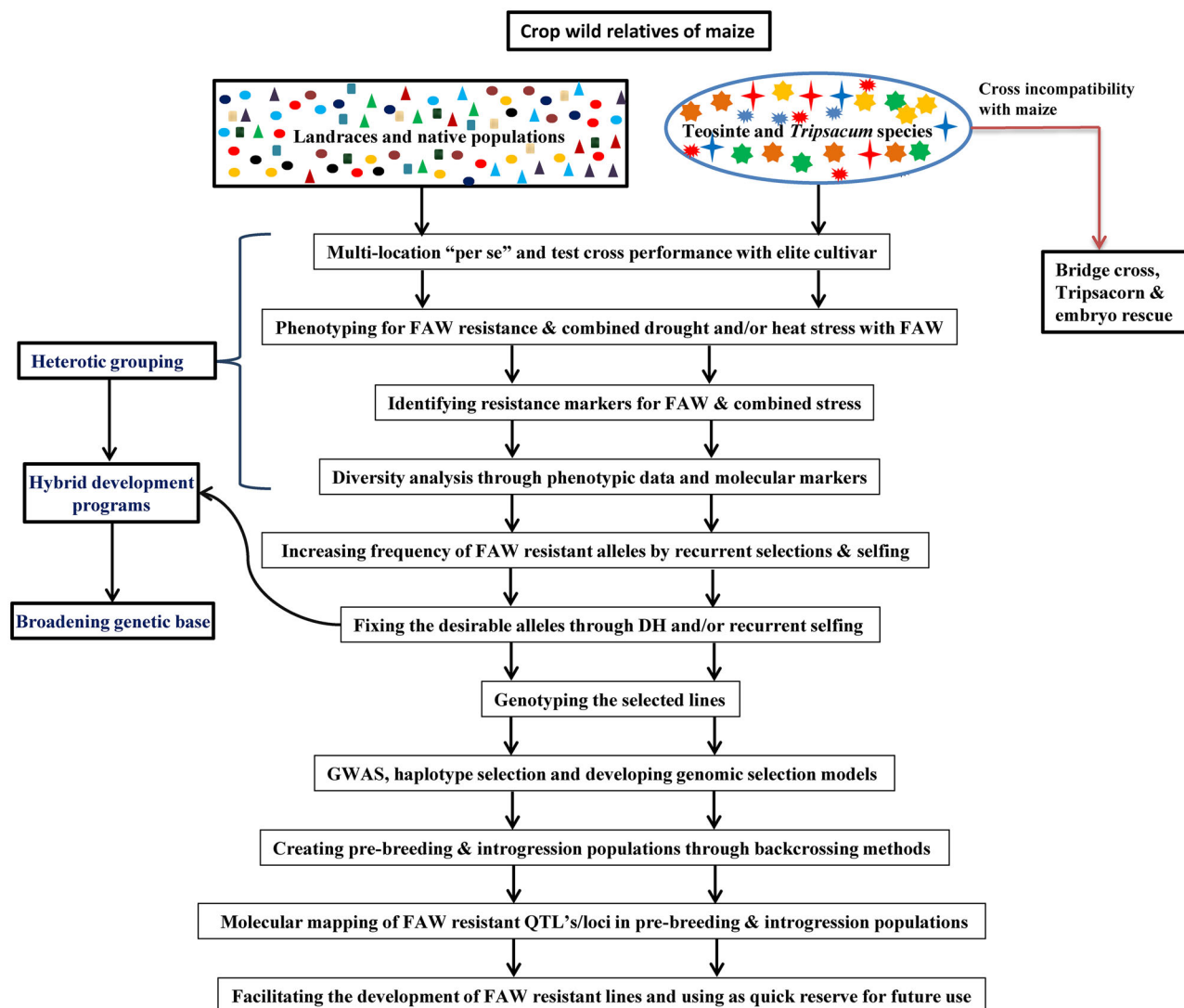


FIGURE 3 An empirical prebreeding scheme for facilitating the development of fall armyworm (FAW)-resistant maize lines

Cross-incompatibility between interspecifics and intergenerics limits the use of potential wild relatives; however, various techniques, such as embryo rescue and bridge cross, could help to overcome this limitation (Eubanks, 2006; Hajjar & Hodgkin, 2007). For example, eastern gamagrass generally produces sterile F_1 hybrids with maize (Eubanks, 1997). To transfer novel traits from eastern gamagrass to maize, Eubanks (2006) developed a technique where eastern gamagrass was crossed with diploperennial teosinte, to obtain fully fertile hybrid recombinant called 'tripsacorn,' which is cross-compatible with maize. This gamagrass–teosinte genetic bridge opens the way to transfer desired alleles from eastern gamagrass into maize. The tripsacorn is intended to provide pest and disease resistance and drought tolerance. Further, it has been claimed to possess features including apomixis, totipotency, perennialism, tolerance of harsh soil conditions, and adaptation to high-carbondioxide conditions (Eubanks, 2000).

In Mexico, farmers traditionally increase the genetic base (and allele exchange) of cultivars via a method called creolization, where two distinct maize populations are grown in adjacent farms to facilitate gene flow between commercial maize lines (Yumurtaci, 2015). Meanwhile, backcrossing is an effective and traditional method of transferring traits controlled by one or two genes; it can also be used to transfer quantitative traits (Nass & Paterniani, 2000). Prior identification of molecular markers through genome-wide associations and mapping studies facilitates using marker-assisted back crossing with foreground selection for FAW resistance and background selection for elite or adapted cultivar genome, which also minimizes linkage drag to some extent (Abdulmalik et al., 2017). Further, Prischmann et al. (2009) evaluated *Tripsacum*-introgressed maize lines for western corn rootworm tolerance, obtained from backcrossing tripsacorn to maize for nearly 14 generations including recurrent selection, backcrossing, and selfing, and a few lines were found to be

tolerant to western corn rootworm. Liu et al. (2016) developed 928 near-isogenic lines by pollinating B73 inbred line with pollen from 10 *Teosinte* accessions, followed by repeated backcrossing of F₁ populations of each accession to recurrent parent (B73) until BC₄, which was further pollinated with a haploid inducer to produce BC₄DH and simultaneously selfed to generate BC₄S2 and BC₄S4. The near-isogenic lines derived from this carry ~4% of the teosinte genome in the B73 background, which can be used for trait mapping studies. Iqbal et al. (2019) produced an autotetraploid maize–eastern gamagrass–perennial teosinte tri-genomic hybrid, which was backcrossed to Mo17 inbred for two generations and observed that 75% of the stained pollen of this backcross population was fertile, and this population could be further used for interspecific and intergeneric gene flow and trait mapping. Furthermore, exploiting mutation breeding and modern biotechnological tools, like the CRISPR-Cas9 system, can create additional genetic variation related to FAW resistance.

5 | CONCLUSIONS

Present and future predicted increases in temperature and drought conditions may increase FAW infestation and other crop pest damage. In a laboratory experiment using Mexican maize landraces, FAW developed faster at larval stage, and each life cycle stage was shorter at high temperatures (Díaz-Álvarez et al., 2020). A simulation study based on 4-yr FAW monitoring indicated that a one-degree increase in weekly mean temperature may nearly double FAW populations (Garcia et al., 2019). Meanwhile, drylands, which constitute 40% of the planet's land surface and are home to 2.5 billion people, are becoming more vulnerable to ongoing climate changes and have less buffering capacity against crop yield losses and climate-change-induced food insecurity (FAO, 2011; Nellemann et al., 2009; Shah et al., 2009). Hence, conserving and bioprospecting for wild novel alleles, which have been thriving under harsh climatic conditions with minimal human care, and introgressing them into elite lines to breed climate-smart and pest-resistant cultivars are essential for sustainable maize production and eco-friendly cultivation.

Further, breeding for resistance to insects should focus more on identifying new resistance genes and understanding the mechanisms of previously identified resistance-related traits (Smith, 2021). Developing rapid screening strategies for wild relatives to accelerate genetic gains with the help of molecular markers, genomic selection models, haplotype identification, and speed breeding might attract more researchers and stakeholders to use plant genetic resources more fully. As suggested by Tanksley and McCouch (1997), evaluating germplasm accessions only based on phenotypes is sometimes misleading in the case of quantitative traits. So, directly searching for desirable genes based on quanti-

tative trait loci from wild relatives and species mapped in prebreeding populations may unleash the full genetic potential of accessions. Exploring and developing new morphological, biochemical, and molecular diagnostic markers for FAW resistance and understanding their mechanisms could improve phenotyping and introgression. Meanwhile, CIMMYT has recently announced three FAW-tolerant hybrids (FAWTH2001–2003) for eastern and southern Africa, which showed significantly higher yields (7.05–8.59 t ha⁻¹) than commercial check hybrids (0.94–1.03 t ha⁻¹) under “no-choice” conditions with FAW artificial infestation in screen houses at Kiboko, Kenya (CIMMYT, 2021).

Prebreeding is a long and laborious process, and immediate products from prebreeding are uncommon. But creating bridging and introgression populations to improve allelic diversity in the primary gene pool might help in the efficient use of genetic resources. Further, insect pests are known to interact with abiotic stresses such as drought and heat. Hence, per se and testcross performance of germplasm under combined stresses of FAW, drought, and heat could help identify and characterize lines with novel alleles for anticipated global warming and FAW expansions. Increasing the expression of genes like *mir1*, *tps23*, *p*, *c2*, and *whp1* through molecular biology tools may elevate the host-plant resistance, but care should be taken to avoid developing resistance by FAW against these major genes. Linkage drag is a major disadvantage in introgression of genes from CWRs, but repeated backcrossing, testcross, and use of DNA markers help in breaking linkages between desired and deleterious alleles. Overall, exploring new resistant sources with desirable alleles and developing pest-resistant maize lines or populations should be an ongoing process for maintaining stable yields under future climate variations and pest outbreaks.

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AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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