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Fall armyworm (*Spodoptera frugiperda*) in Africa: insights into biology, ecology and impact on staple crops, food systems and management approaches

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The fall armyworm (FAW), *Spodoptera frugiperda*, is a polyphagous pest native to the American continent that was first detected in Africa in 2016, where it has since become a major constraint to agriculture. This species severely damages staple crops like maize, sorghum, and rice, threatening food security and the livelihoods of millions of smallholder farmers. Maize, the most vulnerable crop in sub-Saharan Africa, suffers significant annual losses due to the destructive impact of FAW, which affects agricultural productivity and overall rural economies. The pest displays complex biological and ecological patterns that are highly dependent on environmental factors, host plant availability, and natural enemy diversity, making control efforts challenging. This review explores the traits driving FAW's invasive success in Africa, summarizing key findings on its biology and ecology while outlining current management strategies. It underscores the importance of Integrated Pest Management (IPM), which includes cultural practices, biological control, mechanical/physical methods, host plant resistance, and judicious application of chemicals. Regular crop monitoring and surveillance principles are also discussed as prevention and early detection measures to mitigate FAW damage. Future directions emphasize the need for collaboration among stakeholders, including international research organizations, to effectively control FAW invasion. Given the economic risks of the FAW outbreak in Africa, adopting IPM solutions is crucial for reducing pesticide reliance and ensuring stable agricultural production. This review offers valuable insights into achieving this goal.

KEYWORDS

fall armyworm, integrated pest management, food security, crop loss, host plant resistance

1 Introduction

Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae), originally native to America, has rapidly spread across the African continent as a highly destructive polyphagous pest. Since its first reported occurrence on the continent in early 2016 (Goergen et al., 2016), FAW has severely impacted food security and the livelihoods of millions of smallholder farmers.

Studies have reported that FAW feeds on more than 350 plant species, primarily from the Poaceae, Asteraceae, and Fabaceae families (Wyckhuys and O'Neil, 2006; Badhai et al., 2020; Jing et al., 2021). Affected crops include major staples such as maize, sorghum, and rice, along with other important crops like cotton, sugarcane, cabbage, okra, beet, groundnut, soybean, alfalfa, onion, pearl millet, tomato, and potato, as well as pasture grasses (Day et al., 2017; Montezano et al., 2018; Akutse et al., 2020; Ahissou et al., 2022).

Despite its broad host range, FAW poses the greatest threat to maize in sub-Saharan Africa. This crop provides essential nutrients and supports livestock feed production across the region (Ekpa et al., 2019; Galani et al., 2022; Makuachukwu et al., 2022). With over 27 million hectares cultivated to feed more than 300 million people (Akutse et al., 2020), its reliability is crucial for food security. However, FAW infestations have led to significant yield losses, exacerbating agricultural instability, particularly for vulnerable populations.

In response, many farmers rely heavily on synthetic pesticides, which increase production costs and reduce farm income. The decline in production leads to higher food prices, limiting access to nutritious food. Additionally, FAW outbreaks disrupt agricultural supply chains, creating market uncertainties from farms to consumers in affected regions (Amusan and Olelekan, 2018; Banson et al., 2020).

The persistent and evolving nature of FAW infestations necessitates sustainable and resilient agricultural practices. This review provides a comprehensive analysis of FAW's biology, ecology, and its impact on agricultural production. It also evaluates current FAW management strategies and highlights integrated pest management (IPM) as a sustainable approach to enhance resilience within African agriculture. Furthermore, the review explores future directions, emphasizing a holistic and adaptive framework to protect crops, sustain livelihoods, and ensure food security across the African continent.

2 Knowledge of FAW biology and ecology

2.1 Adult behavior and dispersal

Spodoptera frugiperda adults are highly active at night, seeking mates and expanding into new territories while staying elusive during the day (Patel Sagarbhai et al., 2021). Research has confirmed that the males of FAW are more attracted to light than females (Vilarinho et al., 2011). Studies have also documented that FAW moths from the same generation can travel more than 500 kilometers before they are ready to lay their eggs (Prasanna et al., 2018; Acharya et al., 2020; Badhai et al., 2020). Male and female *S. frugiperda* are shown in Figures 1a, b, respectively.

2.2 Reproduction and oviposition

Oviposition typically occurs at night, with females laying inconspicuous egg clusters on the undersides of leaves to shield them from predators (Kasige et al., 2022). In some cases, the eggs are laid in layers and covered with scales for added protection. The upper leaf surface and whorl of host plants may also harbor some egg batches (Sharanabasappa et al., 2018). A single FAW female can lay an average of 1500 eggs, showing the high fecundity of the pest (Prasanna et al., 2018). FAW eggs hatch into tiny neonate larvae within 3 to 4 days at an average temperature of 28°C. Eggs of *S. frugiperda* are shown in Figure 1c.

2.3 Larval stage, damage and behavior

Soon after hatching, the larvae disperse from the site and infest nearby plants, often aided by the wind (Ortiz-Carreón et al., 2024). The larval stage of FAW consists of six instars and lasts about 14 days in warm conditions and up to 30 days in cooler weather (Prasanna et al., 2018). This stage is the damaging phase of FAW's life cycle (Sagar et al., 2020). Caterpillars primarily feed at night, but activity may also occur in the late evening or early morning (Schlemmer, 2018; Patel Sagarbhai et al., 2021). They feed on the leaves, the tender stem, the silks, and the ears of host plants. As they grow, their appetite intensifies, causing severe damage to host plants. Day et al. (2017) and Flanders et al. (2017) reported that the largest larvae can cause up to 77% of plant damage.

During the vegetative phase of the host crops, continuous feeding results in skeletonized leaves and heavily windowed whorls filled with larval frass (Goergen et al., 2016).

Cannibalism is an important biological phenomenon within the FAW larval stage. This intraspecific behavior frequently results in a significant reduction in larval numbers, leaving only one larva per plant. The eliminated cohabitant either succumbs to cannibalism or relocates to another plant where competition is less intense. According to Ren et al. (2020) and Ahissou et al. (2022), a high density of larvae on a maize plant suggests that the larvae have not yet reached advanced developmental stages. Chapman et al. (2000) observed that the larvae of FAW exhibit cannibalistic behavior from the third instar (L3) stage onward, allowing them to dominate interspecific competitors and reduce intraspecific competition. Larva of *S. frugiperda* is shown in Figure 1d.

2.4 Pupation and adult emergence

At the 6^{th} instar, larvae undergo metamorphosis within a woven silky cocoon. Pupation usually occurs in the soil (Figure 1e) at a depth of 2-8 cm (Ojumoola, 2021). During summer, the pupal stage

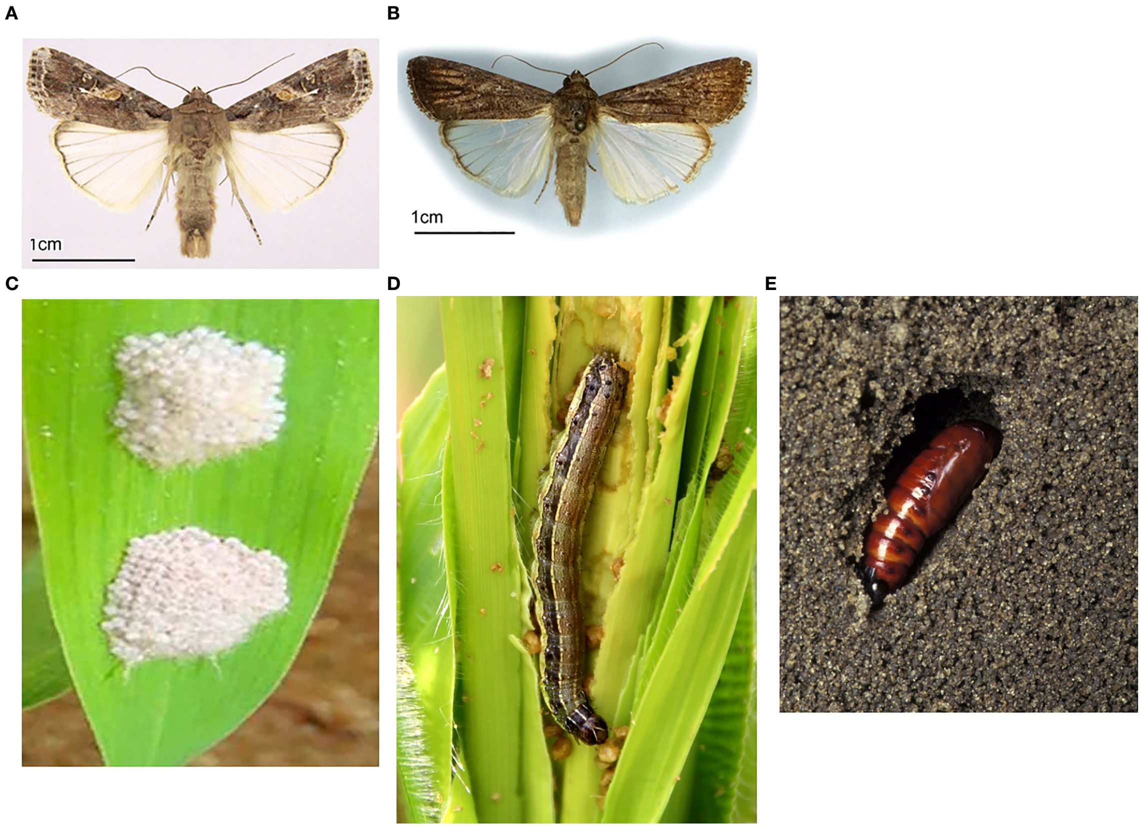

FIGURE 1
Life cycle stages of FAW: **(a)** Adult male, **(b)** Adult female, **(c)** Egg mass, and **(e)** Pupa.

lasts about 8-9 days. Studies conducted by Huang et al. (2021) and Montezano et al. (2018) revealed that the pupal developmental stage was shorter in female FAW than in males. After pupation, adult moths emerge and live for an average of 14 days (Prasanna et al., 2018). The total life cycle of FAW (a generation time) is about 30–40 days at 28°C but extends to approximately 55 days in cooler seasons (Prasanna et al., 2018; Ashok et al., 2020; Lekha et al., 2020). This is supported by Kenis et al. (2022), who found that the FAW life cycle can extend to 90 days at lower temperatures. Tendeng et al. (2019) found that the total cycle is between 22 and 28 days at 25°C with an average of 25 days in laboratory conditions.

2.5 Environmental factors influencing FAW development

Environmental factors such as temperature, relative humidity, soil moisture, and host plant characteristics (quality, diversity, availability and phenology), and the presence of natural enemies influence the development, distribution, abundance and population dynamics of FAW (Kenis et al., 2022).

Several studies have demonstrated the direct impact of temperature and relative humidity on various biological activities, including adult mating, egg production and hatching, larval development, pupal survival, and adult longevity (Table 1). Studies have indicated that FAW egg-to-adult development requires a specific number of degree days, with potential differences in developmental duration between sexes (Schlemmer, 2018; Malekera et al., 2022). Additionally, research has shown that larval and pupal development is optimal at temperatures ranging from 28 to 30°C, while lower temperatures tend to prolong the developmental period compared to warmer temperatures (Du Plessis et al., 2020). Schlemmer (2018) and Kumara et al. (2022) noted that temperatures around 30°C favor the growth and development of FAW, resulting in the fastest larval growth rate and the lowest mortality. Gergs and Baden (2021) found that lower ambient temperatures, combined with poor diet quality, increase the duration of FAW's life cycle.

Researchers typically observed the effect of temperature on pupal weight, noting the highest weights at 25°C and decreasing weights as temperatures deviate from this optimal point (Huang et al., 2021).

Rising temperatures due to global warming may increase the number of FAW generations, facilitating its spread and establishment in new regions (Garcia et al., 2018; Yan et al., 2022). In African climatic conditions, the pest reproduces continuously, producing up to 15 generations annually (Tendeng et al., 2019; Barkessa et al., 2024).

Studies have shown that relative humidity (RH) also plays an important role in FAW biology. According to He et al. (2021), an

TABLE 1 Influence of various temperatures on the mean development time (day), egg hatchability and larval mortality of fall armyworm.

Biological parameters	Temperature ranges						References
	18°c	22°c	25°c	30°c	32°c	35°c	
Egg (days)	–	–	–	2.2	–	2.8	Kumara et al. (2022)
	6.0	4.3	–	2.4	2	–	Savadatti et al. (2023)
	–	–		1.5	1.3	–	Malekera et al. (2022)
	6.4	4	–	2	2	–	Du Plessis et al. (2020)
	–	–	5.0	–	–	–	Tendeng et al. (2019)
1st instar larva (days)	–	–	3.3	–	–	–	Prasanna et al. (2018)
	–	–	–	2.3	–	2.8	Kumara et al. (2022)
	4.2	4.0	–	2.9	2.0	–	Savadatti et al. (2023)
	4.9	3.7		2.7	2.7	–	Du Plessis et al. (2020)
2nd instar larva (days)	–	–	1.7	–	–	–	Prasanna et al. (2018)
	–	–	–	1.9	–	2.4	Kumara et al. (2022)
	4.5	3.0	–	2.3	1.4	–	Savadatti et al. (2023)
	–	3.0	–	1.9	1.3	–	Du Plessis et al. (2020)
3rd instar larva (days)	–	–	1.5	–	–	–	Prasanna et al. (2018)
	–	–	–	2.1	–	2.7	Kumara et al. (2022)
	4.9	2.6	–	1.7	1.2	–	Savadatti et al. (2023)
	5.0	2.5	–	1.4	1	–	Du Plessis et al. (2020)
4th instar larva (days)	–	–	1.5	–	–	–	Prasanna et al. (2018)
	–	–	–	2.0	–	3.2	Kumara et al. (2022)
	5.2	2.7	–	1.7	1.6	–	Savadatti et al. (2023)
	5.2	2.9	–	1.6	1.5	–	Du Plessis et al. (2020)
5th instar larva (days)	–	–	2.0	–	–	–	Prasanna et al. (2018)
	–	–	–	2.8	–	4.0	Kumara et al. (2022)
	5.6	3.4	–	2.2	1.8	–	Savadatti et al. (2023)
	6.2	3.4	–	2.2	1,8	–	Du Plessis et al. (2020)
6th instar larva (days)	–		3.7	–	–	–	Prasanna et al. (2018)
	–	–	–	3.7	–	5.2	Kumara et al. (2022)
	6.7	5.0	–	2.2	2.0	–	Savadatti et al. (2023)
	8.6	5.1	–	2.0	2.1	–	Du Plessis et al. (2020)
Total larval stage (days)	–	–	–	14.8		20.3	Kumara et al. (2022)
	31.5	20.7	–	13.1	10.1	–	Savadatti et al. (2023)
	–		–	12.6	–	–	Malekera et al. (2022)
	34.4	–	–	11.4	10.5	–	Du Plessis et al. (2020)
	–	20.6	14.0	–	–	–	Tendeng et al. (2019)
Pupa (days)	–	–	–	8.6		5.8	Kumara et al. (2022)
	30.9	12.6	–	7.0	6.0	–	Savadatti et al. (2023)
	–	–	–	7.6	–	–	Malekera et al. (2022)

(Continued)

TABLE 1 Continued

Biological parameters	Temperature ranges						References
	18°c	22°c	25°c	30°c	32°c	35°c	
	30.7	17.1	–	9.0	7.8	–	Du Plessis et al. (2020)
	–	–	7.0	–	–	–	Tendeng et al. (2019)
	30.7	17.1	–	7.8	–	–	Schlemmer (2018)
Egg-adult (days)	–	–	–	36.1		34.5	Kumara et al. (2022)
	48.5	–	–	28.6	20.7	–	Savadatti et al. (2023)
	–	–	–	–	–	18.4	Barfield et al. (1978)
	71.4	41.6	–	22.4	20.3	–	Du Plessis et al. (2020)
	–	–	26.0	–	–	–	Tendeng et al. (2019)
	71.4	–	–	–	20.3	–	Schlemmer (2018)
Egg hatchability (%)	30.0	52.0	–	90.0	44.0	–	Savadatti et al. (2023)
Larval mortality (%)	60.0	40.0	–	22.0	30.0	–	Savadatti et al. (2023)
	71.0	37.0	–	4.0	28.0	–	Du Plessis et al. (2020)

RH of 80% was optimal for FAW to achieve its highest intrinsic rate of increase, finite rate of increase, and net reproduction rate. Additionally, the authors noted that soil moisture ranging from 6.80% to 47.59% supports FAW pupation, survival, and eclosion.

Another key factor influencing the ecology and population dynamics of FAW is host plant selection. The preference of FAW for a particular host plant depends on the strain type (Tiwari, 2022). Two distinct strains have been identified within the FAW population: the C-strain and R-strain (Schofl et al., 2009; Groot et al., 2010; Dumas et al., 2015; Jing et al., 2021). Although these strains have morphological similarities, they differ in several key biological aspects including host plant preference, reproductive behaviors, genetic profiles, and pheromone compositions. The C-strain predominantly feeds on maize, sorghum, and cotton, whereas the R-strain demonstrates a greater affinity for rice, sugarcane, and pasture grasses (Dumas et al., 2015; Jing et al., 2021).

Beyond host specificity, these strains also exhibit differences in their dispersal abilities and resistance to environmental stressors. Studies suggest that the C-strain is more adapted to agricultural landscapes with annual crops, while the R-strain thrives in more stable, perennial grassland environments (Nagoshi et al., 2017). Additionally, inter-strain hybridization has been reported, potentially leading to increased genetic diversity and adaptive capabilities in invasive populations (Nagoshi et al., 2019). The presence of both strains in Africa has raised concerns about their combined impact on food security, as they contribute to the rapid expansion and persistence of FAW populations across diverse agroecosystems (Assefa, 2019).

3 The invasive potential of the FAW

The invasive success of the FAW is attributed to its biological, ecological, and behavioral traits. These include its strong migratory capabilities, high reproductive rate, adaptability to diverse habitats and a broad host range (Jing et al., 2021; Barkessa et al., 2024). FAW is a multivoltine pest that lacks diapause, allowing it to maintain continuous infestations in suitable environments (Barkessa et al., 2024).

Africa's favorable climatic conditions and the abundance of suitable host plants further facilitate FAW's establishment and spread, increasing the likelihood of it becoming endemic (Chimweta et al., 2020; Kenis et al., 2022). Furthermore, the overlap of maize cropping seasons and relay planting allows FAW to move from rain-fed to flood-recession crops, thereby intensifying its presence and impact (Chimweta et al., 2020). Bioclimatic factors, particularly temperature, rainfall, and land use, significantly influence the pest's distribution (Fan et al., 2020; Liu et al., 2020; Barkessa et al., 2024; Dessie et al., 2024; Huang et al., 2024). Several studies have confirmed that FAW habitat suitability in Africa is strongly associated with temperature and rainfall patterns (Early et al., 2018; Cokola et al., 2020; Abdel-Rahman et al., 2023).

Other key factors contributing to FAW's invasive potential in newly invaded regions include the absence of native natural enemies and favorable environmental conditions that support its survival and reproduction, leading to unchecked population growth (Early et al., 2018; Prasanna et al., 2018; Tendeng et al., 2019; Jing et al., 2021). The Enemy Release Hypothesis (Joshi and Vrieling, 2005; Elton, 2020) helps explain why FAW has become a devastating pest in Africa. In its native range in the Americas, FAW populations are regulated by a diverse community of over 150 natural enemies, including various species and families of pathogenic microorganisms, parasitoids, and predators (Wyckhuys and O'Neil, 2006; Meagher et al., 2016; Molina-Ochoa et al., 2003). However, when introduced to new regions, invasive species often escape these natural controls, leading to rapid population expansion and greater ecological and economic impacts (Harrison et al., 2019; Kenis et al., 2019). In Africa, FAW has encountered significantly fewer natural enemies, resulting in severe infestations and crop damage (Early et al., 2018).

Studies across Africa have documented around 20 natural enemy species of FAW, including 11 identified in Zambia alone, but their overall parasitism rate remains low at 10.5% (Sisay et al., 2018; Ahissou et al., 2021; Chipabika et al., 2023). This reduced effectiveness compared to FAW's native range underscores the lag time before local natural enemies adapt to the pest and highlights the need for biological control interventions (Prasanna et al., 2018; Pal et al., 2024). The introduction of specialized parasitoids from the Americas has been proposed as a potential strategy to enhance FAW management and mitigate its economic impact (Agboyi et al., 2020).

4 Agronomic and economic impact of fall armyworm in Africa

FAW infestations pose significant threats to crop development, agricultural ecosystems, and economic stability across Africa. In maize, damage during early and mid-whorl stages (first to ninth vegetative leaf stages, V1-V9) significantly reduce plant height, stalk thickness, leaf size, and fresh and dry plant biomass (Marenco et al., 1992). Defoliation reduces the photosynthetic area and leads to seedling loss, both of which can lower grain production (Vilarinho et al., 2011; Overton et al., 2021). However, at this stage, maize can compensate and keep defoliation below 50%, unless recovery is hindered by factors such as soil conditions, plant genetics, and poor cultural practices (Kasoma et al., 2020). Infestations during late whorl stage (V9-R1) result in increased ear damage and reduced crop yields (Marenco et al., 1992). FAW feeding during tasseling stage results in decreased pollen production (Kasoma et al., 2020), while silk damage leads to poor fertilization rates and fewer kernels per ear (Kasoma et al., 2020). Infestations at grain filling stage cause direct yield losses as larvae feed on ears, cobs, and seeds (Overton et al., 2021). Additionally, FAW damage facilitates fungal infections, increasing mycotoxin contamination and further reducing both marketability and overall grain quality (Overton et al., 2021). Beyond direct crop damage, FAW infestations threaten biodiversity and disrupt agricultural ecosystems and natural habitats, affecting the balance of local flora and fauna by consuming non-crop plants (FAO, 2018, 2022; Ayra-Pardo et al., 2024). The heavy reliance on chemical pesticides for FAW control harms beneficial insects, soil microorganisms, and aquatic life, leading to ecological imbalance and affecting ecosystem services (FAO, 2022; Mlambo et al., 2024).

Economically, FAW attacks on maize, rice, sorghum, millet, and other important crops result in substantial yield losses, posing a direct threat to food security and livelihoods of the rural population (Kasoma et al., 2020). FAW infestations across sub-Saharan Africa cause estimated annual economic losses of up to US$13 billion in maize, rice, sorghum, and sugarcane (Abrahams et al., 2017; Overton et al., 2021).

FAW's widespread presence in Africa has severely reduced maize yield, affecting millions of smallholder farmers whose livelihoods depend on this crop (Tambo et al., 2021). The pest has been reported to cause damage ranging from 25% to 50% in Zimbabwe, with farmers noting a 58% yield reduction (Chimweta et al., 2020). In Zambia, estimated yield losses during the 2016/17 cropping season ranged from 38% to 62% (Day et al., 2017). Prasanna et al. (2018) reported that 12 African countries experienced annual maize yield losses ranging from 21% to 53% in 2017. Additionally, FAW-induced yield losses were reported to range from 22% to 67% in West Africa (Day et al., 2017) and 32% in East Africa (Kumela et al., 2019). Day et al. (2017) stated that Sub-Saharan Africa loses approximately 13.5 million tons of maize annually, valued at USD 3.06 billion, due to FAW infestations. Eschen et al. (2021) and Cokola et al. (2023) have noted a total monetary value of approximately USD 9.4 billion due to FAW on maize in Africa. Chimweta et al. (2020) reported that, without effective control measures, FAW could reduce maize yield by 8.3 to 20.6 million tons annually in Africa.

Beyond maize, FAW has also been reported to affect other staple crops. Rice is among the most vulnerable, with infestations significantly reducing both yield and grain quality. Rwomushana et al. (2018) estimated that without effective control measures, annual FAW-induced losses in maize, rice, sorghum, and sugarcane could reach US$13 billion across sub-Saharan Africa. In Ghana, a survey by Koffi et al. (2020) reported FAW impact on rice (13.6% of respondents), millet (5.79%), and sorghum (5.41%), highlighting the pest's broad impact. FAW infestations in sorghum have also been shown to cause substantial yield reductions (Day et al., 2017), although specific figures on economic losses for sorghum in Africa remain limited. Similarly, household surveys conducted in Ghana and Zambia in 2018, indicated that only 2-4% of farmers reported FAW damage to millet, suggesting a relatively lower economic impact on this crop (Rwomushana et al., 2018). Additionally, FAW outbreaks disrupt agricultural trade at local, regional, and global levels, amplifying economic risks (FAO, 2018). Addressing FAW's agronomic and economic impacts requires sustainable pest management strategies that balance productivity, ecosystem stability, and farmer resilience.

5 Integrated pest management strategies specific to *Spodoptera frugiperda*

IPM is a decision-based process that uses a coordinated combination of methods to effectively control complex pests, including insects, pathogens, weeds, and vertebrates, while promoting environmental and economic sustainability (Ehler, 2006). FAW IPM requires a combination of two or more compatible management strategies. It also includes regular field monitoring and surveillance as essential operations for assessing the Economic Injury Level (EIL) and the Economic Threshold (ET). The EIL and ET are used as decision-making tools to determine when to take appropriate control measures to prevent economic losses caused by insect pests (Togola et al., 2023).

Additionally, several strategies, including cultural practices, host plant resistance, mechanical control, and biological control, have been employed to manage *S. frugiperda* (Kenis et al., 2022; Tepa-Yotto et al., 2022a; Mendesil et al., 2023; Obala et al., 2023). To reduce pest-related losses and the risk of hazardous chemicals, several International Research Organizations in Africa have actively conducted research to develop effective IPM strategies for FAW management. They have also made various training materials available, including handouts and guides (FAO, 2018; Prasanna et al., 2018; Tefera et al., 2019; Ahissou et al., 2021; Kasoma et al., 2021). Researchers have implemented a range of community-based educational programs to encourage African farmers to adopt FAW IPM technologies. According to FAO and ASARECA (2018), there is a growing awareness of the limitations and environmental impacts of chemical controls, prompting a gradual shift towards IPM strategies.

5.1 Monitoring and surveillance for early detection

Regular scouting of crops for signs of FAW infestations can help with early detection and prompt action before populations reach the economic threshold levels. According to Prasanna et al. (2018), implementing effective monitoring, surveillance, and scouting systems is a critical step in developing a successful IPM of FAW. Essential tools and practices for field monitoring at the farmer level include regular field scouting, use of pheromones (Tepa-Yotto et al., 2022b), and light traps. Pheromone traps are one of the most prominent and effective scientific tools used in pest management programs worldwide. This device enables early detection of pest infestations, tracks pest population dynamics, and supports pest management decision-making (Chiwamba et al., 2018). For small-scale farmers, several advanced technologies are available for monitoring and surveillance of FAW.

The FAW Monitoring and Early Warning System (FAMEWS) has been widely adopted across the continent, enabling farmers to track pest infestations (FAO, 2020). In six Eastern African countries (Ethiopia, Kenya, Tanzania, Uganda, Rwanda, and Burundi), a community-based initiative involving 650 focal persons has demonstrated its effectiveness (Niassy et al., 2021).

Remote sensing, particularly satellite imagery and NDVI analysis, has proven useful for detecting FAW damage. A Sentinel-2 satellite-based algorithm successfully identified biomass loss in maize fields in Zimbabwe, Kenya, and Tanzania (Buchaillot et al., 2022). In Ghana, integrating field surveys with remote sensing improved FAW distribution modeling (Bilintoh, 2019). Predictive models, such as MaxEnt, have been used to simulate FAW distribution under current and future climate scenarios in Ethiopia (Barkessa et al., 2024).

Machine learning is also being explored, with the University of Zambia developing an automated FAW identification system using Convolutional Neural Networks (CNN) that integrates vision and motion sensors with pheromone traps for real-time pest monitoring, reducing field visits, improving data collection efficiency, and enhancing decision-making (Chiwamba et al., 2018).

5.2 Cultural practices

Studies have found that cultural practices such as crop rotation, regular weeding, and destruction of crop residues help to mitigate FAW infestation (Cokola et al., 2023). Maintaining organic soil fertility was found to prevent high FAW density (Bayissa et al., 2023). Using early-maturing cultivars was reported to be effective against FAW, as these varieties have a shorter growth cycle, reducing their exposure to the pest (Day et al., 2017). Also, adjusting the planting schedule to avoid peak periods of FAW activity can help prevent infestations (Ahissou et al., 2022). Other studies have indicated that destroying the ratoons of sorghum and sugarcane, which serve as reservoirs for FAW, also effectively controls the pest's population. Intercropping maize or other cereals with non-preferred or repellent crops (e.g., legume crops, desmodium and Dolichos lablab), as well as practicing mixed cropping, has been shown to attract natural enemies that prey on FAW, making it a proven effective pest management strategy (Ratnadass et al., 2006; Chimweta et al., 2020). However, many leguminous crops that are often grown with maize are known to be hosts for FAW and tend to sprout earlier, which could exacerbate the pest infestations in maize (Rwomushana et al., 2018; Ambia, 2023). Other practices like zero-tillage can reduce overwintering larvae and promote higher densities of natural enemies, making the environment less attractive for FAW populations (Baudron et al., 2019). The number of FAW predators can also be maintained through habitat management techniques like building shelterbelts or live fences that increase biodiversity (Hellmich et al., 2008). Additionally, push-pull technology, which combines trap plants to attract FAW and repellent intercrops to deter it, is cited as an ideal approach for mixed farming systems, effectively reducing FAW larval density and damage to maize and other cereals (Joatya et al., 2022; ICIPE, 2024). However, certain cultural practices, like intercropping cereals with pumpkins, should be avoided as they may inadvertently increase FAW damage by providing shelter for moths and facilitating larval migration. Integrating these cultural practices with other FAW control strategies can significantly improve the management of the pest.

5.3 Host plant resistance

Host plant resistance (HPR) is a key component of IPM strategies for controlling FAW. It involves the inherent defense mechanisms of plants, which include both biophysical and biochemical properties (Meihls et al., 2012; Jin, 2017);.

Studies discovered several traits associated with maize resistance against FAW. Callahan et al. (1992) found that a combination of two specific polypeptides (36 and 21 kDa) is predictive of resistance to lepidopteran insects. Furthermore, Smith et al. (2012) revealed that the terpenoid (E)-β-caryophyllene in maize whorl leaves showed that the plant is naturally resistant to FAW. Other compounds associated with resistance include mir1-CP, oxophytodienoic acid (OPDA), a low protein/total nonstructural carbohydrates ratio, thicker leaves, and higher contents of crude fiber, hemicellulose, and thicker cell wall complexes, as well as the constitutive expression of jasmonic acid genes (Singh et al., 2022). Similarly, Darshan et al. (2024) reported significant negative correlations among morphological traits such as plant height, stem girth, and the presence of trichomes related to FAW incidence. Baudron et al. (2019) and Snook et al. (1993) stated that the rapid accumulation of proteins or phytochemicals like maysin in silks can either poison or starve the pest. Chiriboga Morales et al. (2021) and dos Santos et al. (2020) found a negative correlation between maize leaf toughness at the twelfth vegetative leaf stage (V12) and leaf damage from FAW infestation. Jiang et al. (1995) and Pechan et al. (2000) found that higher levels of the 33-kD cysteine proteinase in plant leaves were associated with lower FAW larval weight, suggesting that the enzyme may serve as a novel insect defense mechanism in plants. Baudron et al. (2019) reported that plant characteristics such as the density of leaf hairs or the density of the cuticular wax layer can reduce foliar damage. In response to pest attacks, some plants activate wound-response pathways and release volatile compounds (Smith et al., 2012).

To date, the International Maize and Wheat Improvement Center (CIMMYT) has disseminated several FAW-tolerant maize inbred lines, including CML71, CML124, CML125, CML338, CML333, CML334, CML370, CML372, and CML574, across 34 countries. Also, the center has developed three high yielding maize hybrids (FAWTH2001, FAWTH2002 and FAWTH2003) with native tolerance to FAW, which are being widely released in Africa. CIMMYT undertook these research efforts in collaboration with various National Agricultural Research and Extension Systems (NARES), advanced research institutes (ARIs), and commercial seed companies (Prasanna et al., 2021). Several other studies have identified different maize germplasms with desirable resistance traits or mechanisms to FAW, as illustrated in Table 2.

The identification of resistant donor lines and the introduction of desired traits into elite maize cultivars represent significant advancements in developing FAW-resistant plants. Exploring molecular markers for FAW resistance can accelerate the breeding process (Sharma et al., 2008; Nashath et al., 2023). Two important tools used in modern breeding are marker-assisted selection and quantitative trait loci (QTLs). They facilitate the identification of genetic traits, accelerate breeding cycles, and enhance the development of insect-resistant germplasms (Mihm, 1997; Singh et al., 2022). These practices help incorporate desired traits while avoiding deleterious alleles. According to Abdulmalik et al. (2017), molecular tools make it possible to select for FAW resistance while keeping the beneficial traits of adapted cultivars. Singh et al. (2022) emphasized that rapid screening strategies and genomic selection can enhance the utilization of plant genetic resources. In a GWAS study, Badji et al. (2020) utilized SNP markers to identify 62 quantitative trait nucleotides (QTNs) linked to FAW resistance traits in maize in four SNP regions. Notably, QTLs on chromosomes 4 and 9 correspond to bi-parental QTL mapping, highlighting their importance they in in developing markers for FAW leaf damage resistance (Womack et al., 2018; 2020).

Emerging biotechnological solutions are being explored to combat lepidopteran pests, including stemborers and FAW. In the African context, genetically modified Bt maize, which is resistant to both pests, has been commercialized in South Africa and is expected to expand to other countries where transgenic maize is already approved as an effective management strategy (Prasanna et al., 2022). Furthermore, advanced molecular technologies, including RNA interference (RNAi) (Kebede and Fites, 2022; Kumara et al., 2022; Nwokeoji et al., 2022) and gene editing using CRISPR-Cas9 (Singh et al., 2022), have been investigated to target essential genes in lepidopteran pests, disrupting their development and reducing crop damage. However, these technologies have yet to be implemented for FAW management in Africa.

5.4 Mechanical control

It has been reported that practices like handpicking larvae, crushing egg and neonate masses, and uprooting infested plants increase the resilience to FAW. However, these options are best suited for shorter cultivars, early to mid-whorl stages, and small-sized fields (Chimweta et al., 2020). Traditionally, small-scale farmers in Africa apply soil and ash to leaf whorls to control the pest (Abate et al., 2000; Ambia, 2023). These mechanical methods are still applicable at the farmer level in SSA due to the relatively small areas of production (Hruska, 2019; Cokola et al., 2023). Other mechanical approaches used in SSA to control FAW include the use of pitfall traps, sticky traps, light traps, or pheromone traps (Prasanna et al., 2018; Bhusal and Bhattarai, 2019; Gebreziher and Gebreziher, 2020; Akeme et al., 2021), as well as ash and detergents (Tambo et al., 2020). Also, legumes such as beans (*Phaseolus vulgaris*), groundnuts (*Arachis hypogaea*), cowpeas (*Vigna unguiculata*) and soybean (*Glycine max*) are intercropped within maize to serve as trap crops for the pest (Akeme et al., 2021).

5.5 Biological control strategies

Biological control is an effective strategy for managing FAW using natural enemies such as predators, parasitoids, entomopathogenic fungi, viruses, nematodes, bacteria, and biopesticides (Assefa and Ayalew, 2019; Abbas et al., 2022). This can be implemented through two primary approaches: augmentative biocontrol, which involves mass rearing and periodic release of beneficial organisms to boost existing populations, and inoculative biocontrol, which entails a single initial release of natural enemies aimed at establishing a self-sustaining population for long-term pest control (Nyamutukwa et al., 2022).

Additionally, proper habitat conservation, maintaining prey availability, and minimizing the use of broad-spectrum insecticides in agricultural and natural ecosystems can support the populations of natural enemies, a practice known as conservation biocontrol. These methods can be effectively integrated as biocontrol-based applications within an IPM framework against FAW (Tefera et al., 2019; Kenis et al., 2022; Ayra-Pardo et al., 2024).

TABLE 2 Some potential sources of resistance in maize to fall armyworm.

Name or code or pedigree	Resistance traits or mechanisms	References
Antigua Gpo2	*mir-1* CP, antibiosis, etc	Kasoma et al. (2020)
Antigua 2D -118	Nonpreference	Kasoma et al. (2020)
T-FAWCC (C5)	Nonpreference & antibiosis	Widstrom et al. (1992); Singh et al. (2022)
Mp704	Antibiosis and Antixenosis due to 33-kD cysteine proteinase; *mir1*- Cysteine proteinase (*mir1*-CP); higher content of crude fiber, hemicellulose, and cellulose in whorls	Prasanna et al. (2022); Singh et al. (2022); Smith et al. (2012); Brooks et al. (2007); Jiang et al. (1995); Callahan et al. (1992)
Mp706	Nonpreference	Williams and Davis (1994);
Cuba Honduras 46-J	Least leaf sheath damage	Singh et al. (2022)
Mp496, Mp701	Higher hemicellulose and crude fiber	Prasanna et al. (2022); Brooks et al. (2007); Williams and Davis (1994); Callahan et al. (1992)
Mp705, Mp713, Mp714 & Mp716		Prasanna et al. (2022)
MpSWCB-4	Antibiosis & nonpreference	Singh et al. (2022); Scott and Davis (1981); Wiseman et al. (1981)
Mp708	E)-β-caryophyllene; Oxophytodienoic acid (OPDA); Low protein/total carbohydrates ratio; Thicker leaves and cell wall complexes; Higher crude fiber, hemicellulose, and cellulose content. Constitutive expression of jasmonic acid genes	Prasanna et al. (2022); Singh et al. (2022); Smith et al. (2012); Brooks et al. (2007); Pechan et al. (2000); Jiang et al. (1995); Callahan et al. (1992)
Perola (Brazilian landrace)	Oviposition. nonpreference & antibiosis	Singh et al. (2022); Nogueira et al. (2019)
PR030-Doce Flor da Serra & MG 161-Branco Doce (sweet corn landraces)	Antibiosis & impaired insect development	Singh et al. (2022); de Souza Crubelati-Mulat et al. (2019)
Zapalote Chico sh2	Maysin and isoorientin	Widstrom et al. (2003); Singh et al. (2022); Viana et al., 2022; Viana and Potenza (2000); Nuessly et al. (2007)
BR 201	Antixenosis	Viana et al. (2022); Viana and Potenza (2000)
CMS14C	Antibiosis & nonpreference	Prasanna et al. (2022); Singh et al. (2022); Viana et al. (2022); Viana and Potenza (2000);
CML67	–	Miranda-Anaya et al. (2002)
CML121-127	–	Prasanna et al. (2018)
FAWTH2001, FAWTH2002 & FAWTH2003	–	Prasanna et al. (2022)
CML71, CML124, CML125, CML333, CML334, CML338, CML370, CML372 & CML574	–	Prasanna et al. (2021)
B49; B52; B64; B68; B96	–	Prasanna et al. (2022)

Ideally, biological control should be based on natural enemies already attacking FAW in Africa rather than organisms from other regions, as these may cause unforeseen problems (Chimweta et al., 2020). In Africa, Abbas (2023) reported 48 species of parasitoids, primarily from the Braconidae family (19 species), followed by Ichneumonidae (11 species), Tachinidae (9 species), and Trichogrammatidae (5 species). The remaining species belong to families such as Eulophidae, Heciridae, Pteromalidae, and Scelionidae, with one species each. The egg-larval endoparasitoid *Chelonus bifoveolatus* (Hymenoptera: Braconidae) commonly targets the eggs of FAW on the African continent, causing the young instars of FAW to hatch alongside the parasitoid's eggs (Obala et al., 2023; ICIPE, 2024). In Africa, *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae), *Coccygidium luteum*, *Telenomus remus* (Hymenoptera: Scelionidae), and *Cotesia icipe* are also common FAW parasitoids. *Cotesia icipe* is known for its strong ability to control FAW in maize crops.

Several studies found that the parasitism rates of those mentioned parasitoids varied across African countries, such as Ghana, Kenya, Niger, Nigeria, Egypt, Uganda, South Africa, Senegal, Tanzania, and Zambia (Agboyi et al., 2020; Abang et al., 2021; Mohamed et al., 2021; Otim et al., 2021; Abbas, 2023; Koffi et al., 2023; ICIPE, 2024).

Trichogramma spp. and *Telenomus* spp. are widely used parasitoids for FAW control because they are easy to rear in laboratories and effective in managing FAW population (Figueiredo et al., 2002; Gutierrez-Martinez et al., 2012; Tefera et al., 2019).

Abbas (2023) reported a total of 17 predators of FAW in Africa, which include seven coleopterans from the Coccinellidae family (*Coleomegilla maculata*, *Cycloreda sanguinea*, *Cheilomenes sulphurea*, *Coccinella transvirsalis*, *Harmonia octomaculata*, *Eriopis* sp., and *Hippodamia* sp.), two coleopterans from the Carabidae family (*Callida* sp. and *Calosoma granulatus*), one coleopteran from the Lampyridae family (*Hematochares obscuripennis*), three dermapterans from the Forficulidae family (*Diaperasticus crythrocephalus*, *Forficula senegalensis*, and *Doru* sp.), one hemipteran from the Geocoridae family (*Geocoris* sp.), one hemipteran from the Pentatomidae family (*Podisus* sp.), one hymenopteran from the Formicidae family (*Pheidole megacephala*), and one lepidopteran from the Erebidae family (*Perprius modiulipes*). Table 3 shows the main families and order/class of FAW's natural enemies in Africa.

Several bio-rational control agents have shown effectiveness in FAW management. These include the entomopathogenic fungi *Metarhizium anisopliae* and *Beauveria bassiana*, as well as the biological pesticide *Spodoptera frugiperda* nucleo-polyhedrovirus (Fawligen, SfNPV) (Akutse et al., 2019). Nematodes, protozoans, and botanical extracts such as powders, volatile and non-volatile oils, and extracts from *Azadirachta indica* and *Jatropha curcas* seed can also be used to control FAW (Adjaoke et al., 2021; Abbas et al., 2022; El-Sappagh et al., 2022; Tepa-Yotto et al., 2022b). Patel Sagarbhai et al. (2021) stated that neem affects insect growth, development, egg laying, and has been shown to have antifeeding and larvicidal activity in FAW. Sisay et al. (2019) noted that extracts from several plants, such as *Milletia ferruginea*, *Phytolacca dodecandra*, *Schinus molle*, *Melia abyssinica*, *Nicotiana tabacum*, *Lantana camara*, *Chenopodium ambroides*, and *Jatropha gossypifolia*, induced high mortality of FAW. The deployment of biological control methods against FAW among African farmers has been progressing. However, adoption remains minimal due to the absence of true native natural enemies. In Zambia, CABI launched a village-based biological control initiative to promote the use of natural enemies and biopesticides, aiming to reduce farmers' reliance on chemical pesticides (CABI, 2023). Additionally, training programs have been conducted to empower young farmers

TABLE 3 Natural enemies (parasitoids, predators and entomopathogenic organisms) of fall armyworm in Africa.

Family	Order	Population importance	Host stage	Status	References
Parasitoids					
Braconidae	Hymenoptera	++++	L, E-L, L-P	Indigenous	Abbas (2023); ICIPE (2024); Agboyi et al. (2020); Otim et al. (2021); Tefera et al. (2019)
Ichneumonidae	Hymenoptera	+++	L, L-P	Indigenous	Abbas (2023); Otim et al. (2021)
Tachinidae	Diptera	++	L	Indigenous	Abbas, 2023; Otim et al. (2021)
Trichogrammatidae	Hymenoptera	++	E	Indigenous	Abbas (2023); Tefera et al. (2019)
Eulophidae	Hymenoptera	+	L	Indigenous	Abbas, 2023;
Pteromalidae	Hymenoptera	+	L	Indigenous	Abbas (2023)
Scelionidae (Platygastridae)	Hymenoptera	+	E	Introduced	Abbas (2023); Otim et al. (2021); Tefera et al. (2019)
Predators					
Coccinellidae	Coleoptera	++++	E, L,P,A	Indigenous	Abbas (2023)
Forficulidae	Dermaptera	+++	E, L,P	Indigenous	Abbas (2023)
Geocoridae	Hemiptera	+	E, L,P	Indigenous	Abbas (2023)
Pentatomidae	Hemiptera	+	E, L,P	Indigenous	Abbas (2023)
Lampyridae	Coleoptera	+	E, L,P	Indigenous	Abbas (2023)
Entomopathogens Class					
Cordycipitaceae (*Beauveria bassiana)*	Sordariomycetes	NA	E, L	Naturally occurring agent	Akutse et al. (2019); Tefera et al. (2019)
(Clavicipitaceae) *Metarhizium anisopliae*	Sordariomycetes	NA	E, L	Naturally occurring agent	Akutse et al. (2019); Tefera et al. (2019)
Baculoviridae (*Spodoptera frugiperda* multiple nucleopolyhedroviruses-SfMNPV)	Naldaviricetes	NA	L	Naturally occurring agent	Hussain et al. (2021); Tepa-Yotto et al. (2024)

E, egg; L, larva, E-L, egg-larval; P, pupa; L_P= lava-pupal; A, adult; (++++) very high number, (+++) high number, (++) moderate number, (+) few number; NA, Non applicable.

to explore business opportunities in the biocontrol sector, further facilitating the adoption of these methods (CABI, 2024).

5.6 Chemical control options and insect resistance management

At present, most African farmers rely on the application of synthetic insecticides to control the FAW (Assefa and Ayalew, 2019). According to Tambo et al. (2020) and Kumela et al. (2019), the most used control measure in Africa for the management of FAW is the application of synthetic pesticides.

Insecticide applications should be based on FAW infestation thresholds after continuous monitoring. Studies have validated several treatment thresholds that consider not only the pest's developmental stages but also the phenological stages of the infested crops (FAO, 2017; Prasanna et al., 2018). To be technically and cost-effective, the pesticide choice should respect these action thresholds (Chimweta et al., 2020).

However, chemical insecticides should be considered as the last resort for managing FAW, as they may negatively impact the environment and the non-target organisms, human health, and biodiversity, including beneficial insects (Harrison et al., 2019; Deshmukh et al., 2020; Idrees et al., 2022). Furthermore, their use is associated with high costs, potential environmental contamination, resistance development, and frequent pest resurgences (Gebreziher, 2020). Studies have demonstrated that repeated, indiscriminate use and misuse of chemical insecticides exert strong selection pressure, leading to the evolution of resistance mechanisms (Togola et al., 2018; Zhang et al., 2021). Cases of FAW resistance to multiple classes of insecticides, including pyrethroids, organophosphates, and carbamates, have been widely documented in different regions, posing a significant challenge to pest management (Carvalho et al., 2013; Yu et al., 2023). The increasing resistance not only reduces the efficacy of chemical control but also requires higher application rates and more frequent spraying, further exacerbating environmental and economic burdens (Gutiérrez-Moreno et al., 2019). To prevent insecticide resistance in FAW, it is important to implement integrated pest management practices. These strategies will help maintain resistance at low levels.

Studies have shown that selection pressure from *Bacillus thuringiensis* (Bt)-resistant maize can lead to FAW resistance. FAW has developed resistance to Bt toxins such as Cry1Ac, Cry1Ab, and Cry1A.105 through mechanisms like metabolic detoxification, target-site insensitivity, and behavioral avoidance (Storer et al., 2010; Huang et al., 2014; Boaventura et al., 2020; Boaventura et al., 2021; Jing et al., 2021; Zhang et al., 2021). This poses significant challenges for FAW-preferred crop growers (Peferoen, 1997; Zhang et al., 2021). Several studies have also shown that FAW has become resistant to different ranges of pesticides, such as carbamates, organophosphates, and pyrethroids (Jing et al., 2021; Zhang et al., 2021).

It is suggested that to break insects from becoming resistant to protein toxins, an insect resistance management (IRM) approach is recommended. One key strategy of IRM is the establishment of refuge areas, either within or adjacent to transgenic fields, to allow non-resistant insect populations to thrive. This promotes random mating between treated and refuge populations, weakening the resistance alleles in the overall population (Vilarinho et al., 2011; Murúa et al., 2019). Several studies have shown that the presence of non-Bt refuges can sustain the long-term efficacy of Bt crops by preventing resistant populations from becoming dominant (Huang et al., 2014; Carrière et al., 2020). Proper implementation of refuge areas requires careful planning, including the selection of appropriate non-Bt host plants, strategic placement, and maintaining a sufficient proportion of the crop area as a refuge. Research suggests that an ideal refuge should be at least 20% of the total crop area (Bourguet et al., 2005; EuropaBio, 2019). Other studies suggest placing refuge areas approximately 800 meters apart to maintain their effectiveness (Vilarinho et al., 2011). Prasanna et al. (2022) suggested that integrating polygenic native resistance with transgenic Bt maize, which typically relies on one gene (monogenic) or a few genes (oligogenic) in conventional cropping systems, could be a key strategy for insect resistance management. This approach would help prevent FAW from overcoming the limited genetic defenses of Bt maize, thereby promoting a more effective and sustainable FAW control strategy.

6 Future directions and recommendations

Emerging technologies such as digital tools (e.g., mobile applications and remote sensing technologies), drones equipped with imaging technology, and computer vision techniques to automatically detect FAW infestation in maize crops can play a significant role in monitoring FAW infestations in real-time, assessing their severity through data analytics and predictive modeling, and allowing timely interventions (Shaurub, 2024; Shinde et al., 2024). Additionally, advanced genetic research, including the development of genetically modified maize as well as native genetic resistance hybrids, offers promising management avenues for FAW (Prasanna et al., 2022; Gouda et al., 2024). Integrated approaches that combine multiple management options are being explored to enhance the efficacy of traditional methods, promoting sustainable agricultural practices against FAW (Anilkumar et al., 2024). These emerging technologies can not only improve management strategies but also help mitigate the environmental impact of pesticide use.

Despite significant progress in FAW management, several research gaps remain that warrant further investigation. For instance, the role of climate change and its impact on the distribution and life cycle and population dynamics of FAW requires deeper exploration, as it could significantly impact the dynamics of the pest and, consequently, agricultural productivity (Ntwari et al., 2024). Also, the socio-economic and environmental aspects of pest management, including farmers' knowledge, adoption of technologies, and access to resources, need thorough investigation to design comprehensive strategies that enhance resilience (Berg and Plessis, 2024). Furthermore, more research is needed to evaluate the effectiveness of biological control agents and their interaction with native ecosystems.

The battle against FAW in Africa underscores the necessity of collaborative efforts among governments, research institutions, nongovernmental organizations, and local farmers. Effective management requires a unified approach, as FAW does not respect borders and can swiftly spread across regions. Collaborative initiatives facilitate the sharing of knowledge, resources, and technology, enabling countries to develop and implement coordinated action plans tailored to local challenges (Karakkottil et al., 2024). For instance, regional networks can enhance surveillance and monitoring efforts, leading to early detection and response to infestations. Moreover, partnerships can support training programs for farmers, empowering them with information on best practices and sustainable pest management techniques.

7 Conclusion

African farmers continue to face regular infestations and outbreaks of FAW, which impact the yields of staple crops, particularly causing severe losses in maize production. Addressing this pest, which hinders crop production across Africa, requires adequate attention. It is important to know about the pest's biology, ecology, and irreversible impacts, and the range of interventions that can serve as alternative control strategies to minimize pesticide applications.

In this regard, there is an ongoing need for the research community to develop IPM strategies to achieve these goals. The research community has made significant progress in developing, testing, and validating IPM options as holistic management solutions for FAW. CIMMYT and its partners, including National Agricultural Research and Extension Systems (NARES), have developed FAW IPM technologies and made numerous field-guides available for training and capacity building purposes.

Moreover, CIMMYT's Global Maize Program has developed high-yielding maize hybrids with native genetic tolerance to FAW, which are being widely released in Africa. Several African countries are employing other options, including biological control, cultural practices, mechanical control methods, and the judicious use of chemicals as effective strategies to control the FAW. Researchers have utilized various knowledge-sharing platforms such as pest diagnostic guides, field demonstrations, training sessions, videos, animations, and Information and Communication (ICT) tools to facilitate the adoption of IPM technologies.

Author contributions

AT(1st author): Validation, Writing – original draft, Writing – review & editing. YB: Funding acquisition, Resources, Validation, Writing – review & editing. RB: Validation, Writing – original draft, Writing – review & editing. GT: Validation, Writing – original draft, Writing – review & editing. MG: Validation, Writing – review & editing. AT(6th author): Validation, Writing – original draft, Writing – review & editing. PB: Funding acquisition, Resources, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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