Egyptian Journal of Biological Pest Control

REVIEW ARTICLE **Open Access**

Fall armyworm management in a changing climate: an overview of climate-responsive integrated pest management (IPM) strategies for long-term control

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Abstract

Invasive alien insects have the potential to pose a significant threat to global agriculture, with their distinctive traits enabling rapid reproduction, successful adaptation to new environments and high distribution capability. These pests can devastate crops, livestock, biodiversity and ecosystem functioning, resulting in ecological damage and substantial economic losses. Climate change plays a crucial role in driving the invasion of these pests, creating favorable conditions for their development, and negatively impacting global biodiversity. Among invasive alien insects, fall armyworm (FAW) (*Spodoptera frugiperda*) (JE Smith) (Lepidoptera: Noctuidae) has emerged as a major pest species, causing significant yield losses in maize cropping outside his native range. Initially, reliance on pesticides for control proved ineffective and led to pesticide resistance. Significant progress has been made in implementing integrated pest management (IPM) strategies that integrate agro-ecological and biological approaches. This review article focuses on the compilation of IPM methods, combining agro-ecological practices and biological control agents such as parasitoids and viruses, for the effective management of FAW. Approaches such as intercropping, agronomic practices, and the use of parasitoids and viruses have shown promising results in controlling FAW. This review article provides insights into successful management methods, recommendations and suggestions for the sustainable control of FAW using agro-ecological practices, biological control agents or their combination.

Keywords *Spodoptera frugiperda*, *Zea mays*, Climate change, Integrated pest management

Background

Invasive alien insects can reproduce quickly, adapt to new environments and spread widely, posing severe threats to agriculture, biodiversity and ecosystem functioning. The fall armyworm (FAW) *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) is a major concern among these pests due to its devastating impact on maize fields worldwide, resulting in significant yield losses (Kenis et al. 2023). Notably, FAW can cause substantial yield losses of up to 80–100% in maize fields, affecting all maize growth stages from seedling to cobbling. Furthermore, it damages a wide range of crops, with maize being the main target, including rice, sorghum, sugarcane, cabbage, beet, groundnut, soybean, alfalfa, onion, grasses, millet, tomato, potato and cotton (Makgoba et al. 2021). Since its introduction to Africa, the FAW has been an issue in maize production, resulting in losses ranging from 8.3 to 20.6 million tons across the 12 major maize-producing countries (Toepfer et al. 2019). According to Houngbo

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et al. (2020), the FAW caused 49% of Benin's maize crop losses in 2018.

Furthermore, climate change plays a critical role in exacerbating the invasion of alien insects by creating favorable conditions for their development in new environments (Bellard et al. 2018). However, the impacts of climate change extend beyond species extinction. Climate change disrupts plant–animal interactions, compromises ecosystem resilience and increases plant stress and vulnerability to insect infestations, ultimately resulting in decreased agricultural productivity and plant growth (Moutouama et al. 2022). The findings by Ramírez-Cabral et al. (2020) emphasize that climate change has the potential to exacerbate issues related to the FAW by creating more favorable conditions for its proliferation. It becomes important to integrate knowledge about climate change into IPM strategies to ensure effective and sustainable pest management.

In the past, using pesticides as the main pest control method for FAW has proven ineffective and unsustainable. Indeed, maize farmers used high pesticide dosages, resulting in high residues that are hazardous to human health and the environment. Additionally, FAW quickly developed resistance to many chemical compounds, making them less effective over time (CABI 2020).

To overcome the challenges posed by FAW and the influence of climate change, significant progress has been achieved in several areas of pest control. These include host plant resistance, agronomy practices, biological control, botanical application, chemical approaches and biotechnology (Agboyi et al. 2020). Integrated pest management (IPM) strategies have emerged as a holistic and environmentally friendly approach that integrates multiple techniques, including agro-ecological, biological and chemical methods.

This review article aims to present a compilation of IPM methods that combine agro-ecological and biological approaches (parasitoids and viruses) for controlling FAW in maize fields. Intercropping, intercultural measures (agro-ecological practices), parasitoids and viruses (biological methods) have all shown promising results for the sustainable management of *S. frugiperda* (Hussain et al. 2021). The review article will highlight successful management methods, recommendations and suggestions for effectively controlling FAW in maize and other relevant crops using agro-ecological practices, biological methods or a combination of both.

The relevance of invasive alien insects will be highlighted in the introduction of the current review article, with a special emphasis on the effects of the FAW on global agriculture. It will then go into detail about how climate change affects the spread of alien insects and the implications this has for agriculture. As well as outlining the drawbacks of conventional pesticide-based pest control techniques, the introduction will also introduce the idea of integrated pest management (IPM) strategies. The review article's scope will then be presented, with a particular emphasis on gathering and assessing agro-ecological and biological methods for controlling FAW in maize fields.

Through a comprehensive review of the available literature, this review article aims to provide valuable insights into successful management methods, recommendations and suggestions for effectively controlling FAW in maize and other relevant crops using agro-ecological practices, biological methods or a combination of both (Hussain et al. 2021).

Constraints to maize production

Maize production, a major food component in Benin, faces challenges due to modifications in both abiotic such as climatic variations and biotic factors, as highlighted by Shiferaw et al. (2011). A wide range of abiotic constraints, including soil depletion, water scarcity, adverse weather conditions and unsuitable temperatures, are well-known for their negative impact on the productivity of food crops. Biotic factors, such as diseases, pests and natural enemies like parasitoids and predators, also, play a significant role in influencing maize production, as discussed by Agboyi et al. (2021).

The FAW, key maize pest

The FAW, a key invasive pest of maize in Africa, coincidentally shares its region of origin with maize itself (Makgoba et al. 2021). Maize was originally domesticated from its wild ancestor by indigenous people in southern Mexico about 10.000 years ago. It subsequently spread throughout Latin America, the Caribbean and North America (Saari and Prescott 1985). During the early sixteenth century, it was introduced to Europe and further disseminated to Asia and Africa (da Fonseca et al. 2015). This introduction was due to maize's ease of cultivation, and high nutritional value for both humans and livestock (Shiferaw et al. 2011). The crop's adaptability to a wide range of climates and the availability of maize varieties specifically bred for different climatic regions have contributed to its widespread cultivation (Shiferaw et al. 2011).

The FAW, scientifically known as *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), became a major maize insect pest in Africa after its outbreak in 2016 (Agboyi et al. 2021). This invasive pest can cause extensive damage to maize cropping, particularly during the early growth stage (Goergen et al. 2016) and cob setting period (Agboyi et al. 2021). In response to its spread, insecticides have been widely used for its control

(Babendreier et al. 2020b). However, the use of insecticides has led to many side effects for human and environmental health, while insects developed resistance to these chemicals. Therefore, there is an urgent need to develop more sustainable approaches for controlling the fall armyworm in maize fields across Africa.

FAW invasion and migration as a result of climate

In the twenty-first century, climate change has become increasingly evident, resulting in various implications including but not limited to more frequent extreme events (prolonged drought, dry spells, floods, heat). Therefore, climate change can have significant impacts on agri-food systems; it can also cause biodiversity loss, thereby increasing food insecurity risks. The effects of climate change on organisms of a poikilothermic nature can be also high, for instance leading to outbreaks of secondary herbivorous insect pests and the introduction and spread of invasive alien species to new territories (Skendžić et al. 2021). However, the introduction of FAW onto the African continent cannot be a consequence of changing climates as crossing the Atlantic Ocean despite good pest flying capabilities is not a possibility. Conversely, climate change can have both direct and indirect effects on the physiology and behavior of insect pests, primarily influenced by factors such as bioclimatic variables, host plant availability and natural enemy resources (Skendžić et al. 2021). In optimal temperature conditions, insect pests can exhibit improved survivability, fecundity and developmental performance (Liu et al. 2021). The FAW is an exceptionally voracious and destructive pest, displaying high adaptability to a wide range of temperatures and geographical distributions (Yan et al. 2022). Its remarkable fertility, extensive migratory capabilities and adaptability make it a significant economic threat (Yan et al. 2022). The FAW inflicts severe damage by voraciously attacking crucial agricultural regions, thereby affecting various host plant species (Winsou et al. 2022). It has been reported to target at least 353 known host plant species from 76 botanical families (Mutyambai et al. 2022). Also, FAW cannot enter into diapause in its life cycle (Huang et al. 2020). This is particularly relevant in sub-Saharan countries where favorable conditions prevail throughout the year, leading to endemic FAW populations (Paudel et al. 2022). In areas where the FAW is not endemic, migratory populations of FAW arrive only when environmental conditions allow (Nagoshi et al. 2022). These populations may have a limited window of opportunity, with as few as one generation before they adapt to the environment (Paudel et al. 2022).

The FAW is a highly migratory pest native to the Americas. It was first detected in Africa in early 2016, likely introduced via international trade and air travel, potentially as egg masses or larvae on imported plant material (Goergen et al. 2016). Following its establishment, FAW rapidly spread across the continent, facilitated by its strong flight capabilities and favorable climatic conditions (Prasanna et al. 2018). FAW has been reported in over 40 African countries (Day et al. 2017). It has adapted to various agro-ecological zones, ranging from tropical to subtropical areas. Factors such as wind patterns, crop availability and environmental conditions such as temperature and humidity, which are crucial for the pest's life cycle and reproduction, influence its spread (Early et al. 2018). Significant outbreaks were first reported in West African countries such as Nigeria, Ghana and Benin (Abrahams et al. 2017). The pest then moved eastward, affecting major maize production areas in East Africa, including Kenya, Uganda and Tanzania (Harrison et al. 2019). Southern African countries like Zambia, Zimbabwe and South Africa have also experienced severe infestations, impacting both smallholder and commercial farming systems (Rwomushana et al. 2018).

Methods for controlling FAW

When FAW first came to Africa the control was based on the widespread of pesticides (Matova et al. 2020). However, relying only on pesticides shows many limitations in the effectiveness of the management of FAW, leading to pesticide resistance, pest resurgence and increased production costs (Matova et al. 2020. To mitigate the economic damage caused by FAW, especially for small-scale producers in Africa, several studies were done to find an alternative to controlling the pest instead of relying only on solely on pesticide application (Winsou et al. 2022). One approach that has been successfully used is the integration of a couple of methods to manage the pest known as integrated pest management (IPM), which combines different strategies such as agro-ecological practices, chemical and botanicals control, push–pull farming systems, biological control and indigenous knowledge to effectively manage FAW (Winsou et al. 2022).

In terms of biocontrol agent approaches numerous natural enemies of the FAW have been identified in Africa since 2017, bringing encouraging news (Agboyi et al. 2021). These natural enemies include various parasitoid species (such as egg, egg-larval, larval and larval-pupal parasitoids) and predators. In Benin and Ghana, ten parasitoids associated with FAW have been identified (Agboyi et al. 2020). These include two egg parasitoids: *Telenomus remus* (Nixon) (Hymenoptera: Platygastridae) and *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), one egg-larval parasitoid: *Chelonus bifoveolatus* Panzer (Hymenoptera: Braconidae), five larval parasitoids: *Coccygidium luteum* Brullé (Hymenoptera: Braconidae), *Cotesia icipe* Fiaboe (Hymenoptera: Braconidae), *Charops sp*. (Hymenoptera: Ichneumonidae), *Pristomerus pallidus* (Kriechbaumer) (Lepidoptera: Crambidae: Spilomelinae) and *D. quadrizonula* (Thomson) (Diptera: Tachinidae), and two larval-pupal parasitoids: *M. cf. testacea* (Granger) (Hymenoptera: Braconidae) and *Metopius discolor* Tosquinet (Hymenoptera: Ichneumonidae (Laminou et al. 2023)).

Entomopathogens consist of a variety of organisms such as bacteria, fungi, viruses, protozoans and nematodes, which are known to cause diseases in insects (Deka et al. 2021). The FAW has shown susceptibility to infection by several entomopathogens, including *Bacillus thuringiensis* (*Bt*), *Metarhizium anisopliae*, *Beauveria bassiana* and *S. frugiperda* multiple *nucleopolyhedroviruses* (SfMNPV) (Abbas et al. 2022). These pathogens have demonstrated their ability to infect and affect FAW populations (Abbas et al. 2022).

Integrated pest management (IPM) against FAW in the context of climate changes

IPM is a science-based approach aimed at reducing the use of chemical pesticides for managing insects, weeds, plant diseases, etc., economically, safely and effectively by applying a variety of pest management methods (Guimapi et al. 2022). The focus is on the prevention, reduction and suppression of factors that lead to pest infestations (Helyer 2014). IPM has proven successful in addressing agricultural pest issues since the 1980s, with applications in forestry, structural landscape and home and garden pest management, leading to reduced costs, environmental risks and improved farmer health (Guimapi et al. 2022). The principle of IPM is based on a decision-making process to prevent pests' occurrence (Helyer 2014). In this approach, all relevant information and treatment methods are considered to effectively manage pests. To prevent organisms from becoming harmful, ecosystem management must be planned by identifying pests from beneficial organisms, monitoring their effect on plants and the environment such as climate activities, weather variations, etc., and making action decisions based on threshold levels. This inclusive approach combines agro-ecological, biological, physical, mechanical, behavioral and chemical methods. It also involves assessing the implemented management plans (Pretty and Bharucha 2015).

However, climate change becomes a major challenge to the agricultural sector, affecting host plant interactions, population dynamics, geographical distribution, activity of pests and efficacy of control methods (Sharma and Dhillon 2018) and subsequently affecting both crop production and food security. Changes in the geographical distribution of insect pests, driven by temperature variations, are particularly obvious as insect species migrate from tropical or subtropical regions to temperate regions and vice versa in areas where their host plants are cultivated (Sharma and Dhillon 2018). Climate change also affects the effectiveness of pest control methods, including host resistance, agro-ecological practices, biological control, biopesticide use and synthetic chemicals application (Aniwanou et al. 2021). The invasiveness, geographical distribution, phenology and natural enemies of FAW are largely influenced by temperature variations, crop damage level and increasing pest developmental length (Yan et al. 2022).

Host resistance: a key component in IPM strategies

Host plant resistance plays an important role in controlling insect pest's damage by reducing their ability to utilize plant species for food and reproduction. It consists of two dimensions: native genetic resistance and transgenic resistance (Fontes et al. 2002). Native genetic resistance involves identifying or developing plant germplasm with inherent resistance to specific insect pests, while transgenic resistance uses genes from external sources to confer resistance in the targeted plant species. This approach is a valuable component of IPM strategies for controlling pests such as the FAW (Prasanna et al. 2018). Significant progress has been made in both native genetic resistance and transgenic resistance methods, particularly in Africa, Asia and Latin America (Singh et al. 2022). The International Maize and Wheat Improvement Center (CIMMYT) has played a central role in identifying and developing diverse genetic resources in maize, including improved germplasm with traits such as drought tolerance, high yield, nitrogen use efficiency, heat tolerance, disease resistance and insect resistance. These resources have undergone rigorous testing, including greenhouse evaluations (Prasanna et al. 2018).

Native genetic resistance to FAW

Native genetic resistance to FAW has emerged as a promising approach for managing this destructive insect pest. Between 1970 and 1990, the International Maize and Wheat Improvement Center (CIMMYT) in Mexico identified genetic variation and the potential to breed native genetic resistance in cultivated plants, including maize, to manage various insect pests, including FAW, stem borers, weevils and post-harvest species such as the large grain borer (Archer et al. 1994). Native resistance in maize against FAW is based on multiple genes and is quantitative, conferring partial resistance (Prasanna et al. 2018). The insect-resistant maize inbred lines from Mexico have been used in Africa and Europe to develop FAW-resistant maize germplasm for some lepidopterans (Prasanna et al. 2018). Several studies have identified specific traits associated with native resistance to FAW, such as leaf architecture, the presence of trichomes and biochemical compounds like phenolic acids and terpenoids (Morales et al. 2021). However, native genetic resistance to FAW is often incomplete, and its effectiveness varies depending on FAW populations and environmental conditions. Breeding for FAW resistance presents challenges due to the complex genetic basis of resistance and the need for extensive field testing (Morales et al. 2021).

Transgenic resistance in FAW control

Transgenic resistance is a powerful technique that involves genetically modifying plants to confer resistance against specific pests or diseases (van Esse et al. 2020). In the case of FAW, transgenic crops have been developed using genes that provide resistance to this devastating pest (Prasanna et al. 2018). One notable example is the use of *B. thuringiensis* (*Bt*) technology, where the gene producing a toxic protein to FAW has been successfully incorporated into various crops. *Bacillus thuringiensis* is a soil bacterium that produces a protein toxic to specific insect pests, including FAW (Prasanna et al. 2018). Researchers such as Dong and Ronald (2019) and Dupuis (2002) have isolated the gene responsible for producing this protein and have successfully inserted it into the genome of various crops, including maize, cotton and soybean. When FAW larvae feed on these transgenic crops, they consume the *Bt* protein, leading to the rupture of their gut cells and subsequent mortality (Horikoshi et al. 2021). Transgenic resistance has demonstrated great promise in controlling FAW, offering effective and targeted pest management (Prasanna et al. 2018). However, it is crucial to address concerns regarding potential environmental impacts and human health risks associated with the use of transgenic crops (Sharma et al. 2002). Therefore, stringent regulations and extensive safety testing are essential before commercial approval and widespread adoption of transgenic resistance strategies (Sharma et al. 2002). While significant progress has been made in laboratory-based studies on host plant resistance, it is crucial to validate the efficacy of these approaches in field conditions but also take into account challenges such as the potential development of resistance by pests like FAW to genetically modified (GM) crops (Kumari et al. 2022). Despite promising results obtained in controlled environments, real-world agricultural systems pose unique challenges that require careful assessment to ensure the successful implementation of transgenic resistance strategies for FAW control.

Agroecosystem management for fall armyworm control

FAW is a highly destructive pest and thereby is a great threat to crops worldwide. FAW infests a wide range of plant species. To control FAW, farmers use various agro-ecological practices, which involve modifying the agroecosystem to minimize pest damage and enhance natural enemies' population.

Agro-ecological practices include all habitat management practices that can help to avoid or reduce damage by FAW through various mechanisms such as early planting. Timely planting plays a key role in minimizing food availability for FAW, as it primarily feeds on young plants (Boukari et al. 2022). Studies carried out by FAO (2018) reported a high yield decline in Kenya due to late maize planting compared to early ones. Weeds are major competitors for maize crops, affecting light, nutrients, water and space. Depending on the weed species, they can serve as either host plants for FAW or reservoirs for natural enemies. To mitigate weed competition, immediate planting after land preparation, planting in rows and timely post-planting weeding practices are highly recommended. Previous research in Africa demonstrated that intercropping of maize with legume crops, such as groundnut, beans and soybeans, limited FAW damage by 31–30, and 21%, respectively (Hailu et al. 2018). The use of push–pull strategies also showed interesting results in reducing FAW infestation and damage, particularly in some African countries with climate-adapted push–pull systems compared to monocropping (Midega et al. 2018). In addition, farmers developed methods such as FAW egg masses and larvae collecting from fields, which have proven to significantly reduce FAW populations (Kansiime et al. 2019). Natural enemies, including predators, parasitoids and pathogens, play an important role in controlling the FAW population (Agboyi et al. 2021). Some natural enemies, such as birds, and spiders, feed on FAW larvae, reducing their numbers (Harrison et al. 2019). Other natural enemies, including parasitoids and pathogens, can infect and kill FAW larvae, reducing their ability to cause damage. Farmers can improve the presence of natural enemies by reducing the use of insecticides, creating suitable habitats and adopting practices that enhance biodiversity. However, the use of natural enemies requires careful management to ensure that they do not harm non-target organisms or disrupt ecosystem balance (Agboyi et al. 2021). Agro-ecological practices offer effective strategies for managing FAW infestations and minimizing crop losses. Integrating these agro-ecological practices with other pest control methods can enhance the overall efficacy of FAW management strategies. Further research is needed to assess the practical application and sustainability of these agro-ecological practices in various agroecosystems.

Biological control of effective pests

Biological control involves utilizing living organisms to mitigate the population density and impact of specific pests, thereby minimizing damage and reducing pest abundance. These organisms play a crucial role in naturally regulating insect populations and can be classified into three groups: predators, parasitoids and entomopathogens, each playing a specific role in controlling pests (Eilenberg et al. 2001).

Parasitoids

Before the invasion of the FAW in Africa, indigenous and non-indigenous lepidopteran pests, particularly those from the families Noctuidae and Crambidae, had already emerged as significant threats to maize production across the continent. These pests had established associations with various natural enemies, making them viable candidates for augmentation and conservation biological control strategies (Abang et al. 2021).

Extensive surveys conducted across Western Africa (Ghana, Benin, Senegal), Eastern Africa (Ethiopia, Kenya, Tanzania) and Southern Africa (Zambia, Mozambique) have identified potential natural enemies of FAW (Durocher-Granger et al. 2020; Koffi et al. 2020b). These surveys documented seventeen species of parasitoids within the order Hymenoptera (primarily from the families Braconidae, Eulophidae, Ichneumonidae, Platygastridae, Trichogrammatidae) and two species of Dipterans (Tachinidae, Chloropidae). The identified parasitoids included the egg parasitoids (e.g., *Telenomus remus* Nixon, *Trichogramma* spp.), egg-larval parasitoids (e.g., *Chelonus bifoveolatus* Szépligeti, *C. curvimaculatus* Cameron) and larval parasitoids (e.g., *Coccygidium luteum* Brullé, *Cotesia icipe* Fernandez-Triana and Fiaboe, *Charops* sp., *Pristomerus pallidus* Kriechbaumer, *D. quadrizonula* Thomson, *Bracon* sp., *Anatrichus erinaceus* Loew, *Parapanteles* sp., *Diadegma* sp., *Enicospilus capensis* Thunberg, *Euplectrus laphygmae* Ferrière). Additionally, two species of larval-pupal parasitoids have been identified (e.g., *M.* cf. *testacea* Granger, *M. discolor* Tosquinet).

Studies on the natural enemies of FAW reveal a great diversity of parasitoids worldwide. (Ashley 1979) identified 53 species of parasitoids in North and South America, predominantly from the families Braconidae, Ichneumonidae and Tachinidae. Molina-Ochoa et al. (2003) recorded 150 species in the Americas and the Caribbean basin, spanning 14 families, with a similar predominance of Hymenoptera, Diptera and nematodes. Hoballah et al. (2004) identified 10 species of Hymenoptera in five families.

Parasitoids have demonstrated significant effectiveness in controlling FAW populations. They lay their eggs on or in the pest, with developing larvae feeding on the host, leading to its death. The introduction of parasitoids from the Americas, such as *T. remus*, has been successful in newly invaded areas (Molina-Ochoa et al. 2003). Parasitism rates of up to 64% were observed in Niger, following the release of *T. remus* in sorghum fields (Caniço et al. 2020). In Ghana, larval parasitism rates varied from 5.1 to 38.8% and with up to 75% in some sites (Agboyi et al. 2020).

Predators

Predators, organisms that hunt and consume multiple prey organisms during their lifetime, are crucial for biological control due to their ability to reduce pest populations. Three predator species associated with FAW in Africa include the hymenopteran species, *Pheidole megacephala* (Fabricius) (Formicidae) and the heteropteran species *Haematochares obscuripennis* Stål and *Peprius nodulipes* Signoret (Reduviidae) (Shylesha et al. 2018). Furthermore, Koffi et al. 2020b have identified additional predator species such as *Orius insidiosus* (Heteroptera: Anthocoridae), *Rhynocoris* sp., *Zelus renardii* (Heteroptera: Reduviidae), *Calleida* sp. (Coleoptera: Carabidae), *Cheilomenes sulphurea*, *Coccinella septempunctata*, and *Cycloneda sanguinea* (Coleoptera: Coccinellidae), *Euborellia annulipes*, *Forficula auricularia* and *Forficula senegalensis* (Dermaptera: Forficulidae), *Polyrhachis lamellidens* (Hymenoptera: Formicidae), *Chrysoperla carnea* (Neuroptera: Chrysopidae), and *Mantis religiosa* (Mantodea: Mantidae) as potential predators of FAW. In Benin, ant species have been also observed to significantly reduce FAW abundance in maize cropping systems (Dassou et al. 2021).

Entomopathogens

Fungi Entomopathogenic fungi (EPF) are specialized to infect insects, encompassing a great diversity of species distributed across 12 classes and six phyla within the fungal kingdom (Araújo and Hughes 2016). These pathogenic fungi for arthropods are primarily found in the divisions Ascomycota, Zygomycota and Deuteromycota (Samson et al. 1988), as well as Oomycota and Chytridiomycota (Shahid et al. 2012). The most well-known entomopathogens belong to the classes Entomophthorales (Zygomycota) and Hyphomycetes (Deuteromycota).

These fungi infect arthropods by adhering to their cuticle and penetrating through enzymatic degradation and mechanical pressure. Inside the host, they multiply in various tissues, destroying them and producing toxins (Idrees et al. 2023), leading to the insect's death in 3 to 14 days (Skinner et al. 2014). The appressoria and other specialized structures facilitate this penetration and propagation. The chitinous exoskeleton and cuticle of insects enable this penetration (Khan and Ahmad 2015).

Most EPF are hemibiotrophic, killing their hosts before producing spores, while some sporulate from the living bodies of their hosts (biotrophic) (Roy et al. 2006). In Hypocreales, the cadavers often remain intact with visible external mycelium (Inglis et al. 2012). The genera *Beauveria* and *Metarhizium* develop inside the host as yeast-like bodies, multiplying through budding (Araújo and Hughes 2016). The host's susceptibility to infection depends on environmental factors, including temperature (Vega et al. 2012).

EPF infect insects from almost all orders, including Hemiptera, Diptera, Coleoptera, Lepidoptera, Orthoptera and Hymenoptera (Idrees et al. 2022). These fungi, such as *Beauveria bassiana*, *Metarhizium anisopliae*, and *Nomuraea rileyi*, are used as biological control agents against various agricultural pests (Khan and Ahmad 2015). Akutse et al. (2019) tested 20 fungi against FAW, finding an efficacy of 92–96% for some isolates of *M. anisopliae*. Shahzad et al. (2021) observed a maximum efficacy of 79% for a strain of *B. bassiana*. Romero-Arenas et al. (2014) reported a 72.5% mortality rate with a native strain of *M. anisopliae*, compared to 32.5% for a commercial strain.

Nematodes Entomopathogenic nematodes (EPN), primarily from the families Steinernematidae and Heterorhabditidae, play a crucial role in the biological control of FAW. Species such as *Heterorhabditis bacteriophora*, *H. indica* and *Steinernema carpocapsae* are environmentally friendly alternatives to chemical pesticides (Mohan 2015). Associated with symbiotic bacteria, these nematodes increase their efficacy (Salvadori et al. 2012). For example, Andaló et al. (2010) demonstrated 100% larval mortality with species of *Steinernema* and *Heterorhabditis*. Garcia et al. (2008) found that 280 infective juveniles of *Steinernema* spp. were needed to kill 100% of third-instar FAW larvae in Petri dishes, compared to 400 juveniles of *H. indica* to achieve 75% mortality. Negrisoli et al. (2010a) showed that the association of nematodes with certain insecticides can improve FAW population control. The efficacy of *H. indica* is enhanced when mixed with the insecticide Lufenuron (Negrisoli et al. 2010b). Additionally, the nematode species *Hexamermis sp.* (Mermithida) has been identified as a natural enemy of FAW in maize fields in Africa, offering a promising new perspective for biological control (Tendeng et al. 2019).

Bacteria Entomopathogenic bacteria (EPB), such as *Bacillus thuringiensis* (*Bt*), play a crucial role in the biological control of FAW. These bacteria primarily infect insects through ingestion and the digestive tract, where they produce enzymes such as lecithinase, proteinase and chitinase to penetrate the hemocoel (Tanada and Kaya 1993b). They are classified among the Eubacteria, divided into Gram-negative (Gracilicutes) and Gram-positive (Firmicutes), with *Bacillus* being the predominant genus for biological control (Jurat-Fuentes and Jackson 2012). Among Bacillaceae, various species have been studied, showing varying efficiencies against FAW, although resistances to *Bt* Cry proteins have been observed in some populations (Dangal and Huang 2015). Recent studies on the microbiome of FAW have also highlighted the importance of microbial diversity in integrated pest management strategies (Botha et al. 2019).

Viruses Baculoviruses, belonging to a family of large, circular dsDNA viruses, primarily infect the larval stages of mainly lepidopteran species, particularly agricultural pests (Chateigner et al. 2015). Their genome size ranges from 80 to 180 kbp, and they are divided into four genera: *Alphabaculovirus*, *Betabaculovirus*, *Gammabaculovirus* and *Deltabaculovirus* (Jehle et al. 2006). The infection cycle of baculoviruses is biphasic, involving two types of virions: occlusion-derived viruses (ODVs) and budded viruses (BVs). ODVs initiate infection in the midgut, while BVs spread within the insect (Braunagel and Summers 2007). Extensive research has been conducted on baculoviruses for their application in biological control as biopesticides, as well as their use in biotechnological fields such as protein production and gene therapy studies in mammals (Makkonen et al. 2015).

Baculoviruses demonstrate a close coevolution with their hosts, resulting in a narrow host range primarily restricted to single or closely related species (Jehle et al. 2006). This high specificity enables targeted and specific control of insect pests without side effects on humans, the environment and beneficial insects. An example of an extremely narrow host range can be observed in alphabaculoviruses that infect *Spodoptera* species, including SfMNPV, SeMNPV, SpliNPV and SpltNPV (Jehle et al. 2006). SfMNPV, in particular, is a widely used virus candidate for FAW biological control (Jehle et al. 2006). Various isolates of SfMNPV are used, some of which exhibit high larval mortality in FAW (Lei et al. 2020). In populations affected by the virus, dead caterpillars serve as crucial sources of inoculum, contributing to the occurrence and maintenance of epizootics (Hussain et al. 2021). Epizootics are desirable for biological control as they facilitate the spread of the virus to healthy, non-infected caterpillars (Hussain et al. 2021). Other baculoviruses, such as SpliNPV, are known to infect FAW and are currently marketed for their biological control (Jehle et al. 2006). However, the effectiveness of other baculovirus isolates in controlling FAW is often lower in inter-host efficacy. Hence, it is crucial to obtain local baculovirus isolates of SfMNPV and/or *S. frugiperda granulovirus*

(SfGV) to effectively manage local FAW populations (Lei et al. 2020).

Baculoviruses offer several advantages over chemical pesticides, including their narrow host range, specificity and ability to control pests without harmful effects on humans, the environment and beneficial insects (Makkonen et al. 2015). Furthermore, baculoviruses hold potential for biotechnological applications in protein production and gene therapy (Makkonen et al. 2015).

Diversity of biocontrol agents (parasitoids, entomopathogens) and their interactions for FAW control

Synergistic interactions between parasitoids and entomopathogens were reported when applying both measures with enhanced host mortality (parasitoids also could carry entomopathogens with them or become vectors, helping in their dissemination within FAW populations, bearing thus great potential for improving FAW control strategies). Furthermore, the presence of entomopathogens can influence the behavior and fitness of parasitoids, potentially enhancing their effectiveness (Koller et al. 2023).

However, many studies showed that some entomopathogenic fungi were able to alter the oviposition behavior of parasitoids. This alteration results from direct competition between the parasitoids and the entomopathogenic fungi while sharing hosts, particularly when parasitized hosts are infected by the entomopathogen. Despite this competition, parasitoids have evolved a strategic response to avoid direct negative interactions. They exhibit adaptive behavior to avoid ovipositing within hosts already infected by the fungus (Rännbäck et al. 2015). However, despite the potential benefits of integrating parasitoids and entomopathogens, several issues need to be solved. These include the optimization of application methods, compatibility between biocontrol agents and other control measures and the identification of suitable combinations for different FAW populations and agro-ecosystems. Future research should focus on unraveling mechanisms underlying the interactions between parasitoids and entomopathogens, exploring their impact on FAW suppression and developing innovative strategies for their combined utilization.

Conclusion and recommendations

This review article emphasizes the importance of adopting a climate-responsive integrated pest management (IPM) strategy for the sustainable management of FAW and its impact on global agriculture. The increasing threat of FAW needs the implementation of sustainable and resilient approaches that can effectively mitigate its damage while minimizing its negative effects on crop production and food security. It highlights the significance of integrating various pest management techniques, including agro-ecological practices and biological control, within a climate-responsive framework. A holistic approach that considers the influence of climate changes on FAW populations, host plant interactions and the efficacy of control methods is crucial for successful long-term management.

Based on the existing information found from the literature, the following recommendations are proposed for the development and implementation of a climate-responsive IPM strategy for FAW:

1. Climate Monitoring and Early Warning Systems: Establish robust climate monitoring systems to track the environmental conditions that influence FAW outbreaks. Integrate climate data with pest monitoring to develop early warning systems that enable timely and proactive pest management interventions.
2. Resilient Crop Varieties: Promote the development and adoption of climate-resilient crop varieties that exhibit natural resistance or tolerance to FAW. Breeding programs should focus on enhancing traits such as plant architecture, leaf characteristics and secondary metabolite production that deter FAW infestation.
3. Agro-ecological management: Encourage the implementation of climate-adapted agro-ecological management that minimizes FAW damage and promotes ecosystem resilience. These practices may include timely planting, crop rotation, intercropping, trap cropping and proper irrigation.
4. Biological Control: Enhance the use of biological control agents, including parasitoids, predators and entomopathogens, as part of a climate-responsive IPM strategy. Research should focus on identifying and promoting effective biocontrol agents that can thrive under changing climatic conditions and exert sustainable control over FAW populations.
5. Integrated Pest Management: Promote the adoption of an integrated approach that combines multiple pest management tactics. This includes the judicious use of chemical control methods, such as insecticides, with careful consideration of their environmental impact and adherence to safety guidelines.
6. Farmer Education and Capacity Building: Provide farmers with training and capacity-building programs that focus on climate-responsive IPM strategies. Empower farmers with knowledge and skills to monitor pest populations, interpret climate data and make informed decisions regarding pest management practices.

Abbreviations

CABI	Centre for Agriculture and Bioscience International
CIMMYT	International Maize and Wheat Improvement Centre
dsDNA	Double-stranded deoxyribonucleic acid
EAT-USAID	Education and Training (EAT) project funded by the United States Agency for International Development
FAO	Food and Agriculture Organization
FAW	Fall armyworm
INSAE	Institut National de la Statistique et de l'Analyse Économique
IPM	Integrated pest management
kbp	Kilobase pairs
SeMNPV	*Spodoptera exigua* multiple nucleopolyhedrovirus
SfMNPV	*Spodoptera frugiperda* Multiple nucleopolyhedrovirus
SpliNPV	*Spodoptera litura* Nucleopolyhedrovirus
SpltNPV	*Spodoptera littoralis* Nucleopolyhedrovirus

Author contributions

KZ wrote the initial draft of the manuscript; EAD, AAS and JMT added their contributions and comments. All authors read and approved the final manuscript.

Availability of data and materials

Not applicable. No datasets were generated or analyzed in this review paper.

Declarations

Consent for publication

All authors read and approve the submission of the article.

Competing interests

The authors declare that there is no conflict of interest.

Received: 8 March 2024 Accepted: 29 July 2024
Published online: 11 September 2024

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