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REVIEW ARTICLE

Crop plants under siege: Molecular insights into plant-fall armyworm interactions and genetic tools for management

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Abstract

Spodoptera frugiperda (fall armyworm), an alien and highly destructive lepidopteran pest, presents a critical concern to global agriculture, particularly to staple crops such as sorghum, rice and maize. Its broad spectrum of hosts, rapid adaptability and increasing resistance to conventional insecticides have intensified the need for sustainable, plant-based pest management strategies. This review highlights recent molecular and genetic advances in enhancing crop resistance to *S. frugiperda*, with an emphasis on their relevance to crop improvement programs. Bt (*Bacillus thuringiensis)* transgenic crops producing Cry and Vip proteins have successfully impaired larval midgut activity while limiting impacts on non-target organisms. RNA interference (RNAi), particularly Host-Induced Gene Silencing (HIGS), offers a promising plant-mediated approach for silencing key insect genes involved in metabolism and development. CRISPR/Cas (Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR Associated Protein) genome editing also opens up new possibilities for developing pest-resistant crops and deepening our understanding of pest biology through functional research. Complementary approaches such as Sterile Insect Techniques (SIT) and gene drives show potential as part of integrated management strategies when combined with plant biotechnology. Despite these advances, challenges remain, including delivery efficiency, regulatory concerns, potential off-target effects and resistance evolution. The integration of genetic technologies with ecological pest management, biosafety frameworks and stakeholder engagement will be essential for achieving durable, sustainable fall armyworm control. Although genetic strategies like Bt, RNAi and CRISPR hold great promise for managing fall armyworm, each approach has specific limitations and varying levels of field applicability. This review critically examines these methods to provide a balanced and practical perspective for their use in crop improvement. This review underscores the central role of plant biotechnology in crop improvement to safeguard agricultural productivity against *S. frugiperda.*

Keywords: CRISPR/Cas; crop improvement; pest resistance; RNA interference; *Spodoptera frugiperda*; transgenic crops

Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), is a highly invasive and damaging pest responsible for significant yield reductions in numerous economically important crops across the globe (1). In India, agriculture is already threatened by several lepidopteran pests, including *S. litura* and *S. frugiperda*, both of which contribute to significant crop damage (2). FAW was first reported as an invasive species in Africa in 2016 and has quickly expanded throughout the Americas and Asia, reaching the Middle East and Indian subcontinent by mid-2018 (3, 4). In rice crops, the estimated annual losses of up to USD 13 billion are caused by fall armyworm infestations (5). In high-income countries like the US, yearly losses to *S. frugiperda* ranges between USD 39 million and 297 million. In Ethiopia, maize losses of $13 billion due to FAW infestation have been reported (6). Its rapid global spread is largely driven by climate change, particularly global warming, which has expanded its potential habitats. The pest's remarkable adaptability to diverse environmental conditions and high reproductive rate has made its management especially challenging, resulting in severe agricultural and economic consequences (7).

The molecular communication between insects and the relationship between pests and their host plants is vital in shaping the outcome of these interactions and ultimately determines the extent of crop damage (8). Climate warming contributes to the northward and altitudinal expansion of FAW infestations by increasing the size of overwintering zones. Rising temperatures allow FAW to survive in previously unsuitable regions by reducing winter-related mortality. In the United States, for example, warmer winters have enabled FAW populations to persist further north than historically observed, increasing the frequency and scale of annual infestations across the Midwest and into Canada (9). Plants recognize chewing insect attacks through a combination of mechanical damage and chemical cues. In addition to the physical injury caused by feeding, plants detect specific molecules present in the insect's oral secretions (OS), which are deposited at the wound sites during feeding (10). These secretions contain a complex mixture of saliva from mandibular and labial glands, gut-associated microbes and regurgitated plant material (11). Consequently, plants are exposed to diverse molecular signals from both insect and microbial origins. In response to tissue injury, plants also produce their own Damage-Associated Molecular Patterns (DAMPs), viz. oligosaccharides released from cell wall breakdown (12). When FAW larvae feed on cowpea (*Vigna unguiculata*) leaves, a fragment resulting from the breakdown of the plant's chloroplastic ATP synthase γ-subunit known as the cATPC protein is generated in the insect's gut called inceptin (13). The release of Herbivore-Induced Plant Volatiles (HIPVs), such as Green Leaf Volatiles (GLVs) derived from fatty acids and simple terpenoids, is vital in regulating plant defense systems (14). In agroecosystems, volatile compounds are key mediators of the complex three-level interactions among plants, herbivorous insects and their natural enemies. *S. frugiperda* relies on these volatiles to locate suitable host plants, while HIPVs often triggered by specific elicitors such as fatty acid-amino acid conjugates (FACs) present in the insect's oral secretions facilitate cross-trophic communication, offering valuable insights into plant-insect interactions and informing novel plant protection strategies (15, 16).

FAW, a polyphagous pest, FAW poses a significant threat to staple crops such as maize, rice, sorghum and cotton (17). The pest's ability to develop resistance to both traditional insecticides and Bt transgenic crops has increased the need for novel management approaches (1, 18). Continued dependence on chemical pesticides has contributed to resistance development and raised concerns about environmental and ecological impacts (19). The inconsistent use of insecticides across regions further complicates efforts to understand resistance mechanisms (20). In addition, the extensive and long-term use of pesticides has resulted in limited baseline susceptibility data, making it difficult to track how resistance develops over time (21). A *S. frugiperda* population collected in Puerto Rico exhibited extremely high resistance to Cry1F over 7700-fold in bioassays and cross-resistance to Cry1Ac (~12-fold), while remaining susceptible to Cry1A.105 and Cry2Ab2 (22).

The improper use of pesticides, combined with the ongoing invasion of pests like FAW, threatens food security and food safety (23). Infestations often go undetected until they have spread widely, making timely interventions difficult (24). This situation underscores the critical need for sustainable and effective strategies for pest control (25). Genetic technologies have long been explored as alternatives or complements to chemical control (26). Advances in biotechnology, particularly genetic engineering, offer promising solutions for managing invasive pests like FAW. Gene drive technologies aimed at controlling *S. frugiperda* are still in early experimental phases, with most research limited to laboratory proof-of-concept studies. Despite their potential for population suppression, these systems raise significant biosafety concerns, including risks of unintended ecological consequences, off-target genetic effects and challenges in containment and reversibility (27). These methods improve pest management by focusing on specific genes or traits, helping to minimize pesticide use and promote more sustainable farming practices (28).

Among these advances, genome editing technologies like CRISPR/Cas9 have demonstrated significant potential. These tools enable precise genetic modifications in both crops and insect pests, offering potential for pest-resistant plants, sterile insect populations and strategies to counter pesticide resistance. Ongoing research focuses on genetic interventions that disrupt pest biology to protect crops (29). Gene drive systems are also under development to spread lethal traits, such as female lethality, in pest populations, thereby reducing reproduction and population levels over time (30). Recent advances in functional genomics, including transcriptomic and metabolomic profiling, have deepened our understanding of plant responses to FAW feeding (31). While this review primarily emphasizes the molecular aspects of plant-FAW (*S. frugiperda*) interactions, it is important to ensure balanced coverage by systematically incorporating genetic approaches such as RNAi, CRISPR/Cas systems and gene drive technologies, alongside their applications in crop protection (32). Moreover, a more structured explanation of insect-plant interactions, including host selection, herbivory-triggered signaling and induced plant responses will provide a clearer understanding of the ecological and physiological dynamics that underpin these interactions (8). A coherent integration of these components will enhance the overall flow and practical relevance of the review.

At the same time, genetically modified (GM) crops producing insecticidal proteins from Bt, such as Cry and Vip toxins, have been extensively used and now cover more than 80 viz. of crop areas in certain regions (33). As crop plants worldwide come under increasing pressure from FAW, understanding the molecular dynamics of plant-FAW interactions is vital for developing effective, durable resistance strategies. This review provides a comprehensive overview of plant-fall armyworm interactions, with a particular emphasis on the molecular mechanisms that govern plant defense responses. It highlights key signaling pathways involved in herbivore recognition and response, including hormonal crosstalk and DAMPs. Advances in functional genomics are discussed, shedding light on the genetic basis of both host resistance and pest adaptability. The review also examines cutting-edge biotechnological approaches such as RNAi and CRISPR/Cas-based genome editing that are being employed to develop durable resistance in crops. Furthermore, it underscores the critical importance of resistance management strategies, ecological safety considerations and regulatory frameworks to ensure the sustainable deployment of these technologies in mitigating FAW infestations.

Plant-*S. frguiperda* interaction

When chewing insects feed on plants, they deposit complex OS at wound sites, which play a vital role in shaping plant defense responses (34). These responses are coordinated through intricate signalling networks triggered by herbivore-associated cues, including elicitors, effectors and physical damage, as well as the plant's own signaling molecules, such as phytohormones and volatiles (35). Pre-interaction events refer to the early, often passive, stages before direct physical contact between the insect and the plant. These include host plant location by the FAW through visual and olfactory cues, guided largely by plant-emitted volatile organic compounds (VOCs). FAW adults use these cues to identify suitable oviposition sites, while larvae rely on contact chemoreception to assess host quality. Understanding these early cues is crucial, as they set the stage for subsequent feeding and plant defense activation (36). To defend against herbivory, plants deploy a sophisticated system that integrates molecular, enzymatic and chemical mechanisms. Understanding the pathways triggered during herbivore attacks offers valuable insights into the functions of reactive oxygen species (ROS), secondary metabolites, antioxidant enzymes, phytohormones and the broader biochemical defenses employed by crops such as maize to combat FAW (37). OS of *S. frugiperda* play a pivotal role in modulating plant defense responses, not merely through wounding but by delivering specific elicitors such as FACs, notably volicitin, which trigger HIPVs and activate downstream signalling pathways (15).

One of the earliest plant responses to biotic stress is the oxidative burst, marked by rapid ROS production, including hydrogen peroxide (H_2O_2). These molecules are directly toxic to herbivores and serve as signalling agents that coordinate and amplify plant defences (37). In maize, infestation by *S. frugiperda* boosts the activity of antioxidant enzymes like superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT), which play a role in limiting ROS damage and supporting plant defense (37). Peroxidases, in particular, play a central role in modulating ROS levels and reinforcing plant cell walls, enabling rapid response to insect injury (38). Jasmonic acid (JA) is the primary phytohormone regulating plant defense against chewing herbivores such as *S. frugiperda*. Its signalling pathway is rapidly activated in response to tissue damage and insect oral secretions, triggering the expression of defense-related genes. This activation leads to the accumulation of protease inhibitors and various secondary metabolites that deter herbivory. In host plants like maize, JA levels are strongly upregulated following FAW infestation, underscoring its central role in mediating anti-herbivore defences (39).

Secondary metabolites add further complexity to plant-insect dynamics. These compounds serve dual functions: they can attract specialist herbivores adapted to specific hosts while deterring generalist or non-adapted species. In addition to their defensive roles, secondary metabolites support ecological balance by deterring pests and pathogens while attracting beneficial organisms like pollinators, seed dispersers and natural predators (40). JA is rapidly induced in plants upon *S. frugiperda* attack, activating defense genes involved in protease inhibitor production and secondary metabolism. It also promotes lignin biosynthesis and cell wall cross-linking, enhancing structural resistance to herbivory (41). The plant-FAW interaction is illustrated in Fig. 1.

Plant-derived elicitors triggered by FAW attack

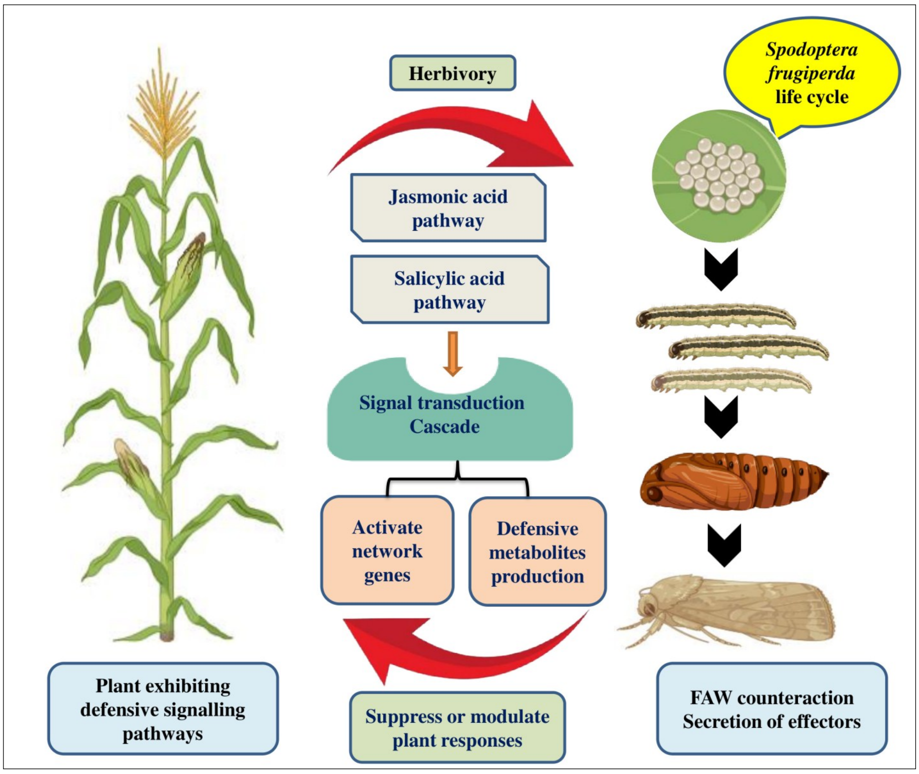

Fig. 1. Schematic representation of the molecular interaction between maize defensive signalling pathways and the life cycle of *S. frugiperda* (fall armyworm, FAW).

- Herbivory by *S. frugiperda* triggers jasmonic acid (JA) and salicylic acid (SA) signaling pathways in maize.
- These pathways activate a signal transduction cascade.
- The cascade leads to activation of defense-related network genes.
- Defensive metabolites are produced as part of the plant's protective response.
- *S. frugiperda* secretes effectors that suppress or modulate plant defense mechanisms.
- The right panel depicts the life stages of *S. frugiperda*: egg, larva, pupa and adult moth.
- The figure highlights the dynamic molecular interaction between plant defenses and insect countermeasures.

Plants are able to differentiate insect herbivory from mechanical injury by sensing herbivore-associated molecular patterns (HAMPs) that are released during feeding (42). In maize, *S. frugiperda* induces substantially lower levels of HIPVs compared to other lepidopteran pests, which contributes to its success as a maize herbivore (43). Larval feeding modifies maize's ability to generate defensive metabolites, notably boosting levels of compounds like linoleic acid that can harm *S. frugiperda* larvae (44). HAMPs are specific herbivore-derived signals that trigger targeted plant defenses, while DAMPs are plant-derived signals from wounded tissue that indicate general damage (45).

Both saliva and regurgitant of *S. frugiperda* are known to activate maize defenses. The application of regurgitant enhances the accumulation of flavonoids as key defensive metabolites and induces genes involved in flavonoid biosynthesis. Furthermore, the caterpillar's regurgitant contains a heat-stable effector that suppresses volatile emissions while promoting flavonoid-based defense (46).

Suppression of plant defense mechanism

In many plant-pest interactions, particularly with plant pathogens, pests suppress host defenses and modify plant traits by releasing effector molecules that disrupt host cellular processes (47). In *S. frugiperda*, glucose oxidase (GOX) present in saliva plays a significant role in modulating HIPV emissions during maize feeding. Silencing the gene encoding GOX reduces this enzyme's expression and impact (16). The GOX enzyme present in OS, catalyzes the oxidation of glucose to gluconic acid, H_2O2 as a by-product. This H_2O2 can suppress plant defense responses by interfering with herbivore-induced volatile emission and altering local signalling, potentially masking feeding sites from natural enemies or disrupting plant defense signalling pathways (48). Feeding by *S. frugiperda* induces linoleic acid accumulation in maize, which has been associated with negative effects on larval development and survival, suggesting a defensive role for this fatty acid in host plants (49).

Additionally, *S. frugiperda* can detoxify maize's primary defense metabolites, benzoxazinoids, by converting them into glycosylated forms (50). Salicylic acid in the insect's OS is also thought to weaken plant defenses by interfering with JA signalling pathways (51).

Metabolomic insights into plant defense and fall armyworm management

Gaining insights into maize's metabolic responses to *S. frugiperda* infestation is key to designing effective pest control strategies. Metabolomics offers a valuable tool for investigating the dynamic changes in maize metabolism induced by pest attacks. This approach offers a holistic strategy for FAW management by leveraging the plant's natural biochemical defenses. Through comprehensive metabolite profiling, metabolomics helps identify key compounds associated with resistance or susceptibility, offering new avenues for crop improvement and integrated pest management (52). Consider adding recent metabolomic studies in maize or FAW-infested systems to support applied relevance.

Key genetic approaches

Progress in molecular biology and functional genomics has transformed the design of genetic approaches for managing pests and vectors. Several genetic approaches have emerged as powerful tools to manipulate gene function, disrupt reproductive cycles or introduce beneficial traits into target populations. Each approach offers unique advantages depending on the target species, desired outcome and ecological considerations (Table 1). Some of the best known examples of all the key genetic approaches are listed into Table 2. To overcome the limitations of conventional pest control, genetic approaches have emerged as innovative, species-specific and environmentally sustainable alternatives. The Table 3 below compares traditional methods with genetic strategies across key parameters.

Traditional approaches like chemical pesticides provide quick control of *S. frugiperda* but pose risks of resistance and environmental harm (53). Biological controls offer sustainability but may lack consistency (54). Modern tools such as Bt crops, RNAi and CRISPR enable targeted action with reduced off-target effects, though challenges like delivery and regulation persist (32). Integrating these strategies lays the groundwork for focused, sustainable pest management.

This section outlines the fundamental principles and applications of these key genetic strategies, highlighting their role in modern biotechnology-driven solutions.

Plant based approaches

Resistant varieties and land races

Host plant resistance offers an economical and sustainable approach to managing insect pests. It is typically cost-effective, environmentally friendly, long-lasting and adaptable to local conditions, making it suitable for sustainable agriculture. In the case of FAW, resistant crop varieties have been developed by leveraging specific morphological characteristics that deter pest behaviour through antixenosis mechanisms (55). Maize genotypes such as BOZM 260, PA 091 and PARA 172 have been identified as valuable candidates for conferring resistance against FAW (56). The maize accessions Mp708 and FAW7050 exhibited resistance to FAW, attributed to elevated levels of defense-related proteins, increased

Table 1. Genetic control strategies: Mechanisms, targets and implementation challenges

Genetic Approach	Mechanism	Application Method	Key Targets/Genes	Advantages	Limitations
RNA Interference (RNAi)	Gene silencing via dsRNA	Topical spray, plant-mediated	Chitin synthase, V-ATPase, detoxification enzymes, metamorphosis related	Target-specific, environmentally safe	dsRNA instability, delivery challenges
Bt Transgenic Crops	Expression of insecticidal proteins	Transgenic maize/ cotton	Cry genes, Vip genes	Proven field use, effective against larvae	Resistance development
CRISPR/Cas9	Genome editing (knockout/knock-in)	Microinjection or viral vector	Phenotypic, reproductive, detoxification, olfactory genes	Precise gene targeting	Off-target effects
Gene Drive	Biased inheritance of engineered traits	Reproductive gene targeting	Sex distortion, sterility genes	Rapid population suppression	Ethical and ecological concerns
Sterile Insect Technique	Gamma rays, X-rays, or high-energy electron beam irradiation	Reproductive damage and sterility	Sterility	Reduce their sexual competitiveness	High initial cost, species-specific approach

Table 2. Genetic approaches for the management of *S. frugiperda*

Genetic Approach	Mechanism	Target Genes/Proteins	Scientific Findings	Key References
Transgenic Bt Crops	Expression of *Bacillus thuringiensis* (Bt) proteins to disrupt insect midgut	Cry1F, Cry1Ac, Cry1Ab, Cry1A.105, Cry2Ab2, Cry2Ae, Vip3A	Bt maize expresses Cry/Vip toxins that kill FAW with minimal impact on natural enemies; gene pyramiding enhances durability of resistance	(59, 33, 61, 106, 64)
RNA Interference (RNAi)	Sequence-specific gene silencing via dsRNA	SfCHSB, SfCHI, SfST, SfHEM, SfCYP321A7, SfCYP6AE43, COPIα, COPIβ, GSTU1, Spofr-AS, Spofr-AT2, SfT6	Gene silencing disrupts vital biological functions (molting, detoxification, immunity); effective delivery and target selection are critical	(67, 68, 69, 70, 71)
Sterile Insect Technique (SIT)	Release of irradiated sterile males to reduce population via mating	Chromosomal integrity affected by irradiation	High-dose X-ray (250 Gy) reduced egg hatch rates; optimal release ratio (12:1 -20:1) achieved 48 %-69 % leaf protection	(73, 74, 75, 76, 77)
CRISPR/Cas-based Genome Editing	Targeted gene disruption using Cas9/ Cas12a systems	sxl, BLOS2, TO, E93, Tssk2, SfDES9, Abd-A, Antp, dsx, Orco, yellow-y, PTTH	Editing reduced fecundity, altered development, impaired mating; Cas12a enabled multiplex edits with eye pigmentation marker	(18, 117, 90, 91, 92, 93, 95, 97, 98, 30)
Gene Drive Technologies	Biased inheritance systems to spread desired genes in populations	Selfish genetic elements or synthetic constructs	Enable rapid dissemination of traits like sterility or lethality; pose regulatory and ecological risks	(79, 80, 81, 82)

Table 3. Traditional methods v/s genetic approach

Method	Specificity	Sustainability	Regulatory Status	Resistance Risk	Environmental Impact
Traditional Approach					
Chemical Insecticides	Low	Low	Widely used	High	High
Biocontrol Agents	High	Depends	Approved	High	Very low
Genetic Approach					
Bt Crops	High	Medium	Approved	Moderate	Low
RNAi	Very high	High	Under evaluation	Low	Very low
CRISPR	Very high	Potentially permanent	Limited trials	Unknown	Depends
SIT	High	Potentially permanent	Approved	Very low	Low
Gene Drive	High	Permanent	Under evaluation	Moderate	Potential for irreversible ecosystem impact

concentrations of amino acids and glucose and a consistent accumulation of JA (57). Previous researchers reported that maize germplasm lines Mp708 and FAW7061 exhibited strong resistance to FAW infestation (58). Numerous resistant sources have been identified globally, offering valuable genetic material that can be utilized in breeding programs aimed at developing resistant or tolerant varieties and hybrids to minimize early-stage crop damage.

Transgenic crops

In the Americas, transgenic maize lines producing insecticidal proteins from Bt have been broadly adopted to manage *S. frugiperda*. These proteins, when ingested, disrupt the insect's midgut lining, causing death and thereby conferring resistance to host plant (59). Unlike traditional pesticides, Bt crops are more selective in their action, sparing beneficial predators and parasitoids. By targeting specific pests using Cry and Vip proteins, these crops contribute to ecological balance and reduce the dependence on synthetic insecticides, thus mitigating environmental contamination (33). Recent metabolomic studies in *S. frugiperda*-infested maize have revealed significant shifts in defensive compounds, such as benzoxazinoids, phenolics and fatty acids, highlighting their applied relevance for resistance breeding and pest management strategies (60).

Various Bt proteins have been incorporated into maize to enhance control of FAW, including Cry1 variants (Cry1F, Cry1Ac, Cry1Ab, Cry1A.105), Cry2 types (Cry2Ab2, Cry2Ae) and Vip3A. These toxins, commonly referred to as Cry proteins or delta endotoxins, are produced as crystalline inclusions during sporulation by Bt and are lethal to select insect pests (61). Metabolomics is increasingly used not only to diagnose plant responses to *S.* herbivory but also for the discovery of resistance-associated biomarkers that can guide breeding programs aimed at developing insect-resistant cultivars (62).

However, deploying genetically modified crops must align with regional biosafety regulations, particularly in maize-growing areas. Strong resistance management plans are crucial to slow the development of pest resistance. One important approach is gene pyramiding, which combines multiple Bt toxin genes within a single crop variety to extend effectiveness and reduce the risk of resistance (63). Extensive research has cataloged various Cry proteins globally and their expression in crops has yielded sustained efficacy against lepidopteran pests. This approach has already proven effective in curbing populations of long-established pest species (64). Cry proteins are crystalline δ-endotoxins produced during the sporulation phase of Bt. Once ingested by insect larvae, they are activated in the alkaline gut, bind to midgut receptors (such as cadherins and ABC transporters) and form pores in the epithelial membrane, leading to cell lysis and insect death. Vip proteins (Vegetative insecticidal proteins), secreted during the vegetative growth phase of Bt, act through a distinct mechanism binding to different receptors (e.g. ribosomal S2 proteins) in the midgut and causing epithelial damage, ultimately leading to insect mortality (65). Modern genetic tools like RNAi, CRISPR/Cas and gene drives offer precise and sustainable strategies for managing *S. frugiperda*. The following subsections outline their mechanisms, applications and progress in FAW control.

RNA interference (RNAi)

The concept of antisense-mediated gene silencing revolutionized the perception of RNA from a passive messenger to an active regulator of gene expression (66). RNAi has emerged as a highly specific and adaptable molecular tool for pest suppression and functional genomics. This technique enables precise disruption of key genes in insect pests, presenting a promising strategy for next -generation pest management. Nonetheless, RNAi effectiveness differs among insect orders and depends on both the choice of target genes and the success of dsRNA delivery methods (67).

In FAW, RNAi has effectively silenced essential genes like COPIα, COPIβ and GSTU1, interfering with vital biological functions and altering pest behavior. Research has also focused on silencing genes responsible for chitin synthesis (SfCHSB, SfCHI), sugar transport (SfST), immune function (SfHEM) and detoxification enzymes (SfCYP321A7, SfCYP6AE43) (68). For instance, silencing neuropeptides like Spofr/Manse-AS and Spofr-AT 2 has been linked to increased juvenile hormone levels and delayed development, implicating these genes in metamorphosis regulation (69).

Moreover, the gene SfT6 has been associated with Cry1Ca1 sensitivity; its downregulation via RNAi reduced Cry1Ca1 toxicity in larvae (70). RNAi efficiency is shaped by several factors, including the strength of the RNAi pathway in Lepidoptera, the stability of dsRNA, the chosen delivery method (such as oral administration or injection), sequence-specific resistance and genetic variation within pest populations (71). Despite its effectiveness, pyramiding insecticidal genes can face limitations such as cross-resistance among toxins with similar modes of action and gene silencing, which may reduce long-term efficacy (72).

Insect based approaches

Sterile insect technique (SIT)

The SIT is an eco-friendly, species-specific pest management strategy that releases sterilized males into the wild. When these males mate with wild females, it results in infertile pairings and a gradual reduction in pest numbers. Sterilization is typically achieved through irradiation methods such as X-rays, gamma rays or electron beams, which disrupt the reproductive chromosomes (73).

The competitiveness of irradiated males is critical. Although often slightly less competitive than wild counterparts, their impact can be enhanced by adjusting release ratios (74, 75). In FAW, studies using 250 Gy X-ray irradiation showed that at a 12:1 sterile-to-normal male ratio, egg hatchability dropped below 26 % and pest population suppression ranged from 58 % to 83 % (76). Another experiment demonstrated that a 100 Gy gamma ray dose induced partial sterility, which was inheritable, marking it as a potential tool for area-wide pest management. Despite its effectiveness, SIT requires continued innovation to improve cost-efficiency and scalability (77). SIT has shown success in controlling other lepidopteran pests, such as *Cydia pomonella* (codling moth) in Canada, providing valuable frameworks for potential FAW control strategies (78).

Gene drive technologies

Gene drive systems are genetic mechanisms that distort inheritance, promoting the transmission of a particular gene at rates higher than those expected under traditional Mendelian genetics (79). These can occur naturally or be synthetically engineered and have the potential to spread desirable traits throughout a pest population, such as sterility or susceptibility to a control agent (80, 81). Designing effective gene drive strategies requires an understanding of their spatial and temporal dynamics, which influence how fast and how far these traits can spread in a population (82). Such technologies are still in early stages for lepidopteran pests like FAW, but their potential for long-term population suppression is significant. Gene drive technologies have shown promising results in mosquito species such as *Anopheles gambiae*, where engineered drives targeting fertility genes significantly reduced vector populations, demonstrating potential for pest suppression in other insect systems (83).

Insect and plant based approach

Traditional strategies for managing FAW include cultural practices such as crop rotation, intercropping and timely sowing, which help disrupt pest colonization and reproduction (84). Mechanical methods like manual removal of larvae or egg masses and the use of pheromone or light traps are also practiced, particularly by smallholder farmers (85). Chemical pesticides remain widely used due to their rapid action, but over-reliance has led to resistance, environmental degradation and non-target impacts (86). Biological control using natural enemies such as parasitoids, predators and entomopathogenic microbes offers a more sustainable approach but often lacks consistency due to environmental variables (87).

To overcome these limitations, genetic technologies like CRISPR/Cas offer precise, scalable and environmentally friendly options for FAW management. These include engineering pest-resistant crops and modifying pest genomes to reduce their survival or reproduction. Integrating such tools with traditional approaches within an Integrated Pest Management (IPM) framework holds promise for more durable and targeted FAW control (88).

CRISPR/Cas-based genome editing

CRISPR/Cas9 genome editing offers a groundbreaking method for insect pest management by allowing precise disruption of target genes. However, its practical use requires solving key challenges, including efficient delivery into insect tissues and minimizing off-target effects (30). Cas12a (Cpf1) offers several advantages over Cas9 in insect genome editing, including a T-rich PAM requirement that expands targetable genomic regions and its ability to process multiple crRNAs from a single transcript enables efficient multiplex gene editing ideal for targeting multiple loci in pest species like *S. frugiperda* (89). CRISPR-Cas9 based knockout of sxl in FAW led to a marked decline in both fecundity and egg survival (18). Other gene targets like BLOS2, TO and E93 revealed vital roles in pigmentation and metamorphosis. Editing Tssk2 affected male fertility without disrupting female reproductive functions (90). Disruption of SfDES9, a gene involved in sex pheromone biosynthesis, affected female mating success, while knockout of Abd-A and Antp genes caused lethal and morphological defects (91, 92, 93). Editing the dsx gene led to malformed genitalia and reduced fertility in both sexes, while Orco, critical for olfactory communication, impacted male courtship behaviour (94, 95). Mutations in yellow-y and PTTH genes led to abnormal pigmentation and premature development, respectively. The experiments were conducted under laboratory conditions and demonstrated a significant reduction in insect fecundity (96, 97).

In addition, the Cas12a system recognizes T-rich PAM sequences and generates staggered DNA breaks, facilitates multiplex genome editing. Cas12a was used to target the TO gene in FAW and successfully induced eye pigmentation changes. In silkworms, Cas12a variants like FnCas12a were employed against BmNPV, suppressing viral replication in cell lines (98, 99). Although these discoveries are promising, ethical, safety and regulatory concerns must be addressed before wide-scale deployment (30). International frameworks such as the Cartagena Protocol on Biosafety provide guidelines for the safe use of living modified organisms, emphasizing risk assessment, public engagement and cross-border regulatory cooperation (100).

Future directions

To maximize the impact of genetic tools for *S. frugiperda* management, key challenges must be addressed, including scalable and efficient delivery systems. For RNAi-based control, the field delivery of dsRNA remains a major hurdle due to degradation and species-specific uptake variability (101, 102). Innovative delivery platforms such as nanoparticles and microbial vectors have shown promise in enhancing dsRNA stability and efficacy (103). Ensuring target specificity is also critical; although CRISPR/Cas is precise, off-target edits necessitate improved gRNA design and validation tools (104, 105). Resistance durability requires strategies like gene pyramiding, trait rotation and integration with ecological practices (106). Incorporating RNAi and CRISPR/Cas into IPM frameworks allows for targeted pest suppression while complementing biological controls.

In parallel, regulatory and ethical concerns must be addressed, especially for gene drives and genome editing in open systems. Strong governance frameworks, such as those outlined in the Cartagena Protocol, are essential for risk evaluation and public oversight (107, 108). Public perception significantly influences technology adoption; thus, participatory risk assessments and community engagement strategies are vital for transparency and trust-building (109, 110) (Table 4 and 5). Future direction includes advanced multi-omics approaches (e.g. transcriptomics, metabolomics) to decode dynamic plant-FAW interactions, as well as the identification of novel insecticidal targets through functional genomics. Strengthening interdisciplinary research that merges molecular biology, field ecology and socio-regulatory sciences will be crucial to translate lab innovations into sustainable, field-ready solutions.

Table 4. Host crop plants and fall armyworm susceptibility (111, 112)

Crop Plant	Stage of Attack	Symptoms of Damage	Natural Resistance
Maize	Seedling to maturity	Leaf feeding, whorl damage	Some landraces reported
Sorghum	Early vegetative	Leaf skeletonizing	Moderate resistance
Rice	Tillering	Dead hearts, leaf cutting	Rarely reported
Sugarcane	Late vegetative	Boring, shoot drying	Under-studied

Table 5. Molecular mechanisms in plant defense against *S. frugiperda*

Defense Type	Molecular Pathway Involved	Key Genes	Type of Response	Reference
Antixenosis	Jasmonic acid signaling	LOX (Lipoxygenase), AOS (Allene oxide synthase), JAZ (Jasmonate zim domain)	Feeding deterrence	(113)
Antibiosis	Protease inhibitors, lectins	PI-I, PI-II (Protease inhibitors), GNA (Galanthus nivalis agglutinin)	Inhibits digestion	(114)
Indirect defense	Volatile organic compounds	TPS (Terpene synthase)	Attracts parasitoids	(115)
Oxidative burst	ROS generation	RBOH (Respiratory burst oxidase homolog), SOD (superoxide dismutase)	Rapid defense signaling	(116)

Conclusion

A deep understanding of the molecular interactions between crop plants and *S. frugiperda* is crucial for designing innovative and long-lasting resistance strategies. These plant-pest interactions influence how effectively plants can detect, respond to and defend against herbivory at the biochemical and genetic levels. Integrating this knowledge with advanced genetic technologies such as Bt crops, RNAi, CRISPR/Cas-mediated genome editing and gene drive systems offers a powerful and targeted arsenal against FAW infestations. These tools disrupt key physiological pathways in the pest with high specificity, thereby minimizing harm to beneficial organisms and reducing environmental impact. Bt crops deliver insecticidal proteins to the pest midgut, RNAi silences essential genes, CRISPR introduces lethal mutations and gene drives facilitate the spread of engineered traits in populations. Together, these strategies provide long-term, ecologically sound pest control solutions. Embedding them within IPM programs, guided by insights into plant defense mechanisms, represents a significant step toward achieving sustainable crop protection and securing global food production.

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Authors' contributions

SG was responsible for planning, framework, editing, compilation and drafting the manuscript. KS, NP, BUR, KT and MP were involved in reviewing the manuscript. AK contributed to editing and software. RA was responsible for developing the concept, supervision and resource acquisition. KA contributed to editing and reviewing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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