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REVIEW

Biology, invasion and management of the agricultural invader: Fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

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Abstract

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is native to the Americas. It has rapidly invaded 47 African countries and 18 Asian countries since the first detection of invasion into Nigeria and Ghana in 2016. It is regarded as a super pest based on its host range (at least 353 host plants), its inherent ability to survive in a wide range of habitats, its strong migration ability, high fecundity, rapid development of resistance to insecticides/viruses and its gluttonous characteristics. The inherently superior biological characteristics of FAW contribute to its invasiveness. Integrated pest management (IPM) of FAW has relied on multiple applications of monitoring and scouting, agricultural control, chemical pesticides, viral insecticides, sex attractants, bio-control agents (parasitoids, predators and entomopathogens) and botanicals. Knowledge gaps remain to be filled to: (1) understand the invasive mechanisms of *S. frugiperda*; (2) understand how to prevent its further spread and (3) provide better management strategies. This review summarizes the biological characters of FAW, their association with its invasiveness and IPM strategies, which may provide further insights for future management.

Keywords: invasive alien species, fall armyworm, *Spodoptera frugiperda*, biological invasions, prevention, management, biosecurity

1. Introduction

Invasive alien species (IAS) seriously threaten agricultural and forestry ecosystems, biodiversity, human health, and cause significant economic losses. The emergence and invasion of IAS are closely linked with increasing trade and have become a major global issue. It is vital to effectively manage IAS (Wan and Yang 2016).

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Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is native to tropical and sub-tropical areas of the Americas (Sparks 1979). FAW has a strong migration ability and in the past three years it has invaded 47 African countries, 18 Asian countries and now Australia where it seriously threatens crop production (https://www.cabi.org/isc/datasheet/29810). FAW is polyphagous and two sympatric host-plant strains have been identified, the "corn-strain" (C-strain) feeding mostly on maize, cotton and sorghum and the "rice-strain" (R-strain) mostly associated with rice and various pasture grasses (Nagoshi and Meagher 2004). In the past few decades, FAW has developed multiple resistance and cross-resistance mechanisms against various kinds of insecticides and transgenic *Bacillus thuringiensis* (Bt) maize, due to the extensive use of the treatments to manage the pest. The synthesis of these biological characteristics has contributed to its spread and invasion, and increased its economical importance. The cost of controlling FAW is enormous: according to statistics from the Food and Agriculture Organization (FAO), Brazil alone spends US$600 million each year in attempts to control FAW (Wild 2017). Due to its perniciousness and invasiveness, it was rated as one of the top ten out of 1 187 arthropod pests by the Centre for Agriculture and Biosciences International (CABI) in the report "State of the World's Plants" in 2017 (Wild 2017).

2. Biological characteristics

IAS are superior in terms of their life cycle, genetics and evolution when compared with related non-invasive species. These characteristics are embodied in the morphology, physiology, ecology, genetics and behavior of the species. It is presumed that FAW invasiveness is associated with its superior biological characteristics including absence of diapause, short generation time, high fecundity, high polyphagy, long-distance migration ability and formidable resistance to insecticides, viruses and Bt toxin.

2.1. Absence of diapause, short generation time and high fecundity

FAW is a lepidopteran insect that undergoes holometabolous metamorphosis. Its life cycle includes egg (2–3 days), larvae (total six instars, 13–14 days), pupae (7–8 days) and adults (7–21 days). FAW has a generation time of approximately 30–40 days during the warm summer months (daily temperature of ~28ºC), and approximately 55 days in cooler temperatures (Prasanna *et al.* 2018; Sharanabasappa *et al.* 2018). It does not have the ability to diapause, so the number of generations occurring in an endemic area depends on environmental conditions, e.g., temperatures and host plants (Prasanna *et al.* 2018). In several regions of North America, FAW occurs seasonally through migration and it dies out in cold winter months. Whereas in the invaded countries, such as most of Africa, it occurs throughout the year with overlapping generations wherever host plants are available and climatic conditions are favorable (Abrahams *et al.* 2017). In southern China, it has been reported that FAW occurred all year round in the winter corn fields without diapause in winter (Qi *et al.* 2020), however, it could not survive when the average temperature was below 10°C for 8–10 days in Anhui Province (Xie *et al.* 2020). Average egg production per female is about 1 500 (a maximum of over 2 000) in Africa, demonstrating high fecundity (Prasanna *et al.* 2018). However, the egg production in India (1 064 eggs per female) and China (1 052–1 323 eggs per female when feeding on different maize varieties) are lower than that in Africa (Prasanna *et al.* 2018; Sun *et al.* 2020). Fecundity appears to be affected by variations in biotic (different hosts) and abiotic (temperature, humidity, etc.) factors.

2.2. Highly polyphagous

FAW has a wide host range of more than 353 recorded plants from 76 families, principally Poaceae (106), Asteraceae (31) and Fabaceae (31). Among them, it has strong preference for maize, rice, sorghum, cotton, pasture grasses and sugarcane (Montezano *et al.* 2018; Dumas *et al*. 2015), which are all major cultivated crops in America, Africa and Asia. Remarkably, FAW has developed two defined strains, C-strain and R-strain, which are morphologically identical but differ in host range (Groot *et al.* 2010), mating behaviors (Schofl *et al.* 2009), genetics (Dumas *et al.* 2015) and pheromone components (Groot *et al.* 2010) in natural and laboratory maintained populations (Velasquez-Velez *et al.* 2011; Dumas *et al*. 2015). The asymmetric distribution of the two strains with selective plant host preference is consistently observed. The C-strain feeds predominantly on maize, cotton, and sorghum while the R-strain feeds primarily on rice and pasture grasses (Dumas *et al.* 2015). However, in Nagoshi *et al.* (2014), a small number of individuals of one strain were found in host habitats dominated by the other strain. In addition, previous laboratory studies indicated that both strains can exploit preferred hosts of the other strain, suggesting that host preference observed in the field cannot fully be explained by differential larval feeding (Groot *et al.* 2010). In addition, strain-specific female oviposition associated with host-preference has been observed under laboratory conditions (Hay-Roe *et al.* 2011).

2.3. Long-distance migration ability

FAW displays high migratory ability (over 100 km per night), through which the moths can find a broad range of habitats within its preferred environmental conditions (Tendeng *et al.* 2019). Laboratory testing has shown that 3-day-old moths have the strongest flight capacity and average flight distance, flight duration and flight velocity in 24 h can be 29.21 km, 11.00 h and 2.69 km h^{-1}, respectively (Ge *et al.* 2019). In its native region, FAW populations can only overwinter in southern Texas and southern Florida, which are considered the northern-most winter-breeding areas available. However, in late summer, FAW are annually detected as far north as Ontario and Québec, Canada, which are considered to be migratory populations (Westbrook *et al.* 2016). The ability to migrate long distances has been confirmed by radar monitoring of noctuid moth species (including FAW) in Texas which identified a 400 km migratory flight displacement in 7.8 h (Westbrook 2008). In addition, in the Caribbean, the FAW can migrate from Puerto Rico to Barbados, a distance of more than 900 km (Nagoshi *et al*. 2017). In its invaded region in Africa and Asia, the spread of FAW also depends on its formidable flight capacity.

In China, FAW quickly invaded almost all maize belts within a year (Jiang *et al*. 2019). There are two main migratory routes for spread and reinvasion in China, the western and eastern routes. The origin of the western route is the westerly winter-breeding region (Myanmar/Yunnan, China) *via* Guizhou and Sichuan provinces through windborne transport. The origin of the eastern route is the easterly winter-breeding region (northern Thailand, Laos, Vietnam and Guangxi and Guangdong, China) *via* east-central China before arriving in the main maize belts (the Huang-Huai-Hai and Northeast Regions) with the help of Asian monsoons (Li *et al*. 2020).

2.4. Formidable adaptability to adversity

FAW has developed high resistance to a range of insecticides. In the mid-1980s, it developed resistance to carbaryl, methyl parathion, trichlorfon and diazinon in the southeastern United States (Pitre 1986). Subsequently, it developed more than 200-fold resistance to organophosphates and carbamate successively in North, Central and South Florida (Yu 1991). In 2002, two field FAW populations in Citra and Gainesville, Florida showed high resistance to carbaryl (626- and 1 159-fold), and moderate resistance to parathion-methyl (30- and 39-fold) (Yu and McCord 2007). In 2016, resistance ratios (RR) of various FAW populations from Mexico and Puerto Rico to chlorpyrifos, permethrin, flubendiamide, and chlorantraniliprole were up to 500-fold; RR to methomyl, cypermethrin and deltamethrin were 20- to 48-fold; and RR to ethyl dodecycin, dodecycin, emamectin benzoate and abamectin were 7- to 14-fold (Gutierrez-Moreno *et al*. 2019). By 2017, FAW had developed resistance to at least 29 insecticides, including carbamates, organophosphorus, pyrethroids and Bt insecticidal proteins in the Americas (https://www.pesticideresistance.org/). Currently, polyfungicide is the preferred pesticide for FAW control in corn fields and is applied three times during a growing season in Brazil. FAW has developed resistance to polyfungicide in Brazil, as well as to cyhalothrin, chlorpyrifos, and guanidine, and transgenic Bt maize Cry1F and Cry1Ab (Li Y P *et al*. 2019). Some studies have shown that the FAW population that invaded China carries resistance to organophosphate and pyrethroid pesticides (Zhang *et al.* 2020).

The transgenic insect resistant Bt maize has also been widely used to control FAW (Buntin *et al.* 2001). When exposed to Bt-maize toxin, FAW can develop monogenic (based on a single gene) or oligogenic (based on a few genes) resistance to these transgenic crop varieties (Huang *et al.* 2014). For example, Cry1F resistance in FAW has been detected in maize fields from Puerto Rico (Storer *et al.* 2010), southeastern mainland USA (Huang *et al.* 2014), Brazil (Farias *et al.* 2014), and Argentina (Chandrasena *et al.* 2018). Furthermore, it has developed resistance to other Bt proteins including Cry1Ac, Cry1Ab and Cry1A.105 (Storer *et al.* 2010).

Baculoviruses, the biological control agent, are widely used to control lepidopteran pests, and offers a promising alternative to chemical pesticides to avoid insecticidal resistance. However, several studies have now shown that FAW has developed resistance to the *S. frugiperda* multiple nucleopolyhedrovirus (SfMNPV) and *Autographa californica* multiple nucleopolyhedrovirus (AcMNPV) (Martinez *et al.* 2004; Haas-Stapleton *et al.* 2005).

3. Invasion mechanisms

Considering the abovementioned biological characteristics of FAW, and limited distribution in its native regions for more than two centuries, the sudden invasion and spread in Africa and Asia were unexpected. The fast rate of invasion has driven scientists to explore the underlying mechanisms. Genome research has greatly assisted in understanding the invasive mechanisms for alien species (Wan *et al.* 2019). With the development of genome sequencing, "Invasion Genomics" has increased investigations of invasion mechanisms as well as the prevention and management of IAS (Huang *et al.* 2019). In studies of FAW invasiveness, genomic data mining has improved our understanding of different biological characteristics and behaviors (Kakumani *et al.* 2014; Gouin *et al.* 2017; Nandakumar *et al.* 2017;

Gimenez *et al.* 2020; Gui *et al.* 2020; Xiao *et al.* 2020; Zhang *et al.* 2020).

3.1. High adaptability to diverse hosts

The expansion of gene families is generally believed to be associated with the invasiveness success of invasive species. That is especially the case for chemosensory and detoxification related gene families, which contribute to the polyphagy and adaptive evolution to host plants for the invasive species (Huang *et al.* 2019). For example, the gustatory receptor (GR) genes of invasive polyphagous moths *Helicoverpa armigera*, *Spodoptera litura* and *Hyphantria cunea* were significantly expanded compared to monophagous or oligophagous non-invasive moths (Cheng *et al.* 2017; Pearce *et al.* 2017; Wu N *et al.* 2018). The detoxification gene families cytochrome P450 (P450), UDP glucuronosyltransferase (UGT), glutathione *S*-transferase (GST) and carboxylesterase have expanded in the invasive species *H. armigera*, *Bemisia tabaci* and *S. litura*, which contribute to their adaptive success in diverse host plants (Chen *et al.* 2016; Cheng *et al.* 2017; Pearce *et al.* 2017). Similarly, the GR gene family has expanded dramatically in FAW, especially the recurrent tandem duplications of "bitter" receptors, compared with non-polyphagous lepidopteran species (Gouin *et al.* 2017; Xiao *et al.* 2020). In addition, P450 and GST were also expanded in genomes of both strains (Gouin *et al.* 2017; Gui *et al.* 2020). There are signatures of positive selection and copy number variation (CNV) in these genes involved in chemoreception, detoxification and digestion (Gouin *et al.* 2017; Gimenez *et al.* 2020).

3.2. Insecticide resistance or tolerance

The resistance or tolerance mechanisms of FAW to insecticides compose two aspects: the detoxification metabolic mechanism and the target resistance mechanism (Zhang *et al.* 2020). The increased activity of detoxification metabolizing enzyme is an important reason for the FAW insecticide resistance (Yu *et al.* 2003). Therefore, some of the above detoxification related gene families, such as mixed function oxidases (MFO), GSTs, P450, esterases (ESTs), alkaline phosphatase, trypsin, aminopeptidase and chymotrypsin (Table 1) are also associated with insecticide resistance, which contribute to the invasiveness of FAW (McCord Jr and Yu 1987; Yu *et al.* 2003; Zhu *et al.* 2015).

Previous studies have indicated that the amino acid substitutions in acetylcholinesterase (AChE), VGSC and RyR result in resistance or tolerance to organophosphate, pyrethroid and diamide insecticides, respectively (Table 1). A genome-wide association study (GWAS) of 105 FAW samples from 16 provinces in China indicated that the single-nucleotide polymorphisms (SNPs) in AChE (AA201, AA290) contribute to its high risk of resistance to conventional pesticides and confirmed that the FAW population invading China is resistant to organophosphate and pyrethroid insecticides by scanning of resistance-related genes (Zhang *et al.* 2020) (Table 1).

3.3. Bt crop resistance

The resistance mechanisms of target pests to Bt crops are composed of toxin activation, mutation of toxin receptor and regulation of the immune system (Xiao and Wu 2019). Until

Table 1 Mechanism of pesticide resistance or tolerance reported in the fall armyworm

Active ingredient	Resistance category	Mechanism of resistance or tolerance	Reference
Acetylcholinesterase (AChE)			
Methyl-parathion	Detoxification metabolic	Increased activity of mixed function oxidases (MFO), glutathione *S*-transferases (GSTs) and esterases (ESTs)	McCord Jr and Yu (1987); Yu *et al.* (2003)
Carbaryl	Detoxification metabolic		
Acephate	Detoxification metabolic	Increased activity of alkaline phosphatase, aminopeptidase, trypsin and chymotrypsin, P450, GSTs	Zhu *et al.* (2015)
Chlorpyrifos	Target resistance	Mutation of AChE (A201S, G227A, F290V; AA201 and AA290)	Carvalho *et al.* (2013); Zhang *et al.* (2020)
Malathion	Target resistance	Mutation of AChE (AA201 and AA290)	Zhang *et al.* (2020)
Phoxim	Target resistance	Mutation of AChE (AA201 and AA290)	Zhang *et al.* (2020)
Ryanodine receptor (RyR) allosteric modulator			
Chlorantraniliprole	Target resistance	Mutation of RyR (I4790M)	Boaventura *et al.* (2020)
Voltagegated sodium channel (VGSC)			
Lambda-cyhalothrin	Target resistance	Mutation of VGSC (T929I, L932F, L1014F)	Carvalho *et al.* (2013); Zhang *et al.* (2020)
Beta-cypermethrin	Target resistance	Mutation of VGSC (AA932)	Zhang *et al.* (2020)
Fenvalerate	Target resistance	Mutation of VGSC (AA932)	Zhang *et al.* (2020)
Deltamethrin	Target resistance	Mutation of VGSC (AA932)	Zhang *et al.* (2020)

recently, there was very little knowledge on the mechanism of FAW Bt-resistance. Some research showed that toxin activation and mutation of toxin receptors are associated with FAW resistance to Bt toxin proteins. The down-regulated expression of Bt receptor alkaline phosphatase (ALP) in FAW populations was related to Cry1F resistance (Monnerat *et al.* 2015; Jakka *et al.* 2016). The mutation of ABCC2 (ATP-binding cassette sub-family C member 2), which is the receptor of both Cry1F and Cry1A.105, resulted in cross-resistance to Cry1F and Cry1A.105 (Flagel *et al.* 2018). The down-regulated expression of serine protease may reduce the FAW sensitivity to Cry1Ca1 toxin, which indicated that serine protease is involved in toxin activation (Rodriguez-Cabrera *et al.* 2010).

3.4. Mechanism of migration and high fecundity

The comparative genomic analyses between FAW and the related species *S. litura*, showed that the elevated ratio of potential host adaptation genes were contributing to FAW invasiveness. Twenty-three of those invasiveness-related genes were under positive selection, including: 1) gustatory receptor (GR) and acetaldehyde oxidase, which contribute to host detection in invasion and expansion processes; 2) mitochondrial adenosine triphosphate synthase β-subunit and ferritin heavy chain, which contribute to long-distance migration during invasion and rapid expansion, due to enhanced locomotion and resistance; and 3) replacement in one site of chorion protein, which affects the protein function to maintain higher hatchability and ensure genetic resources for expansion (Cui *et al.* 2020).

4. Invasion, outbreak and damage

In the past two centuries, the distribution of FAW was limited to tropical and sub-tropical areas in the Americas, with several outbreaks at irregular intervals (Sparks 1979). However, in recent years, it has successfully invaded into Africa and Asia, and is in the process of invading Oceania (Fig. 1).

FAW was first detected in West and Central Africa in January 2016, and spread to the islands of São Tomé and Príncipe within 2 months (Goergen *et al.* 2016), followed by sudden outbreaks in 46 African countries including many countries in central, eastern and southern Africa (Fig. 1) (https://www.cabi.org/isc/datasheet/29810). Molecular identification of FAW showed that the invasive population in Africa includes both C-strain and R-strain (Assefa 2019). The invasion into India was first reported in May 2018 (Mahadevaswamy *et al.* 2018; Sharanabasappa *et al.* 2018), and then quickly spread to Sri Lanka, Thailand, Yemen, Nepal, Myanmar and Bangladesh (Farmer 2019). Genetic diversity studies showed that the FAW population in India belongs to R-strain based on polymorphisms in the cytochrome oxidase subunit I (*COI*) gene (Mahadevaswamy *et al.* 2018) and triose-phosphate isomerase (*Tpi*). These findings suggest a small, shared founder population as the source of FAW in Africa and India (Nagoshi *et al.* 2019). FAW invaded Yunnan, China in December 2018 (Sun *et al*. 2021), spread rapidly and subsequently outbreaks were detected in 26 provinces (autonomous regions, municipalities) (Jiang *et al*. 2019). Both *COI* and *Tpi* showed that the invading populations in China were C-strain (Zhang *et al*. 2019). According to reports from the European and Mediterranean Plant Protection Organization (EPPO), FAW was first found in January 2020 on the islands of Saibai and Erub, in the Torres Strait and then at Bamaga, in the northern Queensland, Australia. By May of 2020, it had spread to 11 regions of Queensland, three regions of the Northern Territory, and three regions of Western Australia (https://gd.eppo.int/taxon/LAPHFR/distribution). In addition, Timor-Leste and Mauritania have also confirmed FAW in 2020 (http://www.fao.org/fall-armyworm/monitoring-tools/faw-map/en/).

Maize yield losses have been estimated at 15 to 73% when infested with FAW (Hruska and Gould 1997). The annual economic losses in Ghana and Zambia have reached US$177.3 million and US$159.3 million, respectively (Abrahams *et al*. 2017). Collectively, maize, rice, sorghum and sugarcane, have suffered total economic crop losses of US$13 billion per annum in sub-Saharan Africa (Abrahams *et al*. 2017). Estimation of the potential economic loss of maize in China caused by FAW indicates a range from US$5.4–47 billion per annum (Qin *et al.* 2020).

5. Prevention and management

5.1. Monitoring and scouting in fields

For migratory invasive insects, monitoring and scouting are extremely important for timely responses to the dynamics of pest occurrence and development as well as crop health. This enables the formulation of comprehensive measures for better prevention and control. These actions must be taken based upon minimum cost parameters to keep the FAW population below the economic threshold level.

In China, entomological radar and vertical-pointing searchlight-traps have been used to monitor the population dynamics of migratory insects, such as *H. armigera* (Feng *et al.* 2009), *Cnaphalocrocis medinalis* (Fu *et al.* 2014), *Mythimna separata* (Zhao *et al.* 2009), *Loxostege sticticalis* (Feng *et al.* 2004), and *Spodoptera exigua* (Feng *et al.* 2003). The monitoring result of vertical-pointing searchlight-traps showed that the FAW population was first trapped in

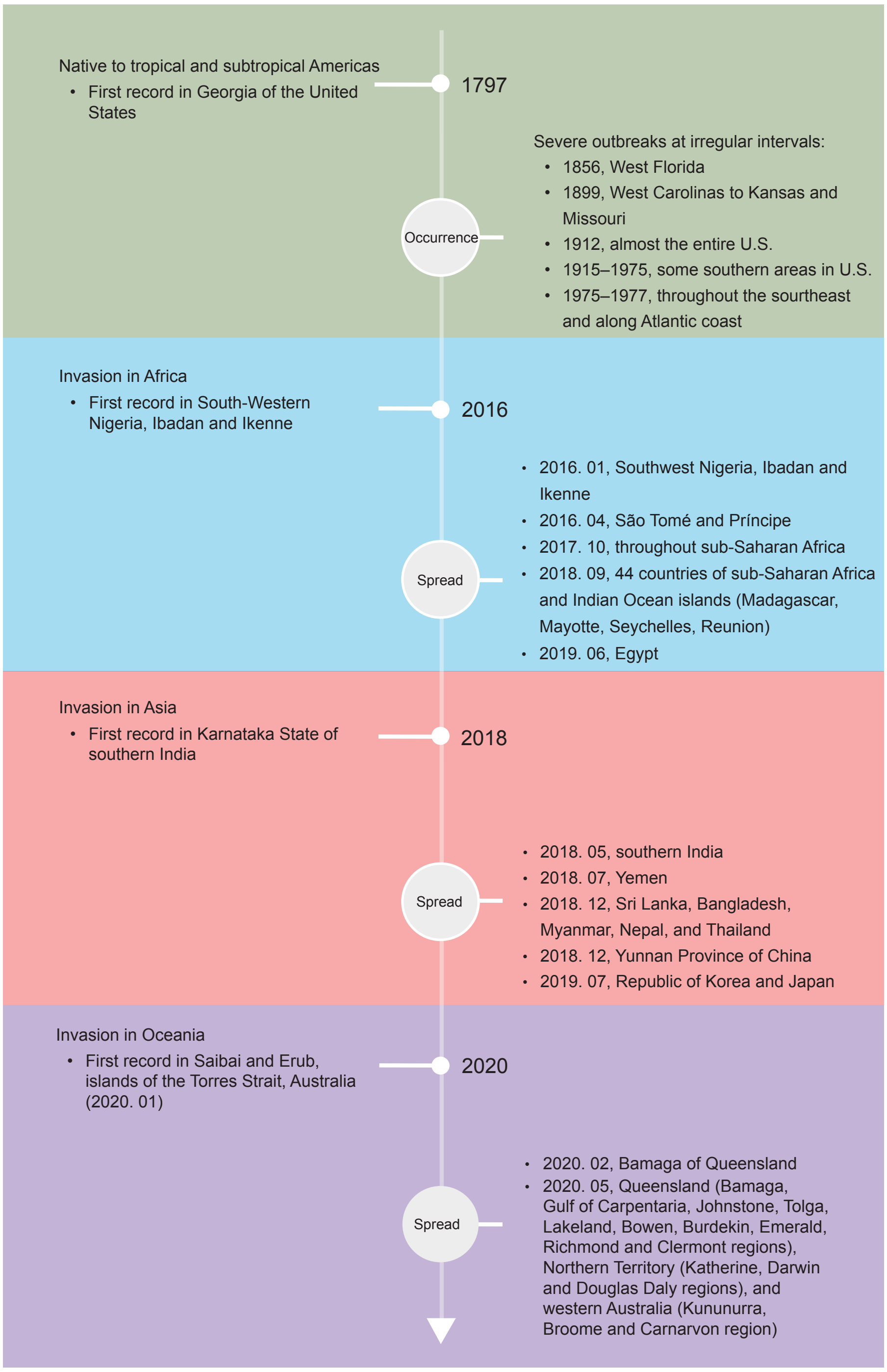

Fig. 1 Invasion and outbreak of fall armyworm (FAW) in its native and invaded regions.

June and the observation peaks appeared from August to October in eight provinces of China in 2019 (Jiang *et al.* 2020). The blacklight and commercial male traps are recommended to farmers to monitor the field population dynamics of FAW. It is recommended that the height of pheromone traps hanging should be 1.5 m above ground and the interval between two traps should be 50 m (Malo *et al.* 2013).

Farmers are recommended to scout the different plant growth stages and crop damage to determine the optimum stages for spraying insecticides based on action thresholds, which are expressed as percentages of plants with typical FAW damage/injury symptoms (Prasanna *et al.* 2018). For the early whorl stage, from vegetative emergence (VE) to 6-leaf (V6) stages, the action threshold is 10–30% of the seedlings infested as well as the tassel and silk stages, while it is 30–50% for the late whorl stage (Prasanna *et al*. 2018). For farmers, the method of scouting in the field involves randomly selecting five locations, or using a "W" or "Ladder" pattern, while avoiding edges (possibility of edge effects). Twenty plants should be examined for each location (Prasanna *et al.* 2018).

5.2. Agricultural control

For smallholders, a series of low-cost agricultural control measures is an optimum option to implement as part of an effective IPM strategy against FAW. These agricultural approaches use the complex interactions between organisms and their environment to develop techniques to minimize the damage of pests on crops. In this review, a few agricultural measures that can be effective against FAW are discussed.

Traditional pre-planting, using some measures such as deep ploughing can decrease the FAW population in advance of sowing by exposing pupae to sunlight and predatory birds (Prasanna *et al*. 2018). Planting transgenic/Bt insect-resistant maize varieties is also a very effective measure to decrease the damage by FAW and is an alternative method to pesticides. Bt maize is commonly used to control FAW, influencing the bioindicators of FAW including oviposition preference (Tellez-Rodriguez *et al*. 2014), larval dispersal (Malaquias *et al*. 2017), control efficacy (Horikoshi *et al*. 2016; Botha *et al* 2019) and fitness costs (Jakka *et al*. 2014). The use of transgenic maize expressing bacterial Bt proteins (e.g., Cry1F) has been commercially employed to control this pest since 2003 (Siebert *et al*. 2008). As stated above, in 2010, resistance of the FAW population to transgenic maize with Cry1F toxin was first detected in Puerto Rico (Storer *et al*. 2010). Developing new insecticidal targets is an urgent need due to the emergence of Bt-resistant FAW populations.

Other mechanical or physical methods are also recommended as management options, for smallholders, to reduce the economic loss caused by FAW, such as handpicking and crushing the egg masses and larvae, or using ash, sand, sawdust or dirt into whorls to desiccate young larvae (FAO 2018). The "push and pull" strategy is another very useful agroecological method to control agricultural pests such as FAW. Planting minor attractant plants or repellent plants in crop fields can decrease pest damage to major crops. Field experiments showed that maize intercropped with other plants helps to reduce the abundance of FAW. Compared with monocultured maize, intercropping with leguminous crops of bean (*Phaseolus vulgaris*), soybean (*Glycine max*) and groundnut (*Vigna unguiculata*) significantly decreases FAW attack by up to 40% (Hailu *et al.* 2018) (https://www.insectslimited.com/history-of-pheromones). Some other plants, i.e., row intercropping with marigold (*Tagetes erecta*) and border intercropping with Napier grass (*Pennisetum purpureum*) have also been reported as effective for sustainable management of FAW (http://www.icipe.org/news/icipe-push-pull-technology-halts-fall-armyworm-rampage).

5.3. Divergence of sex pheromone and sex attractant application

Sex pheromones are applied worldwide for pest control as they present several advantages compared to traditional pesticides, such as nontoxicity, high specificity, and the possibility to apply minimal dosages. The first major pheromone component of FAW, (Z)-9-tetradecenyl acetate (Z9-14:OAc), was identified in 1967 (Sekul and Sparks 1967). Subsequently, other minor components were identified by analyzing the female pheromone glands and volatiles, including dodecyl acetate (12:OAc), (Z)-7-dodecenyl acetate (Z7-12:OAc), 11-dodecenyl acetate (11-12:OAc), and (Z)-11-hexadecenyl acetate (Z11-16:OAc) (Tumlinson *et al.* 1986). The effectiveness of trapping in fields was first investigated in 1976 (Mitchell and Doolittle 1976). Since then, sex pheromones have been used to suppress and monitor FAW populations worldwide for more than 40 years and research has focused on investigating their differences and applications.

The practical effect of sex pheromones varies with geographical ranges and strains. The pheromone lures from North America and Europe were not effective against FAW in Brazil (Batista-Pereira *et al.* 2006), Costa Rica (Andrade *et al.* 2000) or Mexico (Malo *et al.* 2001). Some evidence points to geographic differences of the female sex pheromone blend in FAW (Batista-Pereira *et al.* 2006; Unbehend *et al.* 2014; Cruz-Esteban *et al.* 2018). For example, while females from Brazil (Batista-Pereira *et al.* 2006) produce (E)-7-dodecenyl acetate (E7-12:OAc), those from Florida, Louisiana or French Guyana do not (Tumlinson *et al.* 1986; Groot *et al.* 2008; Lima and McNeil 2009). For the Florida populations, the ratios of sex pheromone components from female glands were 4.9 (12:OAc):3.1 (Z7-12:OAc):1.7 (11-12:OAc):3.5 (Z11-16:OAc):86.9 (Z9-14:OAc). For the Brazilian populations, the sex pheromone consisted of Z7-12:OAc, E7-12:Ac, 12:OAc, (Z)-9-dodecenyl acetate (Z9-12:OAc), Z9-14:OAc, (Z)-10-tetradecenyl acetate (Z10-14:OAc), tetradecyl acetate (14:OAc)/(Z)-11-tetradecenyl acetate (Z11-14:OAc), Z11-16:OAc, and their relative proportions were 0.8:1.2:0.6:traces:82.8:0.3:1.5:12.9, respectively (Batista-Pereira *et al.* 2006). In addition, by adding E7-12:Ac to the major component Z9-14:OAc and critical secondary component Z7-12:OAc, the effectiveness of trapping for Brazilian populations was significantly improved (Batista-

Pereira *et al.* 2006).

Two groups have independently studied the strain-specific differences of the component concentration of sex pheromone in female FAW under laboratory and field environments. Both studies have shown that there are strain-specific differences in relative amounts of the different pheromone components (Groot *et al.* 2008; Lima and McNeil 2009; Unbehend *et al.* 2013). One group found a significantly higher relative amount of Z11-16:OAc, and lower relative amounts of Z7-12:OAc and Z9-12:OAc in the corn-strain females compared to rice-strain females in the Florida population (Groot *et al.* 2008). The other group found the opposite result with a significantly larger relative amount of Z9-14:OAc as well as lower relative amounts of Z7-12:OAc and Z11-16:OAc in corn-strain females compared to rice-strain females in the Louisiana population (Lima and McNeil 2009). These diametrically opposed results suggest that both geographic variation and strains contribute to the differentiation of sex pheromone composition of FAW females.

In China, the effects of four different commercial sex attractants on trapping FAW showed that the production of Shenzhen Bailebao Bio-Agricultural Technology Co., Ltd., was optimum to monitor the occurrence dynamic of FAW. The average number attracted by BLB lure was 137 individuals per trap, and the trapping performance of BLB lure was stable within the first 30 days. However, the numbers significantly decreased during the following 30 days, particularly after 50 days (Che *et al.* 2020).

5.4. Chemical control

Chemical insecticides are heavily used to control FAW (Yu *et al.* 2003). Before the 1980s, insecticides, from organophosphates (methyl parathion, etc.), carbamates (carbaryl, etc.) to pyrethroids (cypermethrin, etc.), were the main method to control FAW in most countries in the Americas (Pitre 1986). Until recently, more than 57 active chemical ingredients with nine modes of action were used against FAW (Table 2). Among them, 47 active ingredients were used in the Americas in FAW native regions, while 34 and 20 active ingredients were respectively used in FAW invaded regions in Africa and Asia (Prasanna *et al.* 2018; Gutierrez-Moreno *et al.* 2019).

In the native regions in the Americas, FAW has developed resistance to more than 29 insecticides with six modes of action (Gutierrez-Moreno *et al.* 2019). Some insecticides are prohibited in the invaded regions of Africa and Asia, such as methomyl (Pitre 1988), thiodicarb (Gutierrez-Moreno *et al.* 2019), tralomethrin and fluvalinate (Leibee and Capinera 1995) (Table 2), due to the high resistance developed in FAW. To delay the development of insecticide resistance, eight compound preparations (emamectin benzoate×indoxacarb, emamectin benzoate×hexaflumuron, emamectin benzoate×lambda-cyhalothrin, emamectin benzoate×chlorfenapyr, emamectin benzoate×lufenuron, emamectin benzoate×tebufenozide, lambda-cyhalothrin×chlorantraniliprole, and lambda-cyhalothrin×diflubenzuron) were recommended by the Ministry of Agriculture and Rural Affairs of China for emergency prevention and control of FAW as there are no currently legally registered insecticides for FAW.

Although 57 chemicals are listed in Table 2 that could be used against FAW, some of them are highly hazardous pesticides (HHPs) that are acknowledged to present particularly high levels of acute or chronic hazards to human health or the environment according to internationally accepted classification systems such as the World Health Organization (WHO) and the Globally Harmonized System of Classification and Labelling of Chemicals (GHS). If these HHPs are used, adequate precautions must be taken during application.

5.5. Biological control

Biological control can reduce contamination of the environment and offer an economically and environmentally safer alternative to synthetic insecticides that are currently being used. Natural enemies include parasites, predators and entomopathogens. A great diversity of natural enemies of FAW has been reported in the Americas, Africa, and Asia (Molina-Ochoa *et al.* 2003; Prasanna *et al.* 2018; Shylesha *et al.* 2018). As the native regions for FAW, the Americas have the most abundant parasitoids (~150 taxa) against FAW, which have been recorded from 13 families, nine in Hymenoptera, and four in Diptera (Molina-Ochoa *et al.* 2003). Among them, the egg parasitoids (*Trichogramma pretiosum*, *T. atopovirilia* and *Telenomus remus*) (Beserra *et al.* 2005; Pomari *et al.* 2013), larval parasitoids (*Campoletis sonorensis* and *Chelonus insularis*) (Jourdie *et al.* 2009), and pupae parasitoids (*Diapetimorpha introit* and *Ichneumon promissorius*) (Molina-Ochoa *et al.* 2003) were widely used to control FAW. In Africa, eight parasitoids of FAW from three families were recovered in West, Central and East Africa, including *Chelonus curvimaculatus*, *Chelonus cf maudae*, *Coccygidium luteum*, *Cotesia icipe*, *Cotesia* sp., *Charops ater*, *Charops* sp., and *Telenomus* sp. Studies in southern India recorded five species of larval parasitoids: *Coccygidium melleum*, *Campoletis chlorideae*, *Eriborus* sp., *Exorista sorbillans*, and *Odontepyris* sp. (Sharanabasappa *et al.* 2019). In China, *T. remus* (Zhao *et al.* 2020), *T. pretiosum* (Zhu *et al.* 2020), *T. dendrolimi* (Tian *et al.* 2020), and *T. chilonis* (Li Z G *et al.* 2019) are the dominant parasitoids of FAW.

Table 2 Chemical insecticides used against the fall armyworm

Active ingredient	Applied region
Acetylcholinesterase (AChE) inhibitors	
Chlorpyrifos	America, Africa
Methomyl	America
Thiodicarb	America
Acephate	America, Africa, Asia
Carbaryl	America, Africa
Carbosulfan	Africa
Trichlorfon	America
Profenofos	Africa
Phenthoate	America
Methyl-parathion	Africa
Methamidophos	America
Malathion	America, Africa
Fenitrothion	America, Africa, Asia
Diazinon	America, Africa
Dimethoate	America, Africa
Sodium channel modulators	
Permethrin	America, Africa
Zeta-cypermethrin	Africa
Deltamethrin	America, Africa, Asia
Alpha-cypermethrin	America, Africa
Beta-cyfluthrin	America, Africa
Beta-cypermethrin	America
Bifenthrin	America, Africa
Cyfluthrin	Asia
Cypermethrin	America, Africa
Fenpropathrin	America, Asia
Gamma-cyhalothrin	America
Lambda-cyhalothrin	America, Africa, Asia
Tralomethrin	America
Pyrethrum	America, Africa
Fluvalinate	America
Etofenprox	America
Esfenvalerate	America, Africa
Nicotine acetylcholine receptor (nAChR) allosteric modulators	
Spinetoram	America, Asia
Spinosad	America, Africa
Acetamiprid	America, Africa, Asia
Cartap	Asia
Thiamethoxam	America, Africa, Asia
Thiacloprid	America
Imidacloprid	Africa
Inhibitor of chitin biosynthesis	
Triflumuron	America, Africa
Chlorfluazuron	America, Africa
Teflubenzuron	America
Novaluron	America
Lufenuron	America, Africa, Asia
Diflubenzuron	America, Asia
Hexaflumuron	Asia
Ryanodine receptor (RyR) allosteric modulator	
Flubendiamide	America, Africa
Chlorantraniliprole	America, Africa, Asia
Cyantraniliprole	America, Africa, Asia
Tetrachlorantraniliprole	Asia
Ecdysone agonists/moulting disruptors	
Chromafenozide	America
Tebufenozide	America, Asia
Methoxyfenozide	America
Glutamate-gated chloride channel (GLUCL) allosteric modulators	
Emamectin benzoate	America, Africa, Asia
Abamectin	Africa
Uncouplers of oxidative phosphorylation *via* disruption of proton gradient	
Chlorfenapyr	America, Africa, Asia
Voltage-dependent sodium channel blockers	
Indoxacarb	America, Africa, Asia

The presence of insect predators for both eggs and larvae is important to keep FAW populations under the control. The earwigs *Doru lineare* and *D. luteipes* prey on FAW eggs and larvae (Pasini *et al.* 2007; Sueldo *et al.* 2010) and the predators *Picromerus lewisi* and *Arma chinensis* mainly prey on 6th instar larvae of FAW (Tang *et al.* 2019a, b). Two species of predacious bugs, *Eocanthecona furcellata* (Wolff) and *Andrallus spinidens* (Fabr.) (Hemiptera: Pentatomidae) were found to effectively prey on FAW (Shylesha and Sravika 2018).

Several reviews have summarized the entomopathogen resources or potential biopesticide options of FAW and their application status (Bateman *et al.* 2018; Chen *et al.* 2019). Bt is a common biopesticide used to control pests including FAW. The soil bacterium *B. thuringiensis* produces multiple crystal (Cry) proteins or vegetative insecticidal proteins (Vip3A) that are toxic to FAW (Singh *et al.* 2010). In addition, the fungi *Beauveria bassiana*, *B. rongniartii*, *Metarhizium anisopliae*, *M. rileyi*, *Nomuraea rileyi* and *Paecilomyces fumosoroseus* have been studied as potential entomopathogens for the control of FAW (Altre and Vandenberg 2001; Carneiro *et al.* 2008; Grijalba *et al.* 2018). The nematodes *Heterorhabditis* and *Steinernema* also effectively control FAW (Garcia *et al.* 2008).

5.6. Viruses associated with *S. frugiperda*

SfMNPV is a member of the Group II *Alphabaculovirus* of the Baculoviridae family, which can cause FAW larval mortality rates of more than 90% (Castillejos *et al.* 2002; Simon *et al.* 2012). Different isolates of SfMNPV have been isolated in North, Central and South America (Berretta *et al.* 1998; Simon *et al.* 2012; Barrera *et al.* 2015). SfMNPV was first studied as a potential bioinsecticide for management of

FAW in 1999. Spraying with 1.5×10^{12} viral occlusion bodies (OBs) per ha caused approximately 40% mortality of FAW larvae at two days post application (Williams *et al.* 1999).

As a biological insecticide, the efficacy of SfMNPV and its speed of killing insects are affected by many factors, such as virulence of different isolates, larval instars, the amount of feeding viral OBs, formulation applied, and environmental conditions. Some studies indicated that diverse isolates had different efficacies: 3AP2 is a fast-killing isolate compared to the wild-type isolate Sf3, and the LT_{50} of the 3AP2 isolate was at least 30 h less than Sf3 when applied in the greenhouse and in the field (Behle and Popham 2012). There is a higher mortality of FAW and longer persistence on crop foliage caused by granular formulation than the aqueous spray application (Castillejos *et al.* 2002). To improve the efficacy of SfMNPV, a variety of SfMNPV formulations were produced for biological control of FAW. Recombinant baculoviruses containing two proteases with insecticidal activity decreased the time to kill insects, thus showing great potential for application in IPM programs (Gramkow *et al.* 2010). Nearly 90% of FAW was controlled by combining SfMNPV with 3 mg L^{-1} Spinosad, which was 12.5–32% greater than the treatment with SfMNPV alone in a maize field (Mendez *et al.* 2002). Some studies indicated that microencapsulated SfMNPV also has the potential for improving FAW management (Gomez *et al.* 2013). A Colombian SfMNPV was microencapsulated by spray drying with a pH dependent polymer. Viral insecticide activity was not affected by microencapsulation, and the process provided effective protection from UVB radiation (Kurmen *et al.* 2015). Wettable powder formulations utilizing microencapsulation of SfMNPV OBs provide useful advantages related to half-life and photostability of viruses and retain the same efficacy under field conditions. In addition, adding 1% boric acid increased the mortality induced by the virus compared to application of granules containing virus alone in a field trial (Cisneros *et al.* 2002). Importantly, it was reported that a leading biopesticide company, Certis, USA, has obtained the license to develop and manufacture a commercial biopesticide product for field application in selected countries around the world based on Corpoica's SfMNPV strain NPV003 and formulation technology.

Spodoptera frugiperda granulovirus (SfGV) is a member of *Betabaculovirus* of the Baculoviridae family. A granulovirus of FAW in Columbia, South America, was first reported by Steinhaus (1957). SfGV attacks only the fat body, causes a proliferation of cells, and requires a relatively long time to produce mortality. One SfGV isolate was evaluated in a co-infection process and was demonstrated to enhance the insecticidal activity of *Lymantria dispar* NPV (Lepidoptera: Lymantriidae), reducing its mean lethal concentration by 13-fold (Shapiro 2000). Other studies obtained a similar synergic effect in co-infection of GV and NPV, due to the enhancins of baculovirus isolates (Hoover *et al.* 2010; Mukawa and Goto 2011). SfGV has been poorly studied compared to SfMNPV, with relatively few SfGV isolates being characterized.

5.7. Botanicals for FAW management

Some plant derived-pesticides, referred to as botanicals, display good performance in insecticidal activity. They have diverse biological activities resulting in high mortality, extended larval duration, decreased pupa weight, insecticidal effects, growth inhibition, antifeedant effects, reduced fecundity, as well as sublethal and acute toxicity. Rioba and Stevenson (2020) have reviewed the opportunities and scope for botanical extracts and products for the management of FAW in Africa (Rioba and Stevenson 2020). They summarized the efficacy and potential of 69 plant species from 31 families including *Azadirachta indica*, *Schinnus molle*, and *Phytolacca dodecandra*. In China, Lin *et al.* (2020) estimated indoor toxicity and control effect of azadirachtin in a maize field for FAW. Azadirachtin has good toxicity and antifeedant activity on FAW, and the control effect reached a peak at seven days after treatment (Lin *et al.* 2020).

6. Future outlooks

FAW invaded Africa, Asia and Oceania extremely rapidly due to its strong flight capability, polyphagy, lack of diapause and quick development of insecticide/virus-resistance. Several biological characteristics associated with its invasiveness and the IPM strategies are summarized in this review, which provides some useful information for the future study of FAW. Furthermore, the five following aspects are worth studying not only for FAW, but also for all IAS.

6.1. Improving monitoring by deep learning

Image recognition by deep learning presents good performance in monitoring alien invasive plants (Qiao *et al.* 2020). It provides researchers a new perspective to monitor IAS including invasive alien insects. Multiple Apps have emerged based on deep learning to identify FAW (Chiwamba *et al.* 2019a; Chulu *et al.* 2019). A system to automate FAW pheromone trapping has also been developed based on machine learning (Chiwamba *et al.* 2019b). There is a significant opportunity for researchers to further develop new monitoring techniques based on deep learning.

6.2. Research on invasion mechanism

FAW has outbreaks with irregular intervals in its native regions for two centuries, before its successful invasion in Africa and Asia. A similar phenomenon, which is called lag-time, has been found in other invasive species, such as the Brazilian pepper (*Schinus terebinthifolius*) which was present as a restricted ornamental for at least 50 years before its rapid invasion (Simberloff and Gibbons 2004). Thus, emerging questions as to why these invasive species have long invasion lag times, what facilitated invasions, and how many species are potential invasive need answering. There is a need to clarify the invasion mechanism to better prevent and control IAS including FAW. The flood of genomic data could provide opportunities for researchers to reveal the respective invasion mechanisms (Huang *et al.* 2019).

6.3. Resistance management

One important reason for the successful invasion of invasive insects is their rapid development of resistance to insecticides, viruses and other environment stresses (Wan *et al.* 2019). The resistance of FAW to transgenic crops, is considered by most researchers to be the result of pyramiding multiple transgenes (in the same plant). This is more effective in terms of FAW control and insect resistance management (IRM) than single-gene-based resistance (Huang *et al.* 2014; Horikoshi *et al.* 2016). Similarly, for resistance to insecticides, pesticides should be applied at the recommended rates, intervals, and seasonal totals according to instructions, which are designed to slow down the development of pesticide resistance for a FAW population (Prasanna *et al.* 2018). In addition, the IPM strategy shown in Table 3 can be used to achieve population control.

6.4. Development of new control techniques for IAS

In recent years, some new techniques have emerged for managing pests, including RNAi, CRISPR/Cas9, and

Table 3 Integrated pest management measures for fall armyworm, *Spodoptera frugiperda*

Management	Method[1)]	Pest stage	Corn growth period
Monitoring & Scouting			
Migration monitoring	Entomological radar, vertical-pointing searchlight-raps	Adult	Whole growth
Light traps	Blacklight	Adult	Whole growth
Pheromone traps	Commercial male trap, 50 m interval between two traps, traps hung at a height of 1.5 m above ground	Adult	Whole growth
Sampling	Random sampling of 20 plants in five locations	Egg and larva	Whorl stage
Agricultural control			
Insect-resistant corn	Transgenic/Bt maize varieties	Larva	Pre-planting
Cultural control (push and pull)	Intercropping with bean or sunflower; trap cropping with castor plant or young corn plants	Egg	Pre-planting
Mechanical control	Handpicking egg masses and larvae	Egg and larva	Whorl stage
Physical control	Deep plowing to kill pupae in the soil/Placing sand or ash in the whorls	Larva and pupa	Pre-planting/Whorl stage
Biological control			
Enemy insects	Egg parasitoids: *Trichogramma pretiosum* and *Trichogramma atopovirilia*, etc. Larval parasitoids: *Chelonus insularis*, Campoletis sonorensis and *Cotesia marginiventris*, etc. Pupal parasitoids: *Diapetimorpha introit* and *Ichneumon promissorius* Predators: *Doru lineare* and *Podisus nigrispinus*, etc.	Egg, larva and pupa	Whole growth
Biopesticides	Virus: SfGV and SfMNPV Fungus: *Metarhizium anisopliae*, *Beauveria bassiana*, seed treatment with *Trichoderma* induces defense Bacteria: *Bacillus thuringiensis* Nematode: *Heterorhabditis bacteriophora*, and *Heterorhabditis indica*, etc. Botanical: *Azadirachta indica*, *Schinnus molle*, and *Phytolacca dodecandra*, etc.	Larva	Whole growth
Chemical control			
Sex attractants	Z7-12:Ac+E7-12:Ac+Z9-14:Ac (0.01:0.01:1.00 mg), or other efficient composite	Adult	Whole growth
Insecticides	A total of 20 insecticides were recommended by Ministry of Agriculture and Rural Affairs, China	Egg and larva	Pesticide sprays at VT (Vegetative–Tassel) stage afterward

1) SfGV, *Spodoptera frugiperda* granulovirus; SfMNPV, *Spodoptera frugiperda* multiple nucleopolyhedrovirus.

nanopesticides. One new technique combines RNAi and a nanocarrier to develop a novel, stable and safe strategy that may greatly improve pest management (Ma *et al.* 2020; Yan *et al.* 2020). For FAW, some scientists have focused on the potential of CRISPR/Cas9 in control programs. Wu K *et al.* (2018) explored the possibility of using the CRISPR/Cas9 system to modify the abdominal-A (*Sfabd-A*) gene to explore new control strategies. Jin *et al.* (2021) generated a *SfABCC2* knockout strain of FAW using the CRISPR/Cas9 system to provide further functional evidence of the role of this gene in susceptibility and resistance to Cry1F (Jin *et al.* 2021). In addition, one study discussed the prospect of studying ORCO using CRISPR techniques in FAW. Due to the efficiency of targeting specific olfactory genes, it is possible to develop new alternative strategies using insecticides and/or microbial sprays to control FAW (Ayra-Pardo and Borras-Hidalgo 2019).

6.5. Global collaboration for biosecurity

Invasive alien species, such as FAW, have serious negative consequences for the environment, economies, and human health and wellbeing, and with the accelerated development of global trade, these species have become a global issue (Bradshaw *et al.* 2016). There is a strong argument for strengthening global collaboration to improve individual country biosecurity defenses to prevent IAS invasions in order to protect food security, biodiversity and human health.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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