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Invasiveness, biology, ecology, and management of the fall armyworm, *Spodoptera frugiperda*

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With 4 figures and 4 tables

Abstract: The fall armyworm (FAW), *Spodoptera frugiperda* (JE Smith, 1797), is a serious pest of several crops, particularly maize and other cereals. It has long been known as a pest in the Americas and has invaded most of Africa and parts of the Middle East, Asia, and Australia in the last six years. Its new status as an invasive species causing serious damage in many regions worldwide has highlighted the need for better understanding and has generated much research. In this article, we provide a comprehensive review of FAW covering its (*i*) taxonomy, biology, ecology, genomics, and microbiome, (*ii*) worldwide status and geographic spread, (*iii*) potential for geographic expansion and quarantine measures in place, and (*iv*) management including monitoring, sampling, forecasting, biological control, biopesticides, agroecological strategies, chemical control, insecticide resistance, effects of insecticides on natural enemies, as well as conventional and transgenic resistant cultivars. We conclude with recommendations for research to enhance the sustainable management of FAW in invaded regions.

Keywords: biological control, biopesticides, genomics, globalization, integrated pest management, invasive species, Noctuidae

1 Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (JE Smith, 1797) (Lepidoptera: Noctuidae) is a highly polyphagous lepidopteran pest (Prasanna et al. 2021). It feeds and develops on the leaves, stems, and reproductive parts of over 350 plant species, primarily Poaceae, causing serious economic damage to key food crops (e.g., maize, sorghum, rice, soybean) and fibre crops (e.g., cotton) (Montezano et al. 2018; Overton et al. 2021).

FAW originates from tropical and subtropical areas of the Americas. Its native year-round distribution includes much of South and Central America, the Caribbean, and southern parts of Texas and Florida. It is also a strong seasonal migrator, causing transient damage in temperate regions of North and South America (Rwomushana 2019). Since its first observation in West Africa in 2016, this pest has invaded many territories worldwide, including most of sub-Saharan Africa, parts of West, East, and South Asia, and parts of Oceania, including southern Australia. FAW is also regularly intercepted on imported plant material in Europe (EPPO 2020). Current control strategies for the management of FAW are challenging due to its high fecundity and mobility, the rapid development of insecticide resistance in insecticide-exposed populations, and its high physiological and behavioural plasticity (Paredes-Sánchez et al. 2021).

The present article provides an updated review on FAW involving four broad areas that affect its status as an invasive insect including: its (*i*) biology, ecology, taxonomy, genomics, and microbiome, (*ii*) worldwide status and geographic spread, (*iii*) potential for geographic expansion and quarantine measures, and (*iv*) management. The management section covers monitoring, sampling, forecasting, biological control, biopesticides, agroecological strategies, chemical control, insecticide resistance, side effects of insecticides, as well as conventional and transgenic resistant cultivars. We conclude by recommending specific research that can help to improve sustainable management of this pest, particularly in recently invaded regions.

2 Taxonomy, biology, ecology, genomics, and microbiome

2.1 Taxonomy and morphology

FAW was originally described as *Phalaena frugiperda* by Smith & Abbot (1797; cited by Simmons & Wiseman [1993]), then placed in the genus *Laphygma* to be finally classified as *Spodoptera frugiperda* in a note published by Todd (1964; cited by Simmons & Wiseman [1993]).

FAW belongs to the *Spodoptera* genus, which comprises about 31 species distributed on six continents; and approximately 15 of these species, including *S. frugiperda*, are important pests of many cultivated plants (Pogue 2002). Little information is available on *Spodoptera* phylogentics, except for the study by Kergoat et al. (2012), showing that, during the diversification of the genus *Spodoptera*, some specialist grass feeders, including *S. frugiperda*, closely tracked the expansion of grasslands in the Miocene, as their mouthpart morphology evolved in response to the selective pressure of abrasiveness of grass leaves.

Misidentification of *S. frugiperda* with other species, such as the beet armyworm *Spodoptera exigua* (Hübner), can occur at all developmental stages (Goergen et al. 2016). However, some morphological characteristics of the larvae can be used to accurately identify *S. frugiperda* in the field. Godfrey (1987) established about 21 detailed morphological characters of the larvae for such identification including “the presence of four pinacula on the eighth terga forming a square, and a line forming an inverted Y shape on the head” (Fig. 1).

Key details of morphological characteristics of the adult moths were given by Todd & Poole (1980) and revised by Pogue (2002). Among them, the male moths have triangular white spots at the tip and near the center of the forewing (Fig. 1). Other morphological characteristics of the species include the following (EPPO 2021):

- the valve of the male genitalia is almost rectangular and there is no marginal notch at the position of the tip of the harpe;
- the pupa is brown with a two-spined cremaster;
- the eggs grouped into a mass, composed of multiple layers, usually stuck on the underside of plant leaves are generally covered with a protective felt-like layer of grey-pinked scales.

In addition, *S. frugiperda*, appears to be an assemblage of two closely related strains referred to as the maize and rice strains (Pashley et al. 2004). They have long been considered morphologically indistinguishable but differ in their host plant distribution. The rice strain is usually associated with millet and grass species associated with pasture habitats, whereas the maize strain is associated with maize and sorghum (Pashley 1986; Pashley 1988; Pashley et al. 1992). More recently, Nagoshi et al. (2020a) reported significant differences in wing size and shape when comparing strains from different habitats, but not between strains within the same habitat, indicating that wing morphology is probably not a reliable indicator of strain identity in field populations where different host plants are available.

2.2 Host range, damage to crops and economic impact

FAW is a highly polyphagous herbivore whose larvae can feed upon the aerial parts of a wide range of cultivated and wild plants. A recent bibliographic survey together with field observations by Montezano et al. (2018) suggested that the pest can feed on 353 host plants belonging to 76 botanical families, with the Poaceae being the most common, followed by Asteraceae and Fabaceae. However, due to the high number of eggs in the FAW egg masses, young larvae, after an initial feeding step, disperse mainly by ballooning onto other nearby plants (Sokame et al. 2020). This suggests that several host records may be due to this behaviour and do not necessarily indicate actual maternal oviposition preference (Prasanna et al. 2021).

The main crops where FAW causes economic injury include cereals, forage and grasses, especially maize, rice and sorghum, and other main arable crops, such as soybean and cotton (Barros et al. 2010; Oliveira et al. 2014; Wu et al. 2021a). Other host crops include various fruits, grapes, citrus, berries, and flowers (Prasanna et al. 2021). It has long been thought that the maize strain prefers maize, sorghum, and cotton while the rice strain attacks mainly rice and other grasses (Sparks 1979). However, it was recently demonstrated in the laboratory that maize is the preferred oviposition host for both strains (Ingber et al. 2021). Nevertheless, the differential distribution of the strains on different hosts in the field remains the defining characteristic of these two populations, with one strain the majority in maize and sorghum while the other predominates in forage grasses and millet (Pashley 1986; Prowell et al. 2004; Murúa et al. 2015). As such, crops at risk in an area can be identified by which of the two strains are present. Both strains are widespread and largely sympatric in the Western Hemisphere but only the group associated with maize and sorghum appears to be significant in the FAW recently found in Africa and Asia (Nagoshi et al. 2017b, 2018, 2020b, 2021). If this condition is maintained, it is likely that consistent FAW infestations in the Eastern Hemisphere will be limited to a narrower host range than documented in the Americas. The whorl and young leaves, ears and tassels are the most consumed plant structures by FAW (Almeida Sarmento et al. 2002). Still,

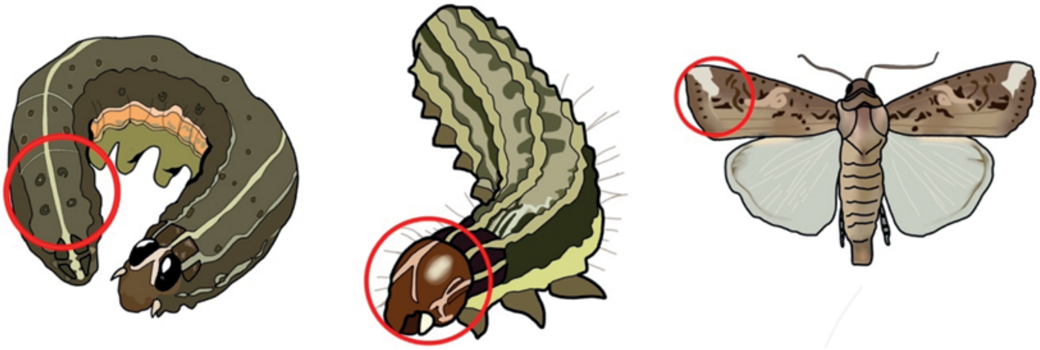

Fig. 1. Typical morphological marks on medium to large-sized larvae of *S. frugiperda* (a square of 4 pinacula on the 8th terga and an inverted Y shape on the head) and white spots on the tip of the forewing of male moths (© Alice De Araujo).

foliar damage of maize may not necessarily translate to high grain yield losses in contrast to ear damage (Kumar 2002; Wightman 2018; Hruska 2019; Prasanna et al. 2021).

Economic losses due to FAW in maize worldwide have been estimated up to 73%, with serious crop damage in many developing countries (Guo et al. 2018; Wu et al. 2021a). In their extensive review, Overton et al. (2021) identified 71 peer-reviewed references that reported yield losses from FAW infestation, with a total of 888 separate yield loss entries. Most studies reported a loss in maize, followed by cotton, sorghum, and sweet corn. Recent studies in Africa highlight the economic importance of the FAW. In Ethiopia, the pest causes an average annual loss of 36% in maize production, reducing yield by 0.225 million tonnes of grain between 2017 and 2019 (Abro et al. 2021). In Kenya, FAW causes losses of about a third of the annual maize production, estimated at about 1 million tonnes, with large variations among regions (De Groote et al. 2020). Eschen et al. (2021) estimated that FAW causes annual yield losses of USD 9.4 billion in Africa alone. The recent invasion of FAW in developing countries also has an important impact on household income and food security. For example, Tambo et al. (2021) showed that households affected by FAW in Zimbabwe had a lower per capita income and were 12% more likely to experience hunger compared to unaffected households.

2.3 Life cycle and developmental biology

FAW must overcome several geographic, environmental, reproductive and dispersal barriers from its native to invaded regions (Richardson & Pysek 2006). Fecundity and fertility of *S. frugiperda* is high (Luginbill 1928; Leiderman & Sauer 1953; Busato et al. 2008; Milano et al. 2008; Montezano et al. 2019) but the reproductive parameters are generally affected by temperature (Ramirez-Garcia et al. 1987), host plant species (Andrews 1988; Wang et al. 2020b) and host plant phenology (Van Huis 1981; Barfield & Ashley 1987; Milano et al. 2008). A female deposits grey-brown or green masses of a highly variable number of eggs. The optimum temperature for egg production is 25°C (Barfield & Ashley 1987). Under optimal temperatures for egg hatching (≈30°C), all eggs hatch in just two days (du Plessis et al. 2020). Larvae usually go through six instars, but the number of instars can vary from five (Leiderman & Sauer 1953; Campos 1970; Escalante 1974; Ali et al. 1990) to 10 (Murúa et al. 2003). A higher number of instars occurs on less suitable host plants and at lower temperatures, increasing survival in adverse conditions (Esperk et al. 2007; Montezano et al. 2019). The entire duration of the larval stage can be as short as 10 days (32°C) and longer than 30 days (<20°C) (Pitre & Hogg 1983; du Plessis et al. 2020). For instance, two to three days are needed for each of the six instars at 26°C. Larval survival is highest between 26 and 30°C. A lower temperature threshold of 10.9°C and 14.6°C is required for larval and pupal development, respectively (Ramirez-Garcia et al. 1987). Larval locomotion ceases at temperatures below 7°C, while the adults show no activity below 3°C (Keosentse et al. 2021). Information on the maximum temperature limits to activity are scarce in the literature.

Pupation typically occurs in the soil. When reared on the same host plant, the longer the larval development time, the larger the resulting pupal stage (Huang et al. 2021). Duration of the pupal stage is about eight to nine days at optimal temperatures (≈30°C), but can be as long as 30 days at 18°C. At lower temperatures, the mortality rate is drastically increased. After emergence, adult females experience a preoviposition period of ~5 days, but some individuals need up to 9 days before initiating oviposition (Luginbill 1928; Habib et al. 1982). During their adult lifetime, mating with more than one partner is common (Simmons & Marti, 1992). Females lay most of their eggs during the first five days following maturation but continue to produce some eggs during their entire lifespan, which is typically between two and three weeks. Each female produces an average of 1500 eggs at optimal temperatures (Huang et al. 2021). However, this number is drastically reduced below 20°C. The longevity of FAW moths decreases with increasing temperatures between 21 and 30°C (Barfield & Ashley 1987). Both larval and adult diets affect the longevity and the fecundity of FAW moths (Luginbill, 1928, Simmons & Lynch, 1990). For instance, provision of honey to adults increased longevity and prolonged the oviposition period in females (Simmons & Lynch 1990).

The egg-to-adult development requires 391 degree-days (du Plessis et al. 2020). Whether females and males experience similar egg-to-adult development duration is unclear. Huang et al. (2021) showed that females developed faster than males due to a shorter pupal stage. Montezano et al. (2019) also observed faster pupal development in females. Nevertheless, larval development in females is slower than males and thus, egg-to-adult developmental time is similar between the sexes. Between 18 and 30°C, the development rate increases linearly with increasing temperatures (du Plessis et al. 2020). The optimal range for egg-to-adult development is between 26 and 30°C, while a plateau is experienced at slightly higher temperatures (du Plessis et al. 2020). As a result, the life cycle is completed in about 30 days under optimal conditions (28°C; 65% RH) and can last up to 90 days at lower temperatures. Higher variability in the duration of the life cycle is experienced at lower ambient temperatures, especially if the diet is poor (Gergs & Baden 2021). This pest does not diapause, is chill susceptible and therefore cannot survive extremely low temperatures. The minimal temperature allowing FAW development is between 12 and 13°C, for all stages (du Plessis et al. 2020), whereas critical locomotor activity temperatures seem to be in the range 1.9 to 6.5°C (Keosentse et al. 2021).

The biology of FAW is also affected by its host plant species and varieties. Larval clinal variation has also been observed owing to variation in host plant families across geographic locations (Busato et al. 2005; Murúa et al. 2008; 2015; Nagoshi et al. 2017a; Montezano et al. 2019). Van Huis (1981) reported the highest oviposition during the early whorl and tasselling stages, but in contrast, Barfield & Ashley (1987) reported that more eggs are laid in the late vegetative stage compared to the reproductive stage of maize. Suitable host plants result in high survivorship, shorter larval development time and higher reproductive rates (Wang et al. 2020b).

2.4 Population dynamics and behavioural ecology

FAW cannot survive winters in areas with freezing temperatures (Meagher & Nagoshi 2004; Johnson 2011). Temperature and rainfall significantly affect FAW population densities (Murúa et al. 2006). In general, densities of moths and larvae are higher during the rainy seasons than in the dry season (Silvain & Ti-A-Hing 1985) and lower infestation levels are found at higher elevations where the temperature is lower (Wyckhuys & O'Neil 2006). Surveys in southern Florida and tropical America indicated a bimodal pattern, with peak numbers occurring typically during the spring and fall seasons (Silvain & Hing 1985; Pair et al. 1986a; Raulston et al. 1986; Mitchell et al. 1991).

The maize strain was most prevalent during spring and early summer, as compared to the rice strain (Meagher & Nagoshi 2004). On maize, FAW infestations display a plant age-dependent response, young instars being prominently found on early plant stages (V1-V3), often with more than one larva per plant, whereas older larvae occur on older plant stages, usually with only one larva per plant (Murúa et al. 2006). However, in the tropics, overlapping generations occur, with all FAW developmental stages found on all plant stages.

Due to a high fecundity, a short generation time and a good dispersal capacity, FAW has a strong ability to invade and colonize new regions (Johnson 2011). In North America, seasonal moth migrations occur over thousands of kilometers from southern USA and Mexico to Canada (Pair et al. 1986a; Mitchell et al. 1991; Nagoshi et al. 2012) and, in South America, transient populations reach the northern parts of Argentina and Chile (Pair et al. 1986a). More recently, it has been shown that the moth can move distances of 250 km overnight in China (Jia et al. 2021). The dispersal capacity of this pest can explain why, after the first record in West Africa in 2016 (Goergen et al. 2016) it quickly spreads to most of the continent as well as parts of Asia in just three years (See section 3 below).

Inter-plant dispersal by mean of ballooning occurs in neonates, whereas older larvae migrate by crawling between plants (Sokame et al. 2020a). The capacity of larvae to move to new, non-infested plants is important because larvae are cannibalistic and, usually, only one or two larvae per plant develop to the pupal stage.

2.5 Chemical ecology

2.5.1 Variation in sexual communication

In terms of chemical ecology, sexual communication through the female sex pheromone to which males are attracted is the most studied trait in FAW. The sex pheromone of this species was first identified in 1986 (Tumlinson et al. 1986) and consists of Z-9-tetradecenyl acetate (Z9-14:OAc) as the major component, and Z-7-dodecenyl acetate (Z7-12:OAc) as a critical secondary component without which FAW males are not attracted. In addition, two other compounds are generally found in the female gland, namely (Z)-9-dodecenyl acetate (Z9–12:OAc) and (Z)-11-hexadecenyl acetate (Z11–16:OAc), but their importance for male attraction seems less critical (Tumlinson et al. 1986; Unbehend et al. 2013). One additional minor component (E)-7-dodecenyl acetate (E7–12:OAc), that was identified from FAW females in Brazil (Batista-Pereira et al. 2006), was not found in other regions.

In addition to the long-range sex pheromones of females, male moths may also emit short-range pheromones by extruding abdominal hairpencil scales (Birch et al. 1990; Cardé & Haynes 2004). Even though FAW males possess and overtly display their hair pencils during courtship, and female choice has been observed (Schoefl et al. 2009), no male pheromone has been identified.

2.5.1.1 Strain- and geographic variation in the female sex pheromone

In the Americas, where the maize and rice strains differ by as much as 2% in their genome (Kergoat et al. 2012), some strain-specific differences exist in the female pheromone composition (Groot et al. 2008; Lima & McNeil 2009; Unbehend et al. 2013). However, since the strain-specific pheromone variation mentioned above differed between studies, geographic variation probably influences the strain-specific pheromone composition.

Within Africa, several other *Spodoptera* species are present (Brown et al. 1975), and some share the same major sex pheromone component Z9-14:OAc (see pherobase.com). Cross attraction with other noctuid genera may also occur, as was shown in Togo, where traps baited with FAW lures caught large numbers of *Leucania loreyi* (Duponchel) males (Meagher et al. 2019). If such cross attractions resulted in viable hybrid matings, large changes in behaviour and chemical ecology could result, but this remains to be investigated. So far, the only study that assessed the sex pheromone composition of FAW in West Africa, where FAW invasion was first identified, found a similar sex pheromone composition as in the Americas (Haenniger et al. 2020).

2.5.1.2 Strain- and geographic variation in the male response

Throughout the Americas, several field attraction experiments have been conducted (Mitchell et al. 1985; Tumlinson et al. 1986; Andrade et al. 2000; Malo et al. 2001; Batista-Pereira et al. 2006). However, the first field experiment that assessed strain-specific attraction in FAW was conducted by Pashley et al. (1992), who used 1–2-day old live virgin females of maize or rice strains as bait in pheromone traps in fields that contained both types of host plants in Louisiana in two consecutive years. Even though this study found a slight but significant strain-specific attraction, specifically of rice strain males to rice strain females, this was likely due to a much larger abundance of the rice strain population at the time of the experiment. More recent field trapping experiments in the Americas mostly showed that both strains are similarly attracted to pheromone lures and that geographic variation is more pronounced than strain variation (Unbehend et al. 2013; Unbehend et al. 2014).

Host plant volatiles may affect the attraction to sex pheromone (Unbehend et al. 2013). In field experiments conducted in Florida, the maize strain pheromone blend (containing less Z7-12:OAc than the rice strain blend) attracted more males of both strains than the rice strain blend in a maize field, whereas these blends were equally attractive in a grass field. This suggests that habitat-specific volatiles may influence male attraction to pheromones.

2.5.2 Attraction to host plants

Host plants play an important role in the chemical ecology of FAW by attracting females for oviposition, larvae for feeding, parasitoids for parasitism and potentially some predators for predation.

Although FAW is a generalist herbivore that is probably more influenced by common or nonspecific stimuli for host selection, females are attracted to specific maize volatiles and prefer to oviposit on plants that are not damaged by herbivores (Signoretti et al. 2012). Females are also less attracted to maize plants with conspecific eggs (Peñaflor et al. 2011). Females generally prefer to lay eggs on Poaceae than on other plant families (Whitford et al. 1988; Silva et al. 2017). The female moths are electrophysiologically responsive to a range of Poaceae volatiles such as linalool, beta-ocimene, alpha-pinene and several short chain alcohols such as hexan-1-ol (Malo et al. 2004a). Few studies to date have addressed the variation in attraction to plants for oviposition between maize- and rice strain females. In general, maize appears the preferred host for oviposition in both strains (Ingber et al. 2021). However, Whitford et al. (1988) observed a preference for maize and sorghum in the maize strain and for bermuda grass in the rice strain. Meagher et al. (2011) observed a preference in the rice strain to oviposit on pasture grass compared to maize, whereas the maize strain did not show any oviposition preference between these two plants.

FAW neonates are attracted to damaged maize leaf tissue (Stuhl et al. 2008). In older FAW larvae, Carroll et al. (2006) observed an attraction to linalool, a constitutive plant volatiles emitted by plants infested by conspecific larvae as compared to undamaged plant odours. Also, the larval feeding experience can influence their preference/acceptance for a host plant (Huang et al. 2019). For example, Boiça et al. (2017) showed that FAW larvae prefer feeding on more susceptible soybean cultivars, especially when the larvae were previously exposed to resistant cultivars. However, differences in FAW larvae preference for different host plants are probably also due to their genetic lineage (Silva-Brandao et al. 2017; Zhou 2019) and gut microbiome (Acevedo et al. 2017).

Several studies have reported that the volatiles emitted from plants infested by FAW larvae attract specific parasitoid species (Loke et al. 1983; Dmoch et al. 1985; Hoballah et al.

2002; Block et al. 2018) and even parasitoids of other host species (Sokame et al. 2020b). However, herbivory by FAW larvae may also reduce the emission of herbivore-induced plant volatiles and, thus, attractiveness to natural enemies as compared to other herbivores (Peñaflor et al. 2011; De Lange et al. 2020). Even oviposition on maize may reduce both constitutive (linalool) and induced host plant volatiles (terpenes and aromatic compounds) involved in host finding by parasitoids (Peñaflor et al. 2011).

2.6 Genomics

The FAW genome is typical of Lepidoptera. It is comprised of 31 chromosome pairs with a Z/W system for sex determination (Robinson 1971). The amount of haploid DNA is 396+/– 3Mb (Gouin et al. 2017). The advent of next-generation sequencing (mainly Illumina and 454) has prompted the publication of several genome assemblies for two well-established cell lines and laboratory-reared strains (Gouin et al. 2017; Kakumani et al. 2014; Nandakumar et al. 2017). However, those assemblies were all highly fragmented. Pac Bio allowed for better chromosome level assemblies from laboratory and invasive strains (Gui et al. 2020; Nam et al. 2020; Gimenez et al. 2020; Zhang et al. 2020). The current reference assembly in NCBI is from an isolate of an invasive populations from Zhejiang University, China (Xiao et al. 2020). Across the seven assemblies deposited in NCBI, the median sequence length is 391.6 Mb. It is a rather AT-rich genome with a GC content of about 36.4%, reflecting a high prevalence (approxiamately 29%) of repeat elements (Gouin et al. 2017). Gene annotation in this context is always difficult, but thanks to a growing number of lepidopteran genomes (from only three assemblies in 2012 to 1,184 assemblies in 2021) and orthology tools (Kriventseva et al. 2019), a median count of 26,254 proteins has been reported. A striking feature of the gene repertoire is the expansion of gustatory receptor genes (Gouin et al. 2017), that have also been found in other polyphagous noctuids (Cheng et al. 2017; Pearce et al. 2017). The recent worldwide invasion of FAW has been the driver of genome assemblies from multiple sources and provides an incentive to develop population genomics approaches (Nam et al. 2020; Gimenez et al. 2020; Zhang et al. 2020, Xiao et al. 2020; Schlum et al. 2021) to better understand the FAW population genetic structure and to uncover the genetic basis of adaptation to new environments and ecological niches.

A complicating aspect of FAW genomics is the status of the two host strains associated with differences in host plant preferences (Pashley et al. 1988). The strains are morphologically indistinguishable and are identified by molecular markers that include mitochondrial haplotypes and nuclear polymorphisms that are limited to the Z-chromosome (Nagoshi 2010; Prowell et al. 2004). The latter suggests that strain divergence is driven by one or more sex-linked genes, a supposition supported by the Z-chromosome location of a function responsible for incomplete hybrid sterility between strains (Kost et al. 2016). Also, at least one autosome has been implicated in influencing strain differences in mating time (Pashley et al. 1992; Schofl et al. 2009; 2011). However, whole genome comparisons between strains have given contradictory results with substantial nuclear genome differentiation between strains found in specimens from Mississippi (Gouin et al. 2017), but not in comparison with collections from other locations (Schlum et al. 2021). The reasons for this discrepancy are unclear, but the high level of genetic variation observed within this species (Gouin et al. 2017) may complicate the identification of strains if a relatively small number of genes is driving strain divergence. Another complicating factor is that the two strains appear capable of significant, though restricted, interbreeding in the field (Prowell et al. 2004), with the potential for substantial gene flow. Therefore, it would not be surprising if the level of genetic differentiation between strains is regionally variable, dependent on the level of sympatry dictated by the local distribution of host plants.

Despite great progress on genomics, functional genomics studies on this insect remain rare. One of the main reasons is its recalcitrance to RNA interference (RNAi). RNAi works efficiently in some insects such as beetles and is used in functional genomics (Zhu & Palli 2020). Unfortunately, RNAi is inefficient and variable in most insects, including FAW (Zhu & Palli 2020). Degradation by dsRNAses present in lumen and inefficient intracellular transport and endosomal entrapment are considered reasons for RNAi inefficiency in FAW (Shukla et al. 2016; Yoon et al. 2017). Nanoformulation of dsRNA prepared using polymers (chitosan and poly- [N-(3-guanidinopropyl)methacrylamide] and lipids (Cellfectin) improved RNAi in FAW (Parsons et al. 2018; Gurusamy et al. 2020a, 2020b). Also, the expression of *Caenorhabditis elegans* systemic RNAi defective protein 1 gene in transgenic FAW improved RNAi in a tissue-specific manner (Chen et al. 2020a). The FAW expressing SID-1 showed an improvement of RNAi in tissues such as Verson's glands but not in the midgut. Genome editing technologies, especially CRISPR/Cas9-based method, could also help in advancing functional genomics studies in FAW. Programmable nucleases such as the zinc-finger nucleases (Maeder et al. 2008), TAL (transcription-activator-like) effector nucleases (TALENs) (Boch et al. 2009; Bogdanove and Voytas 2011; Moscou and Bogdanove 2009), and CRISPR (clustered regularly interspaced RNA–guided Cas (CRISPR-associated protein) endonucleases (Mali et al. 2013; Cong et al. 2013; Jinek et al. 2012) are being used to edit genomes of animals and plants. The CRISPR/Cas9 system was adopted to perform genome editing experiments in several pests. Genome editing has been attempted in FAW (Zhu et al. 2020; Jin et al. 2021; Wu et al. 2018). Wu et al. (2018) applied the CRISPR/Cas9 genome editing method to knockout the abdominal-A homeotic gene and the mutants showed the typical abdominal-A phenotypes such as fused segments. Knock out of the ATP-binding cassette transporter C2 gene resulted in insects being tolerant to Cry1F toxin (Jin et al. 2021). Zhu et al. (2020) employed CRISPR/Cas9 genome editing methods to knockout three target genes, including E93, and developed a method to completely silence the target gene in one generation by injecting the Cas9 protein and multiple sgRNAs.

2.7 Microbiome

Insect hosts are affected by all the gut microbiota components, bacteria, archaea, fungi, protozoa, and viruses (Gurung et al. 2019), which can play important roles in host defence and nutrition (Janson et al. 2008). Nevertheless, current knowledge regarding the lepidopteran gut microbiome and its function is very limited (Voirol et al. 2018). Moreover, despite a proliferation of metataxonomic studies, which determine the taxonomic profile by amplifying a marker gene (Marchesi & Ravel 2015), few have addressed whether those taxa are active cells (Brinkmann et al. 2008; Shao et al. 2014; Chen et al. 2016), and even fewer have analysed their functional role (metatranscriptomics) (McCarthy et al. 2015; Rozadilla et al. 2020). In this respect, high taxonomic abundance does not necessarily entail high metabolic activity (Shao et al. 2014; Chen et al. 2016).

Several studies have analysed the FAW gut microbiota, both in field-collected and laboratory-reared larvae, using culture-dependent approaches (Acevedo et al. 2017; De Almeida et al. 2017; Mason et al. 2019, 2020; Gomes et al. 2020) and next-generation sequencing (NGS) methods (Jones et al. 2019; Rozadilla et al. 2020; Gomes et al. 2020; Gichuhi et al. 2020; Ugwu et al. 2020; Mason et al. 2021). The latter have mainly used metataxonomics to describe the bacterial profile (Jones et al. 2019; Gomes et al. 2020; Gichuhi et al. 2020; Ugwu et al. 2020; Mason et al. 2021), but one study analysed the gut metatranscriptome (Rozadilla et al. 2020). All the metataxonomic analyses identified Proteobacteria and Firmicutes as the dominant phyla, and Actinobacteria and Bacteroidetes in much lower proportions. In contrast, the metatranscriptomic analysis showed Actinobacteria, Proteobacteria and archaea as the most active members of the community, expressing genes involved in nitrogen and carbohydrate metabolism. At the genus level all these studies showed great variability, although *Enterococcus* was found in all the NGS analyses, and *Enterobacter* and *Pseudomonas* in most. Similarly, a recent review found that *Proteobacteria* was the most widespread phylum in 30 lepidopteran species, and *Enterococcus, Enterobacter* and *Pseudomonas* were amongst the most common genera (Voirol et al. 2018). Detailed analysis of other,mostly metataxonomic studies, confirmed this trend (Belda et al. 2011; Shao et al. 2014; Ranjith et al. 2016; Li et al. 2018; Bapatla et al. 2018; Phalnikar et al. 2018; Chen et al. 2018; Gao et al. 2019; Martínez-Solís et al. 2020; Wang et al. 2020c), although gut bacteria were very variable across, and even within lepidopteran species with differing diets and exposure to pesticides.

Variable patterns of bacterial gut colonisation in lepidopterans relate to host species, ontogeny, diets, resistance to pesticides and geographical regions (Shao et al. 2014; Chen et al. 2016, 2020b; Li et al. 2018; Hammer et al. 2017; Phalnikar et al. 2018; Gao et al. 2019; Jones et al. 2019; Mason et al. 2020, 2021; Gichuhi et al. 2020; Martínez-Solís et al. 2020; Ugwu et al. 2020), which makes it difficult to establish their indigenous or transient nature. Moreover, environmental factors and microbiomes not only influence the FAW's biology and ecology (Hu et al. 2018; Real-Santillán et al. 2019; Howard et al. 2020) but can also shape its gut microbiota (Gomes et al. 2020). To conclude, a growing body of evidence indicates that gut bacteria are not entirely transient since they are established and maintained through larval instars (Mason et al. 2020), transmitted across developmental stages (Chen et al. 2016; Gao et al. 2019; Gichuhi et al. 2020), can facilitate nutrient acquisition and digestion in the host (Li et al. 2018; Xia et al. 2017; Rozadilla et al. 2020), aid against plant anti-herbivore defences (Visôtto et al. 2009; Acevedo et al. 2017; Xia et al. 2017) and protect the host from pathogens (Shao et al. 2017).

3 Worldwide status and geographic spread

FAW is native to the Americas, where it is widely distributed and frequently reaches outbreak densities and has long been regarded as a pest (Luginbill 1928; Andrews 1980). The 15th-century Madrid and Borgia Codices both described it as a pest of maize in Mesoamerica (Bricker & Milbrath 2011) However, in Honduran subsistence maize production natural enemies often suppress FAW populations (Wyckhuys & O'Neil 2006).

The native, year-round distribution of FAW extends from Argentina to southern US, and it is found in suitable habitats throughout Central America and the Caribbean feeding on many different host plants (Fig. 2) (Vickery 1929; Pogue 2002; Casmuz et al. 2010; Montezano et al. 2018). As FAW does not diapause and cannot survive low temperatures, its year-round distribution is limited to tropical and subtropical regions. However, it is able to migrate long distances to seasonally suitable areas (Johnson 1987), greatly extending the area over which it can cause crop damage. Thus, while in the US it only overwinters in southern parts of the Gulf States (Florida and Texas), it seasonally migrates north and has been recorded as far north as Canada. Most states to the east of the Rocky Mountains are affected seasonally to some degree. In 2021, infestations in the mid-southern states were unusually early, widespread, and severe (Stewart 2021). In South America, populations observed in Argentina and Chile are also mostly transient (Johnson 1987; See also section 4.1)

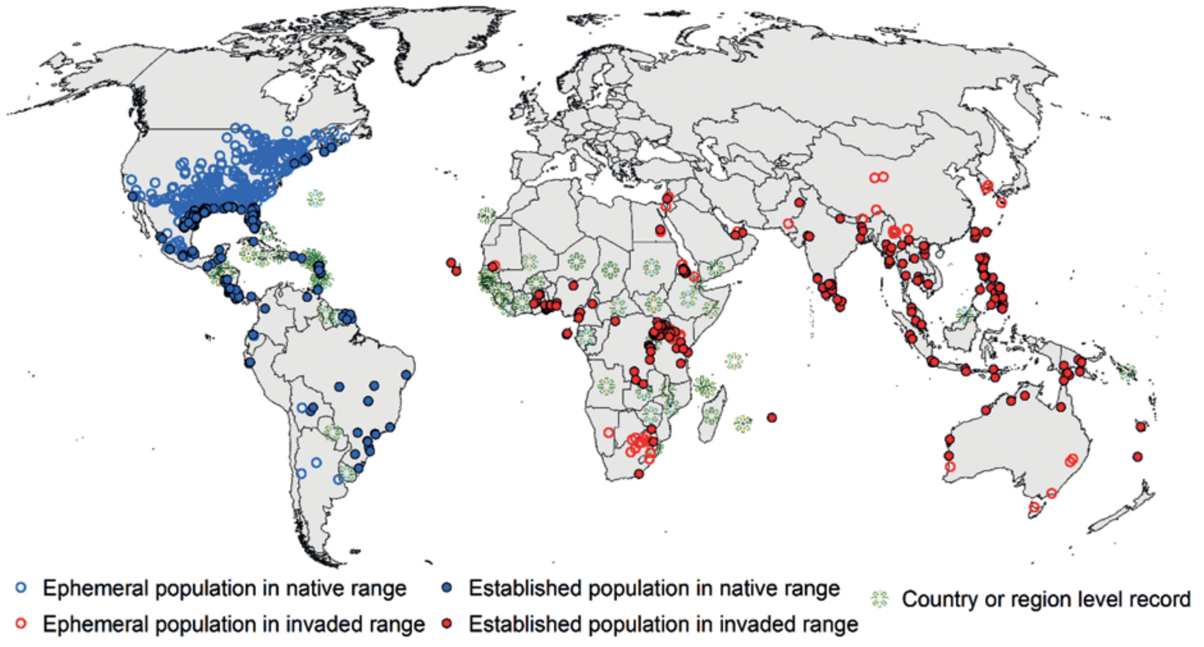

Fig. 2. Global distribution of fall armyworm. Populations are categorised as established or ephemeral based on modelling (du Plessis et al. 2018).

FAW was first found established outside its native range in early 2016, in Benin, Nigeria, São Tomé and Príncipe, and Togo (Goergen et al. 2016). Cock et al. (2017) suggested that it was most likely to have arrived as a hitchhiker on an international flight, rather than as a commodity contaminant, although the latter is possible as it has frequently been intercepted in the Netherlands in consignments from Latin America, particularly Capisum and Solanum shipped from Suriname (EFSA PLH Panel et al. 2017). Lepidoptera can survive in the wheel-bays of planes on long haul flights (Russell 1987) and FAW is known to lay eggs on non-plant surfaces (Sparks 1979; Thomson & All 1984). Porter & Hughes (1950) found nearly 1% of planes arriving at Miami airport from South America and the Caribbean had Lepidoptera eggs on them, mostly FAW. Genetic analysis by Nagoshi et al. (2017b; 2018) indicated the West African population originated in the area of Florida and the Antilles. Following the initial report, FAW was also found in Ghana in late 2016 (Cock et al. 2017).

By 2018, FAW was found in most countries in sub-Saharan Africa. It is now thought to be present in all mainland sub-Saharan and Sahelian countries except Lesotho (Fig. 2) (FAO 2021). It is also present in Egypt (IPPC 2021) and the Indian Ocean islands of Madagascar, Mauritius, Mayotte, Réunion, and the Seychelles (CABI 2021; EPPO 2021). Larvae have also been sampled in Comoros (Nagoshi et al. 2022). The Mediterranean fringes of North Africa have pockets of a suitable environment for FAW (Early et al. 2018; du Plessis et al. 2018; Paudel Timilsena et al. 2022), but there have been no reported sightings except in Egypt (IPPC 2021), and EFSA PLH Panel et al. (2018) considered it unlikely that FAW could fly across the Sahara.

Most of the areas where FAW is found in Africa appear to support year-round populations. However, in South Africa and neighbouring countries, many areas may be too cold for populations to persist (Early et al. 2018; du Plessis et al. 2018). The damage reported in at least some parts of Zimbabwe (Baudron et al. 2019; Chimweta et al. 2020; Tambo et al. 2020a) and Zambia (Tambo et al. 2020b; Kasoma et al. 2021a) might therefore be due to immigrant populations.

In Asia, Yemen was the first country where FAW was found, possibly as early as April 2018 (USAID 2018), although it was not detected in the United Arab Emirates until two years later (IPPC 2021). It was discovered on maize plants in Karnataka, India (Sharanabasappa et al. 2018; Ganiger et al. 2018; Shylesha et al. 2018) in May 2018, and by July it was found in several neighbouring states. The following month it was found in several states to the north of Karnataka, and by October it was reported from states in the north-west and north-east, as well as from Kerala in the south-west (Rakshit et al. 2019). Early in 2019, it was found in the Indian states to the east of Bangladesh (Firake et al. 2019), and by August 2019 it was recorded in the northern states (Rakshit et al. 2019). In 2020 FAW was detected in almost all maize growing areas of India including the hilly areas bordering Pakistan and Tibet (Desk 2020; Sharma 2021). FAW was already present in the Andaman and Nicobar Islands by September 2019 (Giles 2019), around 1400 km to the east of India.

In Sri Lanka, FAW was first detected in August 2018, soon after it was observed in the neighbouring area of India (Perera et al. 2019; Rajapakse 2021). Similarly, the first detection of FAW in Bangladesh was made with pheromone traps in November 2018 (Alam et al. 2018), around the time it was found in the neighbouring states of India. However, in Pakistan, the first report was not until March 2019 (Ullah et al. 2019; Gilal et al. 2020). FAW was found in Nepal (Ratna et al. 2019) and Bhutan (Mahat et al. 2021) later in 2019.

In the Middle East, FAW was observed during 2020 in Israel (EPPO 2021), Jordan (IPPC 2021), and Syria (IPPC 2021; Heinoun et al. 2021) where it was assumed to have arrived by natural spread from Jordan. Wiltshire (1977) reported receiving FAW adults collected in Israel in 1967, but that is thought to be either a misidentification (CIE, 1985) or a transient population that did not establish (EFSA PLH Panel et al. 2017). However, Gilligan & Passoa (2014) reported larvae identified as FAW that originated from Israel had been intercepted at U.S. ports prior to February 2014.

The invasion of South-East Asia appeared to follow the invasion in South Asia, with Thailand and Myanmar first being affected in late 2018 (IPPC, 2021). Indonesia, Malaysia, Laos, and the Philippines reported FAW in 2019 (IPPC 2021), Vietnam (Hang et al. 2020) and East Timor in 2020, Cambodia and Brunei Darussalam in 2021 (IPPC 2021). Singapore reported FAW to be absent in a survey (IPPC 2021).

In East Asia, FAW was reported from China in December 2018, South Korea in June 2019 and Japan in July 2019 (Sun et al. 2021b; FAO 2019; IPPC 2021). It cannot overwinter in many parts of Eastern Asia, but Yang et al. (2021a) found that it is able to persist in the tropical and sub-tropical parts of southern China, but not in areas further north where most of China's maize is grown, and to which seasonal migration occurs. In 2019 alone, 1.125 million hectares of crops were infested in China, with maize accounting for 98.1% of the total affected area (Zhou et al. 2021).

In Oceania, FAW was detected in Papua New Guinea in February 2020 on young maize plants (Pacific Community 2020). The arrival of FAW in Australia had been expected as a hitchhiker or via wind dispersal from the north or north-west, with the latter making eradication efforts futile because of the likely subsequent migrations. In February 2020 FAW was detected in pheromone traps in the northern Torres Strait islands of Saibai (less than 5km from mainland Papua New Guinea) and Erub. Later the same month, FAW was detected on Cape York, in the far north of Queensland, and the Consultative Committee on Emergency Plant Pests concluded that it was not technically feasible to eradicate FAW. It was subsequently detected in Western Australia and the Northern Territory, and then New South Wales (September 2020) and Victoria (December 2020). It has been detected as far south as north-western Tasmania (April 2021) and on Norfolk Island (March 2021). FAW has also been found in the arid interior of Australia at Alice Springs, associated with an irrigated site. The CLIMEX model of du Plessis et al. (2018) shows that in wet years this area could be suitable for year-round persistance (DJK, unpub. data). The models of Maino et al. (2021) also show that while populations may probably only persist in the northern parts of Australia, and that it will be restricted by high or low temperatures and dry conditions in the country. However, in some months population growth is likely to be possible in many areas of Australia.

In December 2020, FAW was found in New Caledonia. In an attempt at eradication, the affected maize field was destroyed, but in 2021 FAW was found throughout the territory and eradication is now considered impossible (IPPC 2021). In August 2021 it was discovered in the Solomon Islands (IPPC 2021), where eradication was again considered not feasible. In March 2022 a FAW egg mass was found on the northern Island of New Zealand (NZ Herald 2022)

FAW is regularly intercepted in imports of plant products to Europe (EFSA PLH Panel et al. 2017), but the only field report of FAW in mainland Europe was in 1999 when maize plants in a nursery in Germany were found to be affected (EPPO 2021). The larvae were destroyed, and the insect was not recorded again. FAW was detected in pheromone traps in the Canary Islands (Spain) in July 2020 (Moreno & Gaston 2020). Subsequent surveys found the insect on all the islands, but only on maize and causing minor damage. It is thought that it might have arrived from Africa on strong winds that occurred during March 2020.

Because of variation in the rate with which countries have detected and reported FAW, it is not feasible to give an accurate chronology of its global spread. From the sequence of reports beginning in West Africa, across Africa, then Asia and eventually Oceania, the impression is of progressive spread. However, whole genome analysis by Tay et al. (2022) indicates multiple introductions have played a major role in the apparent rapid spread of FAW, with complex mixing of populations including significant directional gene-flow from Asia into East Africa. Gilligan & Passoa (2014) reported interceptions of FAW in consignments arriving at U.S. ports from China, Indonesia, Micronesia, Netherlands, Turkey, and Thailand, suggesting FAW might have been present in many countries outside its native range before its discovery in West Africa in 2016. More work is required, including sampling of Southeast Asian and Oceania FAW populations for whole genome analysis, to better understand the global spread of FAW and seasonal patterns of migration.

4 Potential for geographic expansion and quarantine measures in place in areas threatened by the pest

4.1 Climate and spread modelling

The potential distribution of FAW has been modelled using a variety of methods (Fig. 3A and 3B) (du Plessis et al. 2018; Early et al. 2018; Timilsena et al. 2022). Each of these models indicates that FAW can establish in warm, moist regions on every continent except Antarctica.

A critical feature of the geographical distribution of FAW in North and South America is its ability to migrate long distances into temperate zones during warmer months to take advantage of seasonal host resources (Gao et al. 2020). The CLIMEX model (Fig. 3A) explicitly captures these range dynamics, clearly distinguishing the areas that are likely suitable for population *establishment* and those areas that are only suitable for supporting *ephemeral populations*. The European Pest Risk Assessment for FAW (Jeger et al. 2017) called into question the concordance of the CLIMEX model of du Plessis et al. (2018) and reported outlying observations in Argentina. A careful examination of the Argentine literature reveals that all the outlying records in Argentina represented ephemeral populations, rather than established populations. For example, Juarez et al. (2012) noted a population in Carmen de Areco, which they concluded was probably a non-permanent population, being re-colonized each year by populations from other regions (northeastern Argentina, Uruguay, or Brazil). In the north-west of Argentina, Murúa & Virla (2004a, b) studied populations from Tucuman province and concluded based on winter trapping, that this was the southernmost limit of FAW in South America, which accords with the modelling results of du Plessis et al. (2018). This conclusion was subsequently supported by genetic analyses (Murúa et al. 2008; 2019). The realized ephemeral range of FAW in South America does not appear to be as widespread as it is in North America, suggesting that while it is a relatively strong flyer, the specific weather patterns in North America play a significant role in transporting *S. frugiperda* populations into high latitudes on an annual basis.

Irrigation plays a critical role in modifying the habitat suitability of xeric areas, such as along the Nile River in Sudan and southern Egypt, effectively creating an invasion corridor across the otherwise inhospitable desert area (Fig. 4). This pattern is also apparent in patches scattered throughout the Middle East, central India, and central Australia.

Comparing the current known distribution (Fig. 2) and the modelled potential distributions (Fig. 3) we can see that FAW has been remarkably effective at expanding its range globally within the area modelled as being climatically suitable. After the first reports of FAW in West and Central Africa in 2016 (Goergen et al. 2016), it spread rapidly, and was reported in most sub-Saharan countries in 2017 (ACAPS, 2017), including South Africa (Jacobs et al. 2018). The potential distribution regions forecasted by du Plessis et al. (2018) is still continuously being infilled by the pest. The area permanently colonized by *S. frugiperda* in South Africa accords with the model, and it can overwinter in Mbombela and as far south as East London (du Plessis, pers. obs.) (Fig. 4).

FAW has already invaded all the regions that were modelled as being climatically suitable for establishment under historical climate conditions. The potential for range expansion is now limited to the Pacific Islands, and in-filling gaps within the invaded continents. In the Western Pacific, FAW has already invaded New Caledonia and has been recorded on Norfolk Island, 750 km to the south and, in March 2022, an egg mass was found in New Zealand (Tauranga, Northern Island) (NZ Herald 2022). In China and Australia, FAW appears to have established an oscillatory dynamic range that matches the seasonal range extension and contraction observed in North and South America. In Australia, the most southerly report was from a trap in Tasmania in Autumn of 2021. In China, FAW overwinters in the south. During the summer of 2019–2020, the ephemeral range extended over more than 1×10^6 ha, reaching as far north as Liaoning Province (41°N) (GH, pers. obs.).

Prevailing seasonal winds at high altitudes can play a central role in supporting regular long-distance migration. In northern America, the Great Plains low-level jet is a prominent atmospheric flow spanning the latitudinal extent of the central USA from Mexico to Canada (Wainwright et al. 2016). At night, this rapid stream of meridional winds has likely plays a role in supporting the migration of *S. frugiperda* across the central USA (Westbrook et al. 2016; Rose et al. 1975). In eastern Asia, the annual East Asian summer monsoon provides a pathway of favorable winds for the airborne transport of migratory organisms (insects, birds, and pathogen spores), to the north in the spring and returning south in the autumn.

Flight mill studies have shown that some individuals of FAW can fly continuously for more than 48 hours, and the longest flight distance and time recorded on a mill were 163.58 km and 46.73 hours (Ge et al. 2021). These studies indicate that the potential for spread in the absence of a suitable tailwind is limited to around 100 km. Trajectory simulations that combined flight behavior and meteorological data were used to simulate FAW migrating from its newly established overwintering regions on the Indochina Peninsula and southern China into the main maize-producing regions of eastern China via two pathways. The western pathway originated in Myanmar and Yunnan province in China, while the eastern one was from Thailand, Laos, Vietnam, and southern China (Li et al. 2020c; Chen et al. 2020c). Based on these simulations, FAW could also migrate to Japan and the Korean Peninsula by crossing the sea from China during the Meiyu season (Ma et al. 2019). The simulated migration paths and

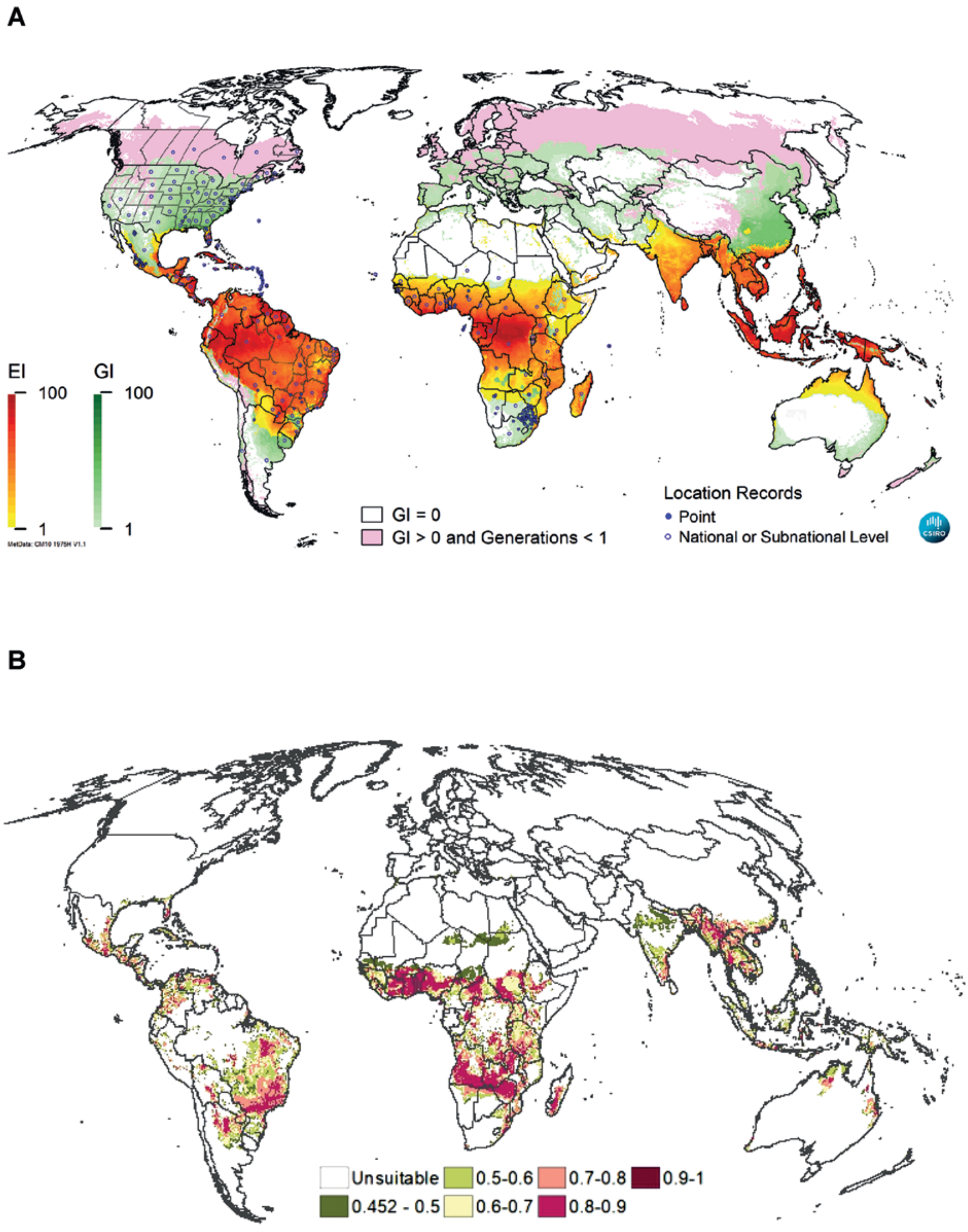

Fig. 3. The global potential distribution of *Spodoptera frugiperda* **(A)** modelled using CLIMEX, du Plessis et al. (2018). The red-orange areas represent climates suitable for the establishment of persistent populations. The green areas represent areas suitable for supporting one or more generations during favourable seasons. **(B)** An ensemble of correlative species distribution models (Regan et al. 2018). The correlative model is cut at a threshold of 0.452, which includes 95% of the known *S. frugiperda* presence records. N.B. in the correlative model the modelled suitability for *S. frugiperda* in the Sahara Desert should be discounted. This result is due to the inclusion in the training dataset of an irrigated site in the Sechura Desert in Peru, which is artificially irrigated.

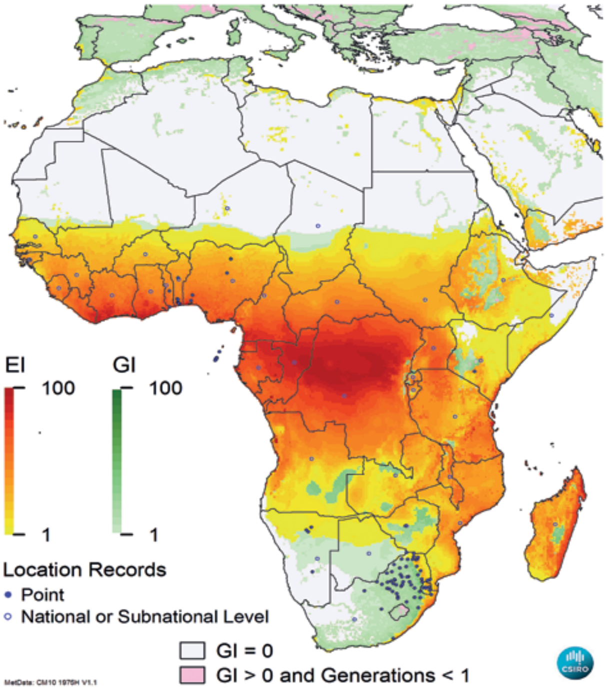

Fig. 4. Potential distribution of *Spodoptera frugiperda* in Africa and the Middle East modelled using CLIMEX (du Plessis et al. 2018).

migratory ranges in these studies were in accordance with its observed spread trends in China, Korea, and Japan in 2019 (Wu et al. 2021b; Li et al. 2020c; Ma et al., 2019; Jiang et al. 2019; Lee et al. 2020).

The potential for FAW to invade the tropical Pacific Islands depends on the wind patterns in the archipelagos (Monsoon storms, trade winds, cyclones, and hurricanes) and trade contamination patterns. Once established in an archipelago, it may be able to spread relatively easily between islands.

4.2 Phytosanitary measures

Increasingly, international trade activities are being linked with the spread of exotic insect pests (e.g., Wu et al. 2017; McCullough et al. 2006; Hulme et al. 2008; Tay et al. 2017; Tay & Gordon 2019). Phytosanitary measures such as pre-border interceptions and species identification underpin a country's ability to reduce the accidental introductions of exotic insect pests and diseases to protect plant health. The efficacy of these measures is often difficult to quantify due to compounding factors such as predetermined 'target species lists' and 'priority pest species and the current understanding of the pest or diseases geographical distributions, as well as its detectability and diagnostics capacity. For example, FAW samples intercepted prior to 2016 may have been disregarded as being implausible if the country of origin involved non-native ranges. Trans-shipped goods that are re-labelled in terms of their country of origin further complicate matters. Finally, market access considerations provide an incentive for invaded countries to avoid or delay officially reporting the presence of invasive organisms. For these reasons, pest interception data is often difficult to obtain. The reporting delays and inconsistencies, especially through Asia, have affected the perceived pattern of invasion by FAW, supporting the "out of Africa" thesis.

The spread of FAW is likely facilitated by both anthropogenic activities and natural dispersal (Early et al. 2018), suggesting that phytosanitary measures could in principle help slow its further spread. The Pacific Islands may therefore be a region where cost-effective phytosanitary measures could be useful for this purpose, as the islands are relatively widely dispersed and represent small targets for migratory moths. Despite the natural geographical advantages afforded to island nations with regards to some forms of biological invasions, the spread of devastating insect pests (e.g., Bedford 1980; Gotzek et al. 2015; Wetterer 2005), including *S. frugiperda* across Indian Ocean islands (e.g., Seychelles, Madagascar, Réunion Island, Mauritius) demonstrates that significant challenges remain when implementing policies and developing strategies to slow the spread of invasive insect pests. New Zealand's assessment is that *S. frugiperda* will likely arrive via wind-assisted flight in the five years following 2021 (https://www.mpi.govt.nz/dmsdocument/45934-Biosecurity-Intelligence-report-the-threat-of-fall-armywork-natural-dispersal-from-australia-to-new-zealand). Accordingly, the Risk Assessment places more emphasis on managing FAW, should it arrive or establish following wind dispersal, than on preventing its import via trade or transport routes. The report, however, does not elaborate on what preparation activities are being undertaken to assist in managing *S. frugiperda* when it arrives. A single egg mass of FAW was found in March 2022 on a spongy moth (*Lymantria dispar* (L.)) trap in the country, but there is no sign of establishment yet (NZ Herald 2022).

5 Management of *S. frugiperda*

5.1 Monitoring, sampling, and pest forecasting

While pheromone trap catches provide early warning of moth activity in a region (Meagher et al. 2008), monitoring and scouting for pest-infested plants provide information on field infestation levels which informs decisions whether to apply control measures (Linduska and Harrison 1986; McGrath et al. 2018).

5.1.1 Pheromone trapping

Since the 1960s, behavioural bioassays suggested that female FAW moths release a blend of chemicals that attracts males. The main chemical component was first identified as (Z)-9-tetradecen-1-ol acetate (Z9-14:OAc) (Sekul & Sparks 1967). Lures were made with this component but trapping results were not successful. Another compound, (Z)-9-dodecen-1-ol acetate (Z9-12:OAc), was later found to be the primary pheromone component and was then used extensively as the pheromone lure (Sekul & Sparks 1976; Jones & Sparks 1979). However, moth numbers in traps were variable and a large amount of the component was required. Further analysis showed that females produce four additional compounds: including (Z)-7-dodecenyl acetate (Z7-12:OAc), (Z)-11-dodecenyl acetate (Z11-12:OAc), (Z)-11-hexadecenal (Z11-16:Ald), and (Z)-11-hexadecenyl acetate (Z11-16:OAc) (Tumlinson et al. 1986). Field tests revealed that Z9-14:OAc and Z7-12:OAc were critical for male attraction (Tumlinson et al. 1986). This two-component blend became commercially available in the US in the mid-2000s. and is still used today. However, lures do not always attract large number of moths (Batista-Pereira et al. 2006; Cruz-Esteban et al. 2020). Furthermore, pheromone blends that attract FAW also attract other noctuids, including species that can be confused with *S. frugiperda*, creating issues for monitoring in newly invaded areas (Fleischer et al. 2005, Meagher et al. 2019). Interestingly, it was also found that the compound Z11-16:OAc interrupts the attraction of non-target sympatric moth species (Fleischer et al. 2005, Cruz-Esteban et al. 2020).

The combination of different traps with different pheromone components and substrates that influence release into the environment guided the development of trapping techniques (e.g., Malo et al. 2001, 2004b; Meagher & Mitchell 2001). Many types of traps were developed with different designs and colours (Adams et al. 1989, Malo et al. 2001, 2018, Meagher et al. 2013, 2019). Trap height (Malo et al. 2004b), trap color (Mitchell et al. 1989, Malo et al. 2018), and host plant volatiles (Unbehend et al. 2013) affect the performance of pheromone-baited traps. Other factors such as weather, crop habitat, and proximity to trees also affect trap captures (Tingle & Mitchell 1979; Koffi et al. 2021a). The use of artificial intelligence as a component of FAW pheromone trapping systems was illustrated by Chiwamba et al. (2019), who used automated traps to provide early warning and near real-time information.

5.1.2 Pest forecasting and early warning

Regional monitoring may provide early warning of pest presence. Barfield et al. (1980) indicated that the development of such a system is knowledge intensive and that the erratic occurrence of this pest made it difficult to predict.

A system that may provide early warning if used by enough farmers in a particular region was developed by the FAO (FAW Monitoring and Early Warning System-FAMEWS) (FAO 2020) to collect data and provide information on FAW population fluctuations over time. The FAMEWS global platform is an online resource for mapping data collected by the FAMEWS mobile app whenever fields are scouted, or pheromone traps are checked, and provides a real-time situation overview with maps and analytics of FAW infestations at global and regional levels.

5.1.3 Monitoring and Sampling

For detection only, a sensitive trapping method that provides presence / absence data is required, while the use of action thresholds requires quantitative information on pest incidence and even meteorological data (Howse et al. 1998). Pheromone trap catches indicate the presence of moths in an area but are not necessarily good indicators of egg-laying intensity and larval numbers (Barfield et al. 1980; Meagher et al. 2008; McGrath et al. 2018). Silvain (1998) reported correlations between FAW trap catches and larval numbers in forage pastures in French Guiana, and accurately estimated, a week in advance, the abundance of larvae in these pastures. Linduska & Harrison (1986) also reported a positive relationship between trap catches and FAW infestation levels.

Decisions to apply insecticides should not be based on moth counts alone (McGrath et al. 2018). Once moths are detected, scouting for eggs and damaged plants should commence. Scouting implies the periodic checking of fields to determine if the incidence of infested plants exceeds predetermined action threshold levels (McGrath et al. 2018). Scouting is especially important when the crop is attacked by a complex of pest species, since pheromones only attract one or closely related species. This is particularly the case in the Americas on crops such as cotton and soybean. Scouting protocols have been described by McGrath et al. (2018) and should begin soon after seedling emergence. Early detection is highly advantageous since insecticide and biocontrol applications are more effective on eggs and early larval stages (Linduska & Harrison 1986; Hernandez-Mendoza et al. 2008; Colmenarez al. 2022; Prasanna et al. 2021).

5.1.4 Action threshold levels

Economic threshold levels for FAW control have not been determined with precision (Overton et al. 2021) and only guidelines exist for use in decision making (McGrath et al. 2018). Large variations exist in the injury resulting from a given level of FAW infestation and in plant responses to injury (Cruz & Turpin 1983; Hruska & Gladstone 1988; Baudron et al. 2019; Van den Berg et al. 2021a). On-farm studies in Zimbabwe suggested that yield loss cannot be predicted from once-off assessments of infestation and leaf damage alone (Baudron et al. 2019). McGrath et al. (2018) and Van den Berg et al. (2021a) suggested that, given the high degree of uncertainty surrounding the relationships between infestation levels, plant damage and yield loss, more conservative thresholds should be used, especially in the case of smallholder farmers.

Action thresholds based on expert opinion have been recommended for FAW control (McGrath et al. 2018). These recommendations have been presented as different thresholds for different maize growth stages as follows: during the early whorl stage, if 20% (range of 10–30%) of the seedlings are infested, or during the late whorl stage, if 40% (range of 30–50%) of the plants are infested, an insecticide application is warranted. During the tassel and silk stage, if 20% (range of 10–30%) of plants are infested an insecticide application may be justified. However, action thresholds should be based on the value of projected yield losses versus the cost of the proposed intervention. Moreover, early application of chemical pesticides usually requires repeated spraying, because natural enemies are impacted to a greater extent than the pest (Meagher et al. 2016; section 5.8.3), and this should be imputed into any calculations. Urgent research is required to elucidate reliable metrics for predicting yield loss.

5.2 Parasitoids, parasitic nematodes, and predators

5.2.1 In the native range

Many publications provide information on natural enemies of FAW in the Americas, with most studies focusing on parasitoids. Molina-Ochoa et al. (2003a) and Bahena & Cortez (2015) provided reviews of the literature regarding natural enemies of FAW and listed from 150 to 200 species of natural enemies for the Americas and the Caribbean. Since then, parasitism has been further studied in various parts of its native range, including, e.g., Hernández-García et al. (2017), Barreto-Barriga et al. (2017), Contreras-Cornejo et al. (2018), and González-Maldonado et al. (2020).

The most frequently cited parasitoid of FAW throughout its native range is the egg-larval parasitoid *Chelonus insularis* Cresson (Braconidae) (Molina-Ochoa et al. 2003a; Bahena & Cortez 2015). Other larval parasitoids that are often recorded are *Campoletis sonorensis* (Cameron), *Campoletis. flavicincta* (Ashmead), *Pristomerus spinator* (F.), *Eiphosoma laphygmae* (often cited as *Eiphosoma vitticolle* (Cresson) but see Gauld 2000 for the taxonomic clarification) (Ichneumonidae), *Euplectrus plathypenae* Howard (Eulophidae), *Cotesia marginiventris* (Cresson), *Aleiodes laphygmae* (Viereck) and *Meteorus laphygmae* Viereck (Braconidae), *Archytas incertus* (Macq.), *A. marmoratus* Townsend, and *Lespesia archippivora* Riley (Tachinidae) (Molina-Ochoa et al. 2003; Bahena & Cortez 2015 and references therein). A useful key for identifying the main larval parasitoids of FAW in the Americas is provided by Cave (1993). Parasitic nematodes of the genus *Hexamermis* (Mermithidae) are also regularly cited attacking FAW larvae (Gardner & Fuxa 1980; Wyckhuys & O'Neil, 2006).

Natural larval parasitism rates are provided in several studies and are often lower than 30% (e.g. Pair et al.1986b; Molina-Ochoa et al. 2004; Wyckhuys & O'Neil, 2006; Murúa et al. 2009; Virgen et al. 2013; Ordóñez-García et al. 2015). However, Allen et al. (2021) argue that larval parasitism rates are probably largely underestimated in most studies in the Americas because of likely biases in sampling and calculation of parasitism rates. Furthermore, the extensive use of pesticides and Bt crops probably negatively affects natural parasitism rates, either by direct effect on parasitoids or because many parasitoids forage in a density-dependant manner (Ramirez-Romero et al. 2007; Desneux et al. 2010; Han et al. 2016). In the southern US, Meagher et al. (2016) observed that FAW larval parasitism rates are much higher in unsprayed fields (44% on average) than in fields sprayed with pesticides (15%), and they recorded a parasitism rate of 97% in one unsprayed field surrounded by diverse vegetation. Other studies measured average parasitism rates higher than 60%, e.g., Gladstone (1991) in Nicaragua and Marenco & Sauders (1993) in Costa-Rica.

Egg parasitioids are commonly mentioned in terms of augmentative biological control strategies (see section 5.6.3) but data on natural occurrences are scarce. *Telenomus remus* Nixon (Scelionidae), introduced from Asia, is only occasionally found naturally in the Americas (Hay-Roe et al. 2015; Varella et al. 2015; Wengrat et al. 2021). *Trichogramma pretiosum* Riley and *Tr. atopovirilia* Oatman & Platner (Trichogrammatidae) are regularly found parasitizing FAW egg masses, but natural parasitism remains below 5% (Beserra et al. 2002; Varella et al. 2015; Jaraleño-Teniente et al. 2020), This is partly ascribed to the difficulty to parasitize eggs in the lower layers of egg masses or egg masses covered by a high number of scales and hair (Beserra & Parra 2005; Goulart et al. 2011a).

Pupal parasitism has been poorly studied due to the difficulty in collecting large numbers of pupae. *Diapetimorpha introita* (Cresson) (Ichneumonidae) is reported as the most abundant pupal parasitoid in Mexico (Molina-Ochoa et al. 2003a). An acugutturid nematode, *Noctuidonema guyanense* Remillet and Silvain, has been reported to attack adults of FAW and other noctuid species (Molina-Ochoa et al. 2003a).

Data on predators in the Americas are rather scarce. The first detailed description of predators on FAW was made by Luginbill (1928). More recently, predation has been primarily studied in the laboratory (de Oliveira et al. 2004; Sueldo et al. 2010), but little is known on their precise impact in the field, except from the life table study of Varella et al. (2015) who considered predation on eggs and young larvae to be much higher than parasitism. Bahena & Cortez (2015) listed 65 species of FAW predators, mainly for the egg and larval stages. The most commonly observed FAW predators include *Orius insidiosus* (Say), *O. tristicolor* (White) (Hemiptera: Anthocoridae), *Geocoris punctipes* (Say) (Hemiptera: Geocoridae), *Zelus longipes* (L.), *Sinea confusa* Caudell (Hemiptera: Reduviidae), *Harmonia axyridis* (Pallas), *Eriopis connexa* (Germar), *Coleomegilla maculata* (De Geer), *Hippodamia convergens* (Guérin-Méneville) (Coleoptera: Coccinellidae), *Doru luteipes* (Scudder) and *D. lineare* (Eschscholtz) (Dermaptera: Forficulidae) (Gross et al. 1985; Isenhour et al. 1990; Varella et al. 2015; Bahena and Cortez 2015). Mites of the genus *Balaustium* have been found preying on eggs of FAW in Mexico (Jaraleño-Teniente et al. 2020). Predatory ants are known to contribute to the biological control of FAW (Hruska, 2019). In maize-based cropping systems in Honduras highlands, ants, especially

Solenopsis geminata (F.), *Brachymyrmex* spp., *Camponotus* spp., *Crematogaster* spp. and *Pheidole* spp. are closely associated with FAW (Wyckhuys & O'Neil, 2006). In Nicaragua, by means of poison baits in maize fields, Perfecto (1991) and Perfecto & Sediles (1992) observed that ant-foraging activity on FAW larvae and pupae was reduced and FAW abundance and damage were increased. Solitary wasps (Wyckhuys & O'Neil 2006; Sousa et al. 2011) and social wasps, in particular *Polistes* spp. (Prezoto & Machado 1999; Southon et al. 2019) are also known to actively prey on FAW. Southon et al. (2019) conducted an experiment in Brazil showing that the presence of *Polistes satan* has a significant effect in reducing FAW population. However, this study was conducted in a screen house. Field-realistic data on the impact of social wasps on FAW are lacking (Brock et al. 2021).

5.2.2 In the invaded range

Many studies have recently been conducted to identify local natural enemies, mostly parasitoids, that could be used for biological control of FAW in newly invaded regions. The presence of various congeneric *Spodoptera* spp. prior to the invasion has allowed the natural transfer of several of their parasitoids to FAW.

In Africa, over 30 indigenous parasitoid species attacking FAW have already been identified in 17 countries (Table 1). The most common larval parasitoids of FAW in Africa are the braconids *Chelonus bifoveolatus* Szépligeti and *C. curvimaculatus* Cameron, *Coccygidium luteum* and *Cotesia icipe* Fernandez-Triana and Fiaboe, the ichneumonid *Charops* sp. and the tachinids *Drino quadrinozula* (Thomson) and *Drino imberbis* (Wiedemann) (=*Palexorista zonata* (Curran)) (Amadou et al. 2018; Sisay et al. 2019b; Agboyi et al. 2020; Durocher-Granger et al. 2021; Abang et al. 2021; Otim et al. 2021). FAW eggs are attacked mainly by *Te. remus* and more occasionally by species of the genera *Trichogramma* and *Trichogrammatoidea* (Kenis et al. 2019; Sisay et al. 2019b; Elibariki et al. 2020; Laminou et al. 2020; Sun et al. 2021a). Both eggs and larvae sometimes suffer surprisingly high rates of parasitism for a non-indigenous species. For example, average larval parasitism rates varied between 5% and 38% in Ghana (Agboyi et al. 2020) and between 13% and 53%, depending on countries and years, in East Africa (Sisay et al. 2019b). Agboyi et al. (2020) also found egg mass parasitism up to 26% in Ghana and 14 % in Benin. In Kenya and Tanzania, Sisay et al. (2019b) recorded egg parasitism rates by *Te. remus* above 50%. In Zambia, larval parasitism rates varied from 8.5% to 33%, the latter being an organic farm, but egg parasitoids were not detected (Durocher-Granger et al. 2021).

Information on predators of FAW is sparse in Africa, although it is common to find various species praying on eggs and larvae. In Ghana, three predator species were found feeding on FAW larvae in the field: the ant *Pheidole megacephala* (F.) and the reduviid bugs *Haematochares obscuripennis* Stål, and *Peprius nodulipes* (Signoret) (Koffi et al. 2020). In Benin, Dassou et al. (2021) found seven ant species in fields infested by FAW and all preyed on FAW larvae in the laboratory. Social wasps are also frequently observed predating on FAW larvae in the field (R. Harrison per obs.). However, the importance of predators in the population dynamics of FAW is unknown and deserves further study to assess their potential as biological control agents in augmentative or conservation biological control.

In Asia, most data on natural enemies of FAW derives from India and China. In India, more than 20 species of parasitoids (Table 2) and several predators have been reported (e.g., Shylesha et al. 2018; Gupta et al. 2019; 2020a; 2020b; Sharanabasappa et al. 2019; Firake & Behere 2020a; 2020b; Anandhi & Saminathan 2021; Navik et al. 2021). Their impact on FAW populations can be significant. In northeast India, Firake and Behere (2020a) reported 57 to 73% FAW larval mortality due to natural enemies in maize fields. In ginger fields in Meghalaya state, Firake & Behere (2020b) recorded 74% larval mortality, mainly due to the egg-larval parasitoid *Chelonus formosanus* Sonan (5%), mermithid nematodes (10%), *M. rileyi* (38.01%) and SfMNPV (21%). In Karnataka state, egg parasitism rates of *Trichogramma chilonis* Ishii and *Te. remus* reached up to 24% and 9%, respectively, whereas larval parasitoids caused 9% parasitism (Navik et al. 2021).

Parasitoids of FAW in China were recorded soon after the first report of its presence in the country in 2019 (Table 2). Egg parasitoids included *Te. remus* and *Tr. chilonis* (Huo et al. 2019; Liao et al. 2019; Tang et al. 2020a). Parasitism rates by *Te. remus* were significant, with 28.9% of the egg masses parasitized in Hainan province (Tang et al. 2020a) and 30.6% in Guangdong Province (Huo et al. 2019). Two egg-larval parasitoids as well as eight larval parasitoids and one pupal parasitoid have also been identified (Table 2). In Hainan, parasitism by the egg-larval parasitoid *C. formosanus*, the larval parasitoid *Microplitis pallidipes* Szépligeti, and the pupal parasitoid *Tetrastichus howardi* Olliff was 12%, 7% and 4%, respectively. An extensive survey for parasitoids was conducted in Java, Indonesia (Tawakkal et al. 2021) where egg parasitism was dominated by *Telenomus* sp. and larval parasitism by *Microplitis* sp.

Predation has also been observed in fields in Asia, but its impact has not been quantified and most observations have been anecdotal. The most extensive study on predators was that of Firake & Behere (2020a), who directly observed 12 predators feeding on FAW eggs and larvae, including predatory bugs (Hemiptera: Pentatomidae and Reduviidae), earwigs (Dermaptera: Forficulidae), spiders (Araneae), paper wasps (Hymenoptera: Vespidae) and a tiger beetle (Coleoptera: Cicindelidae). The most important predator was the pentatomid bug, *Eocanthecona furcellata* Wolf. Various species of ladybird beetles (Coleoptera: Coccinellidae) were also found foraging on infested plants.

Table 1. Parasitoids recorded from *S. frugiperda* in the field in African countries, as mentioned in the references.

Species[1]	Biology[2]	Countries	References[3]
Dipt: Tachinidae			
Drino quadrizonula (Thomson)	Larval-(pupal)	Benin, Ghana, Mozambique, Uganda, Zambia	b,d,f,k
Drino sp.	Larval	Burkina Faso	c
Exorista larvarum (L.)	Larval	Egypt	o
Drino imberbis (Wiedemann) (= *Palexorista zonata* (Curran))	Larval	Ethiopia, Kenya	m
Sturmiopsis parasitica (Curran)	Larval-pupal	Uganda	l
Hym: Braconidae			
Bracon sp.	Larval	Ghana	i
Chelonus bifoveolatus Szépligeti	Egg-larval	Benin, Burkina Faso, Ghana, Senegal, Uganda, Zambia	b,c,f,i,l,o
Chelonus curvimaculatus Cameron	Egg-larval	Kenya, Zambia	f,i,m
Chelonus intermedius (Thomson)	Egg-larval	Egypt	p
Chelonus sp.	Egg-larval	Niger	
Coccygidium luteum (Brullé)	Larval	Benin, Burkina Faso, Cameroon, Ethiopia, Ghana, Kenya, Mozambique, Tanzania, Uganda, Zambia	a,b,c,e,f,i,l,m
Cotesia flavipes Cameron	Larval	Uganda	l
Cotesia icipe Fernandez-Triana and Fiaboe	larval	Benin, Cameroon, Ethiopia, Ghana, Kenya, Tanzania, Zambia	a,b,f,m,
Cotesia ruficrus (Haliday)	Larval	Egypt	p
Cotesia sesamiae (Cameron)	Larval	Cameroon	a
Cotesia sp.	Larval	Niger	d
Diolcogaster sp.	Larval	Uganda	l
Meteorus sp.	Larval-pupal	Uganda	l
Meteoridea testacea (Granger)	Larval-pupal	Benin, Ghana	b,i
Microplitis rufiventris (Kokujev)	Larval	Egypt	o
Parapanteles sp	Zambia	Zambia	f
Hym.: Eulophidae			
Euplectrus laphygmae (Ferrière)	Larval	Nigeria, Zambia	f,k
Hym: Ichneumonidae			
Charops sp. / *C.* cf. *diversipes* Roman	Larval	Benin, Cameroon, Ghana, Mozambique, Niger, Uganda	a,b,d,e,l,
Charops ater Szépligeti	Larval	Kenya, Tanzania	m
Diadegma sp.	Larval	Zambia	f
Enicospilus capensis Thunberg	Larval	Zambia	f
Metopius discolor Tosquinet	Larval-Pupal	Benin, Ghana, Mozambique, Zambia	b,e,f
Pristomerus pallidus (Kriechbaumer)	Larval	Benin	b
Pristomerus sp.	Larval	Zambia	f
Hym: Scelionidae			
Telenomus remus Nixon	Egg	Benin, Cameroon, Côte d'Ivoire, Ghana, Kenya, Niger, Nigeria, Uganda, South Africa, Tanzania, Zambia	a,b,g,h,j,j,k,l,m
Hym: Trichogrammatidae			
Trichogramma chilonis (Ishi)	Egg	Cameroon, Kenya	a,g,m
Trichogramma mwanzai Schulten and Feijen	Egg	Tanzania, Zambia	g,n
Trichogramma sp.	Egg	Benin, Ghana	b
Trichogrammatoidea lutea	Egg	Zambia	n
Trichogrammatoidea sp.	Egg	Niger	d,j
Nematoda: Mermithidae			
Undetermined Mermithidae	Larval	Burkina Faso, Senegal, Zambia	c,f,o

[1] Parasitoids may be wrongly identified in the source reference, and different rows may refer to the same parasitoid species.

[2] Host stage attacked and killed

[3] a = Abang et al. 2021, b = Agboyi et al. 2020, c = Ahissou et al. 2021c, d = Amadou et al. 2018, e = Caniço et al. 2020, f = Durocher Granger et al. 2021, g = Elibariki et al. 2020, h = Kenis et al. 2019, i = Koffi et al. 2020, j = Laminou et al. 2020, k = Ogunfunmilayo et al. 2021, l = Otim et al. 2021, m = Sisay et al. 2019b, n = Sun et al. 2021, o = Tendeng et al. 2019, p = Youssef 2021.

Table 2. Parasitoids recorded from *S. frugiperda* in the field in Asian countries, as mentioned in the references.

Species[1]	Biology[2]	Countries	References[3]
Dipt: Phoridae			
Megaselia scalaris (Loew)	Larval	China, India	v,α
Dipt: Tachinidae			
Exorista japonica (Townsend)	Larval	China	o
Exorista sorbillans (Wiedemann)	Larval	India	u
Exorista xanthaspis (Wiedemann)	Larval	India	n
Peribeae sp.	Larval	India	a
Hym: Bethylidae			
Odontepyris sp.		India	u
Hym: Braconidae			
Apanteles sp.	Larval	Indonesia	β
Aleiodes sp.	Larval		j
Chelonus formosanus Sonan	Egg-larval	China, India	c,d,g,s,y
Chelonus munakatae Munakata	Egg-larval	China	k
Chelonus nr. *blackburni* (Cameron)	Egg-larval	India	s
Coccygidium transcaspicum (Kokujev)	Larval	India	f
Coccygidium melleum (Roman)	Larval	India	u
Cotesia glomerata (L.)	Larval	China	o
Cotesia ruficrus (Haliday)	Larval	India	c
Glyptapanteles creatonoti (Viereck)	Larval	India	w
Meteorus pulchricornis (Wesmael)	Larval	India	h
Microplitis demolitor Wilkinson	Larval	India	x
Microplitis manilae (Ashmead)	Larval	India	c
Microplitis pallidipes Szépligeti	Larval	China	y
Microplitis prodeniae Rao & Kurian	Larval	China	r
Microplitis similis Lyle	Larval	China	z
Microplitis sp.	Larval	Indonesia	β
Hym.: Eulophidae			
Euplectrus laphygmae (Ferrière)	Larval	China	z
Euplectrus sp. nr. *xanthocephalus* Girault	Larval	India	a
Euplectrus sp.	Larval	Indonesia	β
Tetrastichus howardi Olliff	Pupal	China	v
Hym: Ichneumonidae			
Campoletis chlorideae Uchida	Larval	China, India	j,p,u,w
Charops brachypterum Gupta and Maheswary	Larval	Philippines	m
Charops sp.	Larval	Indonesia	β
Diadegma semiclausum (Hellén)	Larval	China	o,z
Eriborus sp.	Larval	India	u
Ichneumon promissorius (Erichson)	Pupal	India	b
Metopius rufus Ashmead	Larval-pupal	India	a
Temelucha sp.	Larval	India	S,a
Hym: Scelionidae			
Telenomus remus Nixon		China, India, Indonesia, Nepal	b,c,i,l,q,y
Hym: Trichogrammatidae			
Trichogramma chilonis (Ishi)	Egg	China, India	n,w,y
Trichogramma chilotraeae Nagaraja & Nagarkatti	Egg	Indonesia	t
Trichogramma sp.	Egg	Indonesia	β
Nematoda: Mermithidae			
Hexamermis cf. *albicans* (Siebold)	Larval	India	c
Hexamermis sp.	Larval	India	d
Ovomermis sinensis Chen et al.	Larval	China	a

[1] Parasitoids may be wrongly identified in the source reference, and different rows may refer to the same parasitoid species.

[2] Host stage host attacked and killed

[3] a = Anandhi & Saminathan 2021, b = Elibariki et al. (2020), c = Firake & Behere 2020a, d = Firake & Behere 2020b, e = Gupta et al.2019, f = Gupta et al. 2020a, g = Gupta et al. 2020b, h = Gupta & Shylesha 2021, i = Huo et al. 2019, j = Keerthi et al. 2021, k = Li et al. 2019, l = Liao et al. 2019, m = Navasero & Navasero 2021, n = Navik et al. 2021, o = Ning et al. 2019, p = Niu et al. 2021, q = Oktaviani et al. 2022, r = Qin et al. 2021, s = Sagar et al. 2022, t = Sari et al.2021, u = Sharanabasappa et al. 2019, v = Sharanabasappa et al. 2021, w = Shylesha et al. 2018, x = Sun et al. 2020b, y = Tang et al. 2020a, z = Tang et al. 2020b, α = Tang et al. 2021, β = Tawakkal et al. 2021.

5.3 Augmentative biological control using parasitoids and predators

5.3.1 In the native range

The only arthropods used or extensively studied in augmentative biological control (ABC) of FAW in the Americas are the egg parasitoids *Te. remus* and *Trichogramma* spp. *Telenomus remus* is considered as one of the most effective ABC agents due to its high fecundity, its hability to parasitize all layers in an egg mass (Cave 2000; Bueno et al. 2014) and its high dispersal and search capacities (Pomari et al. 2013; Pomari-Fernandes et al. 2018). The first introduction of *Te. remus* in the Americas took place in 1971–1972 in Barbados, where field releases resulted in parasitism rates higher than 60% (Cave 2000). Since then, *Te. remus* has been frequently utilized in experimental and commercial field releases in Latin America (Cave 2000; Colmenarez et al. 2022). The most extensive use of *Te. remus* in ABC against FAW took place in Venezuela where it was imported in 1979 and has been commercially produced since the early 1990s (Hernández et al. 1989; Ferrer 2001; 2021). Releases of *Te. remus* in Venezuela resulted in an overall reduction of between 50% to 80% in pesticide use against FAW and parasitism rates up to 90% (Ferrer 2001; 2021).

Not all field experiments with *Te. remus* have been successful (e.g. Varella et al. 2015). Challenges in production and release of *Te. remus* are discussed in Colmenarez et al. (2022), the main ones being the maintenance of an effective strain in laboratory colonies, release strategy (amount, timing, stage released, etc.), and high production costs due to the need to rear *Te. remus* on FAW eggs.

Trichogramma pretiosum and *Tr. atopovirilia* have also been tested as part of ABC against FAW in the Americas, in particular in Brazil (e.g. Figueiredo et al. 2015; Parra 2010) and Mexico (Sanchez et al. 1999; Bahena & Cortez 2016). Inundative releases of *Tr. pretiosum* sometimes resulted in egg mass parasitism of up to 79 % with yield increases of 700 kg/ha (Figueiredo et al. 2015). However, it is generally considered difficult to control FAW with *Trichogramma* spp. alone because females are only able to access the upper layer of the egg masses and cannot easily oviposit through the hairs and scales when this layer is too thick (Beserra & Parra 2005). Research on the simultaneous used of *Tr. pretiosum* spp and *Te. remus* has been carried out in Brazil to combine their advantages as biological control agents (Goulart et al. 2011b) but questions remain concerning the best proportion of the two species, release strategies and rearing technologies.

5.3.2 In the invaded range

Since the invasion of FAW in Africa and Asia, various projects have focused on the development of ABC strategies against the pest. In Africa, a steppingstone was the discovery that *Te. remus* was already present and widespread in the continent (Kenis et al. 2019). The finding of several other African parasitoids attacking FAW (see section 5.6.2) led to research programmes on their potential for ABC. Guides to produce and use *Te. remus* and other egg parasitoids were published (Tefera et al. 2019; Colmenarez et al. 2022). The first field trials were conducted with *Te. remus* and a *Trichogrammatoidea* sp. in Niger, where experimental releases in sorghum fields resulted in 64% parasitism (Laminou et al. 2020).

In East Africa, *Te. remus, Tr. chilonis* and *C. icipe* are being studied. Following promising laboratory observations on their performances as biological control agents (Mohamed et al. 2021a), preliminary field releases of the three species were conducted between December 2020 and February 2021. Post-release assessments showed a significant increase in parasitism by the three species (Mohamed et al. 2021b).

Other experimental field releases showed that ABC with *Te. remus* is not simple and that the technique needs improvement to become efficient and economically viable in Africa (Agboyi et al. 2021). In addition, more information is needed on the cost effectiveness of ABC with parasitoids in an African context (Colmenarez et al. 2022).

Less than four years after the first observations of FAW in Asia, several ABC approaches have already been evaluated, also mostly with egg parasitoids. Field releases of *Te. remus* against FAW in south-east China resulted in parasitism rates of egg masses and eggs of up to 100% and 84%, respectively (Zhao et al. 2020). Chen et al. (2021) showed that *Spodoptera litura* (F.) can advantageously replace FAW as host in the mass rearing of *Te. remus*.

Several *Trichogramma* species were tested in the laboratory and in the field against FAW in China. *Trichogramma chilonis* was tested in maize fields in Shandong Province, resulting in parasitism rates of egg masses and eggs up to 73% and 86% respectively (Yang et al. 2019). Another species, *Tr. dendrolimi* Matsumura, which is used to control several pest species in China (Zang et al. 2021), demonstrated higher biological control potential on FAW under laboratory conditions than three other *Trichogramma* species because it is more able to parasitize eggs through the hair and scales covering FAW egg masses (Sun et al. 2020a). Larval parasitoids were also successfully tested in the laboratory, including *Microplitis pallidipes* (Ju et al. 2021) and *Cotesia marginiventris* (Zhang et al. 2021b).

In India, Varshney et al. (2021) integrated *Tr. pretiosum* into a biocontrol-based integrated pest management (IPM) comprisingpheromone traps, the fungi *M. rileyi* and *M. anisopliae*, neem oil and *Bacillus thuringiensis*. These treatments resulted in 71–76% egg mass reduction, 74–80% larval population reduction and 38–42% gain in yield.

Predators are also being considered as potential ABC agents against FAW in Asia. The predatory stink bug *Eocanthecona furcellata* (Wolff) has been evaluated in China (Li et al. 2020b) and India (Keerthi et al. 2020). While laboratory tests are promising, field releases in India have been hampered by high parasitism rates affecting bug populations. Several other predators have been tested against FAW only in the laboratory, for example the true bugs *Picromerus lewisi* (Fallou) (Tang et al. 2019, Wang et al. 2019), *Orius similis* Zheng (Zeng et al. 2021), *Orius sauteri* (Poppius) (Dai et al. 2019; Di et al. 2021) and *Sycanus croceovittatus* Dohrn (Wang et al. 2020a), the hoverfly *Eupeodes corollae* (F.) (Li et al. 2021), the ladybirds *Coccinella septempunctata* L. (Kong et al. 2019) and *Harmonia axyridis* (Pallas) (Di et al. 2021), the carabid beetle *Chlaenius bioculatus* Chaudoir (Huang et al. 2020a) and the lacewings *Chrysoperla sinica* (Tjeder) (Huang et al. 2020b) and *Chrysopa pallens* (Rambur) (Li et al. 2020a).

5.4 Classical biological control

In the 20th century, several classical biological control (CBC) projects targeted FAW in its native range with introductions of parasitoids. Either parasitoids were moved from one part of the native range to another part where they were absent, or parasitoids of other *Spodoptera* spp. were introduced from other parts of the world. Examples of parasitoids moved within the Americas include *Archytas incertus* Giglio-Tos from Argentina to the USA, *Eiphosoma vitticolle* (probably *E. laphygmae,* see Gauld 2000) from Bolivia to the USA and *Cotesia marginiventris* from the USA to the Caribbean (Cock 1985; Rosen et al. 1994). In addition, several Asian, Australian, and North African parasitoids originating from other *Spodoptera* spp. were introduced in America, mostly in the Caribbean and the USA: *Campoletis chlorideae* Uchida, *C. formosanus, Chelonus heliopae* Gupta*, Euplectrus platyhypenae* Howard, *Microplitis manila* Ashmead, *Microplitis rufiventris* Kokujev, *T. remus, Tr. achaeae* Nagaraja and Nagarkatti, *Tr. chilotraeae* Nagaraja and Nagarkatti and *Trichospilus pupivorus* Nagaraja and Nagarkatti (Cock 1985; Rosen et al. 1994). From all these introductions, only *Te. remus* became established. This egg parasitoid was introduced against *Spodoptera* spp. from India to various parts of the world, including the Caribbean, Colombia, and Venezuela, from where it subsequently spread to most of the distribution range of FAW in the Americas (Wengrat et al. 2021). However, parasitism rates on FAW remained low and it was mainly used in augmentative releases.

The recent worldwide invasion of FAW in Africa and Asia has generated interest for CBC using natural enemies from the Americas (Allen et al. 2021; Tepa-Yotto et al. 2021). However, nowadays, selecting a CBC agent for introduction into a new area is a long process involving careful assessments of potential non-target effects (Hayek et al. 2016). FAW has many natural enemies in its native range (see section 5.6.1 above), but only a few can possibly combine efficiency and specificity. All known predators of FAW are too polyphagous to be considered for introduction. Among the main parasitoids of FAW, few appear specific. *Eiphosoma laphygmae* is one of them and is presently being evaluated for potential introduction in Africa and Asia (Allen et al. 2021). The most abundant and widely distributed parasitoid of FAW in its native range, *C. insularis*, is also known from a few other hosts (Yu et a. 2005). Furthermore, in Africa and Asia, other *Chelonus* species, parasitoids of local *Spodoptera* spp. have been reported among the main parasitoids that have adopted FAW (e.g., Agboyi et al. 2020; Durocher-Granger et al. 2021; Firake & Behere 2020a, 2020b; Gupta et al. 2020a). The potential competition between the native and introduced species needs to be considered in the assessment. The other main parasitoids of FAW in its native range are known as polyphagous but the possible occurrence of cryptic species showing higher host specificity should be investigated.

5.5 Biopesticides

5.5.1 Entomopathogenic fungi

Entomopathogenic fungi (EPF) are ubiquitous and contribute to both natural control of insects and the development of commercial biopesticides. Natural infection of up to 24% with EPFs has been widely reported on FAW in its native region (Guo et al. 2020). Natural epizootics have also been reported in the invaded regions of Kenya (Gichuhi et al. 2020), India (Firake & Behere 2020a; Shylesha et al. 2018; Mallapur et al. 2018) and Indonesia (Ginting et al. 2020a) with up to 79% infection. Most epizootics in all continents are due to *Metarhizium rileyi*, with, in the Americas, occasional reports of *Entomophthora sphaerosperma* Fresenius, *Entomophaga aulicae* (E. Reichardt), *Metarhizium anisopliae* (Metschn.) Sorokin, *Beauveria bassiana* (Bals.) and *Hirsutella* sp. (Gardner & Fuxa 1980; Lezama-Gutierrez et al. 2001; Molina-Ochoa et al. 2003b). Glasshouse and field efficacy of *M. rileyi* against FAW has been demonstrated (Grijalba et al. 2018; Mallapur et al. 2018). For example, in India, field applications of *M. rileyi* resulted in ca. 60% reduction of pest infestation (Mallapur et al. 2018). However, its commercial utility has been limited due to challenges associated with fungal production and storage (Bateman et al. 2021; Grijalba et al. 2018; Fronza et al. 2017).

Other EPF isolates from soil and other arthropods have been screened for efficacy against FAW life stages and potent isolates have been identified (Akutse et al. 2019; Akutse et al. 2020b; Herlinda et al. 2020; Montecalvo & Navasero 2021; Ramanujam et al. 2020; Russo et al. 2021). High infectivity of *M. anisopliae, B. bassiana*, and *Isaria* isolates has been reported on eggs and neonates (Akutse et al. 2019; Lezama-Gutierrez et al. 1996; 2001) as well as adults of FAW (Akutse et al. 2020b). Field efficacy of these isolates has also been established (Ramanujam et al. 2020), and some of them further progressed for commercialization (Akutse et al. 2020a). Current EPF products are focussed on formulations for foliar application against the immature life stages of FAW. However, the compatibility of EPFs with FAW pheromones and their impact on fertility and egg viability highlight the potential for the development of lure and infect application strategies (Rivero-Borja et al. 2018; Gutiérrez-Cárdenas et al. 2019; Akutse et al. 2020b). Furthermore, endophytic colonization of cereals and other hosts with *B. bassiana, M. anisopliae*, and *Metarhizium robertsii* (Metchnikoff) Sorokin, and the impact of such plant colonization on FAW survival, growth, reproduction, and food preference offer a promising potential for incorporating EPFs into FAW management practices (Ramirez-Rodriguez & Sanchez-Pena 2016; Jaber & Ownley 2018; Vega 2018; Mwamburi 2021; Russo et al. 2021; Gustianingtyas et al. 2021).

5.5.2 Baculoviruses

The *S. frugiperda* multiple nucleopolyhedrovirus (SfMNPV), a common pathogen in natural populations of FAW in the Americas (Gardner & Fuxa 1980; García-Banderas et al. 2020), is now reported in India (Raghunandan et al. 2019; Firake & Behere 2020a; 2020b; Firake et al. 2020), Indonesia (Ginting et al. 2020b), China (Lei et al. 2020) and Africa (Wennmann et al. 2021). In the Americas, a small proportion of FAW larvae collected from the wild is observed to succumb to NPV infection, typically <5% (Agudelo-Silva 1986; Valicente & Barreto 1999; Molina-Ochoa et al. 2003b; Gómez-Valderrama et al. 2010; García-Gutierrez et al. 2013). As FAW disperses over large distances, it carries the virus with it as an inapparently sublethal infection (Williams et al. 2017). Vertical transmission of infection from parents to offspring is common (Fuxa & Richter 1991). The transmission and prevalence of SfMNPV is increased at higher temperatures, thus, climate change is likely to alter the dynamics of NPV disease in FAW populations in the future (Elderd & Reilly 2014). In contrast to the NPV, the granulovirus (genus *Betabaculovirus*) is less prevalent in natural populations of FAW and is far slower killing (Valicente 1989; Cuartas et al. 2014;2015, Pidre et al. 2019). The speed of kill by a baculovirus depends on the quantity of inoculum, larval instar, and temperature during the incubation period, and differs between the strains of FAW (Popham et al. 2021).

SfMNPV has attracted attention as the active ingredient in the development of biopesticides against FAW (Table 3). Field tests have been performed in the US, Mexico, Colombia, and Brazil by application of aqueous sprays and by testing more complex formulations. The potential use of a baculovirus bioinsecticide has also been tested for small-scale maize growers in Latin America (Williams et al. 1999). The prevalence of the baculovirus infection in larvae, which can range between 30% and 90%, usually declines as the occlusion bodies (OBs) on leaf surfaces become diluted by the rapid expansion of maize leaves and are sensitive to deactivation by solar radiation (Villamizar et al. 2009). The use of formulations involving the encapsulation of OBs (Behle & Popham 2012; Gómez et al. 2013), feeding stimulants (Castillejos et al. 2002; Farrar et al. 2005), and sunscreens (Wilson et al. 2020) can improve virus persistence but invariably involves extra cost.

A wettable powder formulation of SfMNPV was produced by EMBRAPA in the 1990’s and used on over 20,000 ha of maize per year in Brazil but was subsequently discontinued due to high virus production costs (Moscardi 1999; Haase et al. 2015). The high costs were related to the cannibalistic habits of this species and the need to rear inoculated larvae individually (Chapman et al. 1999), in addition to the liquefaction of the larval integument that can limit the collection of OBs (Valicente et al. 2013). Since then, several commercial products have been developed based on SfMNPV including Spobiol® (Corpoica) (Sosa-Gómez et al. 2020), registered in Colombia, Fawligen® (AgBiTech) now registered in several countries including Bangladesh, Kenya, USA and an Emergency Use Permit in Australia, Spodovir Plus® (Andermatt) currently undergoing testing in Australia and Littovir/RavageX® (Andermatt) now registered in Cameroon (Gou et al. 2020) and undergoing testing in Kenya. In Brazil, four commercial products containing SfMNPV are registered and sold to control FAW (Agrofit, 2022). Unlike the other products, Littovir/RavageX® is a formulation of *Spodoptera littoralis* NPV that is also pathogenic to FAW. It is likely that SfMNPV-based insecticides could soon be available in China, given the history of use of baculoviruses for pest control in that country (Sun 2015). These products are likely to contribute to the rapidly growing need for sustainable control options against FAW and prospects for their use as biopesticide were recently reviewed by Hussain et al. (2021).

5.5.3 Entomopathogenic bacteria

Crystal proteins of the gram-positive bacterium *Bacillus thuringiensis* Berliner (Bt) are the most commonly used biopesticides against lepidopteran pests worldwide. It is also frequently used against FAW (Guo et al. 2020). Two sub-species (Bt *aizawai* and Bt *kurstaki*) are effective against FAW (Bateman et al. 2021), but toxicity may vary largely between strains and proteins (Valicente & Barreto 2003; dos Santos et al. 2009; Liu et al. 2019). Some Bt strains only have sublethal effects such as reduced pupal weight and fecundity (Polanczyk & Alves 2005). The efficacy of Bt biopesticides may also be influenced by the adjuvants used in its formulation (dos Santos et al. 2021). Bt is most efficient against early larval instars because it works by ingestion and older larvae in the whorls are less likely reached (Prasanna et al. 2021)

Bt is registered against FAW and commercially available in several newly invaded countries, alone or mixed with other biopesticides or pesticides (Bateman et al. 2021). In countries such as Ghana, Bt-based biopesticides are among the most commonly used products against FAW (Tambo et al. 2020a). Transgenic maize cultivars expressing Bt crystal proteins are commonly used in some countries (see section 5.8.2.).

5.5.4 Entomopathogenic nematodes

Entomopathogenic nematodes (EPN) are generalist lethal parasites of ground-dwelling insects that are present in soils worldwide (Kaya & Gaugler 1993). They can also be highly

Table 3. Virus induced mortality following application of SfMNPV occlusion bodies (OBs) to maize plants in different countries. Larvae were usually collected shortly after treatment and reared in the laboratory to determine the prevalence of lethal infection.

Country	Dose (OBs/ha)	Application, Formulation	Initial virus-induced mortality (%)	Persistence	Reference
Brazil	2.5×10^{11} 2.5×10^{12}	Aqueous spray (backpack)[1]	71 82	58% mortality in 3 d sample 93% mortality in 3 d sample	Cruz et al. 1997
Brazil	2×10^{11} 1×10^{12} 2×10^{12}	Irrigation water[2]	63 89 91	– – –	Valicente & da Costa 1995
Colombia	1.5×10^{12}	PMAA polymer encapsulation[3]	71–84	Reduced plant damage in 11 d sample	Gómez et al. 2013
Mexico	1.5×10^{12} 3×10^{12} 6×10^{12}	Aqueous spray[4]	30–62 37–61 38–63	7–23% mortality in 9 d sample – 18–27% mortality in 9 d sample	Williams et al., 1999, Martínez et al. 2000
Mexico	3×10^{12}	Aqueous spray	58	84% mortality in 7 d sample	García-Banderas et al. 2020
Mexico	1.5×10^{12}	Maize flour granules[5]	55–63	23% of activity remaining in 8 d sample	Castillejos et al. 2002
Mexico	2.6×10^{12}	Maize flour granules + 1% boric acid	35–80	Increased persistence in 5 d sample	Cisneros et al. 2002
USA	2.5×10^{11} 2.5×10^{11}	Aqueous spray 1% coax[6]	66 84	All samples taken at 5 d post-application	Farrar et al. 2005
USA	$2.5 \text{ x } 10^{12}$	Lignin-based formulation[7]	–	3-fold increase in persistence	Behle & Popham 2012

[1] Virus induced mortality was lower when applied by tractor. Data from Tables 2 and 3 in Cruz et al. 1997.

[2] Virus was applied to irrigation water to treat plants.

[3] PMAA, poly-methacrylic acid used to encapsulate OBs.

[4] Summary of eight field studies in southern Mexico.

[5] Granules applied directly to maize whorl at 6, 18 or 32 kg granules/ha.

[6] Study performed on potted plants. Coax is a feeding stimulant formulation. Samples from Bt transgenic plants experienced 46–69% virus-induced mortality (Table 4 in Farrar et al. 2005).

[7] Spray dried lignin formulation was applied to cabbage plants in field to measure persistence.

pathogenic to FAW (Fuxa et al. 1988; Molina-Ochoa et al. 1999; Andaló et al. 2010; Acharya et al. 2020). In laboratory assays, applying as few as 50 EPN per insect resulted in 100 % mortality of all larval stages of FAW (Acharya et al. 2020). Raulston et al. (1992) showed that natural infection of FAW by EPNs does occur, as about 4% of FAW pupae collected in maize fields were infected and killed by EPN. Moreover, applying EPN onto the soil surface can cause up to 86% mortality of crawling late-instar FAW larvae under greenhouse conditions (Andaló et al. 2010).

However, the efficacy of EPNs to control FAW larvae feeding on maize plants is adversely affected by unfavourable abiotic conditions (Lacey & Georgis 2012). Spraying EPN with water onto vegetative maize was found to reduce FAW infestation, but not consistently across fields (Richter & Fuxa 1990). Negrisoli et al. (2010) found that EPN sprayed with water resulted in less than 25% FAW mortality but showed additive effects when applied in combination with insecticides. The addition of surfactants is not sufficient to improve EPN efficacy to control FAW (Garcia et al. 2008). Developing protective formulations is key to EPN effectiveness against FAW, as was recently shown with EPNs formulated in a carboxymethyl cellulose gel. Applied into the whorl of maize, it was as effective as the chemical insecticide cypermethrin in killing FAW (Fallet et al. 2022).

5.5.6 Botanical-based insecticides

Botanical-based insecticides (BI) are promising for real-world use against insect pests, considering their multiple modes of action and limited non-target effects (Isman 2020). Several BI have been tested against FAW (Rioba & Stevenson 2020), including commercial products (Forim et al. 2010) and extracts which can be prepared by farmers from plants growing in the surroundings of their farms (Pavela 2016; Marchand 2017; Assefa & Ayalew 2019; Sisay et al. 2019a; Silvie et al. 2021). Several plant extracts have insecticidal properties against FAW (Mugisha-Kamatenesi et al. 2008; dos Santos et al. 2008; Ogendo et al. 2013; Silva et al. 2013; Stevenson et al. 2017; Phambala et al. 2020) (Table 4). Montes-Molina et al. (2008) showed that extracts

Table 4. Selected examples of promising plant-borne insecticides applied in the form of aqueous extracts, which have been found effective against *S. frugiperda*.

Plant species	Family	Part used	Effectiveness and tested concentration	Reference
Azadirachta indica	Meliaceae	seeds	Larval mortality > 95% (72 h) – concentration 50 g/l	Sisay et al., 2019
Carica papaya	Caricaceae	seeds	Larval mortality> 95% (96 h) – 15% in artificial diet	Franco et al., 2006
Chenopodium ambrosioides	Amaranthaceae	leaves	Larval mortality > 20% (72 h) – concentration 350 g/l	Sisay et al., 2019
Copaifera langsdorffii	Fabaceae	leaves and bark	Larval mortality > 20% (22 days) – concentration 5%	Sâmia et al., 2016
Croton macrostachyus	Euphorbiaceae	seeds	Larval mortality > 75% (72 h) – concentration 250 g/l	Sisay et al., 2019
Cymbopogon citratus	Poaceae	leaves	Larval mortality > 50% (7 days) – concentration 100 g/l	Phambala et.al. 2020
Cymbopogon flexuosus	Poaceae	leaves	Larval mortality = 100% (240 h) – concentration 4.0 mg mL^{-1} diet)	Oliveira et al., 2018
Duguetia lanceolata	Annonaceae	stem bark	Larval mortality = 100% (92 h) – 135 µg mL-1 of diet	Alves et al., 2020
Gliricidia sepium	Fabaceae	leaves	Significant increase in corn yields (field tests) – 333 g/l	Montes-Molina et al., 2008
Jatropha curcas	Euphorbiaceae	seeds	Larval mortality > 90% (72 h) – concentration 115 g/l	Sisay et al., 2019
Lantana camara	Verbenaceae	seeds	Larval mortality > 40% (72 h) – concentration 400 g/l	Sisay et al., 2019
Lantana camara	Verbenaceae	whole plants	Significant increase in corn yields (field tests) – 1.7% extract	Ogendo et al., 2013
Lippia javanica	Verbenaceae	leaves	Larval mortality > 60% (7 days) – concentration 100 g/l	Phambala et.al. 2020
Malpighia emarginata	Malpighiaceae	fruits	Larval mortality > 35% – concentration 2000 mg L^{-1} diet	Marques et al., 2016
Melia azedarach	Meliaceae	leaves	Larval mortality > 90% (72 h) – concentration 250 g/l	Sisay et al., 2019
Militia ferruginea	Leguminosae	seeds	Larval mortality > 75% (72 h) – concentration 500 g/l	Sisay et al., 2019
Nicotiana tabacum	Solanaceae	leaves	Larval mortality > 50% (72 h) – concentration 250 g/l	Sisay et al., 2019
Ocimum selloi	Lamiaceae	whole plants	Larval mortality = 100% (>48 h) – concentration 4 mg mL^{-1}	de Menezes et al., 2020
Peumus boldus	Monimiaceae	leaves	Larval mortality > 70% (when?) – 8% in artificial diet	Silva et al., 2013
Phytolacca dodecandra	Phytolaccaceae	seeds	Larval mortality > 95% (72 h) – concentration 250 g/l	Sisay et al., 2019
Sapindus saponaria	*Sapindaceae*	seeds	Larval mortality > 60% (14 days) – concentration 1%	Santos et al., 2008
Schinus molle	Anacardiaceae	seeds	Larval mortality> 95% (72 h) – concentration 250 g/l	Sisay et al., 2019
Tagetes minuta	Asteraceae	whole plants	Significant increase in corn yields (field tests) – 1.7% extract	Ogendo et al., 2013
Tephrosia vogelii	Fabaceae	whole plants	Significant increase in corn yields (field tests) – 1.7% extract	Ogendo et al., 2013

from *Azadirachta indica* (neem) and *Gliricidia sepium* reduced plant damage by several pests, including FAW, increasing mean maize yield (9.7 and 8.7 tha^{-1} respectively, compared to 7.2 tha^{-1} for the control).

The insecticidal properies of 69 plant species for control of FAW has been demonstrated by Rioba & Stevenson (2020). However, their wider use should ideally be based on simple aqueous extracts although more complex formulations are reported in the literature. A good example is *Piper guineense* extract as a botanical insecticide to protect maize against FAW. This extract is produced using dry *P. guineense* seeds, crushed and mixed with vegetable oil (1:1). A small amount of a suitable emulsifier, usually a detergent, is added to obtain an aqueous emulsion. Repeated application provided the same efficacy against FAW as a synthetic insecticide comprising lambda-cyhalothrin 15 g l^{-1} + 20 gl^{-1} acetamiprid a.i (Tanyi et al. 2020). Increased maize yields were also achieved in Zambia by Siazemo & Simfukwe (2020), who tested aqueous extracts from *Melia azedarach, Allium sativa*, and *A. indica* in comparison to cypermethrin in the control of FAW. In general, it remains difficult to compare efficacies of different plant extracts considering that different extraction, application, and evaluation methods are used. Ethnobotanical studies among local growers, as well as enhancing the stability and insecticidal efficacy of plant extracts using nanoformulations, remain crucial (Pavoni et al. 2019). In northeast India, Prickly ash (*Zanthoxylum armatum*) fruit extract showed larvicidal, ovicidal, and oviposition deterrent activities against FAW. The LC_{50} against 2nd instar FAW larvae was recorded to be 0.44% solution at 96 hours after treatment (HAT). The extract showed 100% ovicidal effect at ≥ 2.2% concentration (D.M. Firake, unpublished data)

5.6 Mating disruption

Mating disruption (MD) products disrupt chemical communication between sexes by permeating the crop environment with artificially produced sex pheromone plumes that impede male communication with females thereby affecting the insect's chance of reproduction (Rodriguez-Saona & Stelinski 2009). Several compounds are successful for reducing mating of FAW in the field (Malo et al. 2013; Bateman et al. 2021; Rizvi et al. 2021). For instance, mating and oviposition by FAW in a 12-ha maize field in Florida was reduced by an average of 86 and 84%, respectively, following aerial applications of the pheromone (Z)-9-tetradecenyl acetate formulated in hollow fibres (Mitchell & McLaughlin 1982). Malo et al. (2013) showed that the presence of large amounts of (Z)-9-tetradecenyl trifluoromethyl ketone (Z9-14:TFMK), closely-related analogue of the sex pheromone, distrupted FAW mating under field conditions. Further, (Z)-9-tetradecen-1-ol acetate was highly effective in reducing mating under laboratory conditions (Hirai & Mitchell 1982). The increased male antennal sensitivity to Z7–12: dodecenyl acetate in African populations of FAW indicates the possibility of enhancing the efficiency of mating disruption with specific pheromone dispensers (Haenniger et al. 2020). Efficient pheromone emission has been achieved using microencapsulation, hand application, aerial dispensers, and matrix formulations (SPLAT, Specialized Pheromone and Lure Application Technology), (Welter et al. 2005). Regulatory approval of a liquid foliar spray formulation of pheromones for FAW management has been obtained in Brazil, while in Kenya, aerial application of dispensers has been approved. Ideally, dispensers should release pheromones at a constant rate, be mechanically applyable, completely biodegradable, made from affordable and renewable organic materials, and eco-toxicologically inert (Hummel et al. 2013). Considering the high dispersal potential of FAW, this technology is most efficient when applications are made on large surface areas.

5.7 Agroecology

Agroecological approaches are an essential component of IPM strategies. Such approaches affect pests directly or through enhancing the populations and activities of natural enemies (conservation biological control). Agroecological approaches are built around three mutually reinforcing pillars; (i) sustainable soil fertility management, which improves crop vigour and reduces susceptibility to pests and diseases; (ii) promoting biodiversity across a range of spatial scales from the field to the landscape, which provides living space and alternative resources for pest's natural enemies; and (iii) specific management interventions, sometimes referred to as cultural control, aimed at reducing pest populations or their impact (Harrison et al. 2019). Agroecological approaches to FAW management in the Americas have received scant attention, although evidence from smallholder fields in Central America suggests they can effectively suppress FAW populations (Wyckhuys & O'Neil 2006).

5.7.1 Soil fertility management

The promotion of vigorous plant growth is the first line of defence against crop pests and diseases. However, the application of synthetic fertilisers can increase pest damage, especially in soils with low levels of soil organic carbon (Altieri & Nicholls 2003; Morales et al. 2001). Hence, interventions that promote healthy soil biology are recommended, including applying manure or compost and using cover crops, intercropping, crop rotation, minimum tillage and residue retention. Minimum tillage systems can reduce FAW damage and increase yields compared to conventional tillage controls (Andrews 1988; Kumar 2002; Kumar & Mihm 2002; Rivers et al. 2016). Residue retention enhances the diversity and abundance of natural enemies and reduces FAW damage (Rivers et al. 2016; Clark 1993), although some studies found it did not increase yields in minimum tillage systems (Kumar 2002; Kumar & Mihm 2002).

5.7.2 Promoting biodiversity and habitat management

Many native parasitoids, predators and pathogens exploit FAW in its native and invaded ranges (sections 5.2.1 and 5.2.2). Natural pest control services are dependent on the biodiversity inside and around fields (Tscharntke et al. 2007). Different species attack different life stages of the pest or may be active in different seasons or crop stages. Functional redundancy in the natural enemy community may thus stabilise the pest control service (Tylianakis et al. 2006). Infield diversity of FAW natural enemies may be enhanced through interventions such as residue retention (Rivers et al. 2016; Clark 1993), intercropping (Perfecto & Sediles 1992; Smith & McSorley 2000) and weed management (van Huis 1981). On the other hand, many synthetic insecticides have negative impacts on natural enemies, thereby compromising the natural pest control services these organisms provide (Meagher et al. 2016; Perfecto 1991; Sherratt & Jepson 1993). Hence, a crucial step in implementing agroecological approaches is to minimize the use of synthetic pesticides.

Intercrops may also reduce pest oviposition through olfactory camouflage or the release of repellent volatiles. For example, the release of repellent volatiles by *Desmodium* spp. is the main mechanism by which FAW damage is reduced in climate-adapted push-pull (Midega et al. 2018; Hailu et al. 2018; Niassy et al. 2021a). Intercrops or weeds may also reduce FAW damage by providing alternative oviposition sites or directly increasing FAW mortality. In Nicaragua, van Huis (1981) found that ballooning first instar larvae often became entangled in weeds. There is good evidence that intercropping reduces FAW damage and increases yields (Midega et al. 2018; Hailu et al. 2018). In dry areas of East Africa, the climate-adapted push-pull system succeeded in reducing FAW infestation by 87% and increased yields 2.7-fold (Midega et al. 2018). However, this may not apply to all intercrops in all situations. Baudron et al. (2019) found that pumpkin intercropping was correlated with increased FAW damage in surveyed fields in Zimbabwe.

Diverse field margins and habitats around fields can also enhance natural enemy populations and reduce FAW populations (Meagher et al. 2016; Wyckhuys & O'Neil 2007; Niassy et al. 2021b). For example, experimental plantings of field margins with wildflower mixes surrounding turfgrass patches led to increased populations of natural enemies and high FAW predation rates (Braman et al. 2002). In Peru, plants with bracteal extrafloral nectaries attracted the greatest diversity of both parasitoids and predators, including species known to attack FAW (Quispe et al. 2017). At larger spatial scales, the amount of (semi-) natural habitat and diversity of agricultural land cover types (i.e., different arable crops, orchards, vegetables, and pastures) can increase the abundance and activity of natural enemies. However, studies looking at these effects on FAW control are few. One study found a significant positive effect of habitat complexity on FAW control at one site but no effect at two other sites (Menalled et al. 1999). Nonetheless, in Texas, Brazilian free-tailed bats (*Tadarida brasiliensis*) consume up to four billion noctuid moths each night, and consumption patterns correlate with the seasonal migration of pests, including FAW (Lee & McCracken 2005). Hence, the management of landscapes to enhance insectivorous bat and bird populations could reduce FAW infestations. In Zambia and Malawi, fields in landscapes with high tree cover had lower levels of FAW infestation (R. Harrison, *In press*). In addition, some studies have demonstrated the effect of distance from forest fragments on natural pest control and FAW infestation. For example, in Brazil, predatory solitary wasp abundance decreased, and FAW abundance increased, with distance from forest patches (Sousa et al. 2011). However, it should also be noted that landscapes can promote disservices (Tscharntke et al. 2016; Karp et al. 2018). For example, natural forest fragments can harbour noxious weeds or mammalian pests such as crop-raiding primates. Hence, habitat management at larger scales requires a local understanding of potential trade-offs.

5.7.3 Other interventions

Farmers can use homemade products in lieu of chemical pesticides. In Latin America, the application of sugar or molasses onto plants increased parasitism and reduce FAW infestations (Canas & O'Neil 1998; Bortolotto 2014). Smallholder farmers in Africa have tried many approaches to control FAW, including egg crushing or hand-picking larvae, applying soil, sand or ash to the whorl, spraying detergent, and using fish soup (Tambo et al. 2020a; 2020b). Egg crushing and hand-picking larvae are labour intensive but can be effective in the early crop stages. Heavy rain forces FAW larvae out of the whorl, so the efficiency of hand picking may be increased by conducting it immediately after heavy showers. Preliminary results for soil, sand, ash, and soapy water are mixed, suggesting specific characteristics of the materials or their application are important (Babendreier et al. 2020; Aniwanou et al. 2021; Varma et al. 2021). Ash is an unconventional pesticide that acts as a physical poison causing abrasion of insect cuticle, thus exposing pests to death through desiccation. Furthermore, ash interferes with the chemical signals emanating from the host plants, thus blocking the initial host location by pests. Applying fine river sand into maize whorls is a traditional FAW control method in Central America (M. Kenis, unpublished). The effectiveness of sand is mechanical; the microscopic quartz or siliceous particles act as a deterrent against a wide range of insects. These particles penetrate the insect body, creating wounds leading to loss of body fluid.

A promising approach appears to be using fish soup, especially with a bit of sugar added. The mechanism of fish soup is that, when applied in a field, it attracts diverse groups of natural enemies, reducing FAW damage. In addition, under adequate irrigation and soil fertility, plants treated with fish soup recover from defoliation faster compared to untreated plants (S. Niassy, unpublished data). More research is needed to further evaluate the effects of such approaches on FAW control and yield.

To enhance the presence of natural enemies in crop fields, farmers may also provide nesting sites. For example, social wasps are important predators of FAW, and their abundance can be augmented by providing nest boxes (Prezoto & Machado 1999; Southon et al. 2019).

5.8 Patterns of Insecticide Use and Resistance

5.8.1 Insecticide use

In Brazil, the US, and Mexico, management of FAW has relied heavily on insecticide use since the 1970's (Burtet et al. 2017; Brown & Dewhurst 1975). In the first two countries, widespread adoption of Bt crops has augmented insecticides for the past few decades (see Section 5.9.2). In Mexico, 3,000 tons of active ingredient per year have been applied to combat this pest (Blanco et al. 2014). The pattern of insecticide use against FAW in its native range reflects its growing importance and its evolution of resistance. The prevailing use of organophosphate and carbamate insecticides before the 1980´s was succeeded by pyrethroids (Diez-Rodríguez & Omoto 2001; Wood et al. 1981; Yu, 1991; 1992; Yu et al. 2003). Starting in about 2000, spinosyns, avermectins, oxadiazines, insect growth regulators (chitin synthesis inhibitors and ecdysteroid agonists) and diamides have been used intensively in the Americas (Bolzan et al. 2019; Kaiser et al. 2021; Lira et al. 2020; do Nascimento et al. 2016; 2021; Okuma et al. 2018). Bt-based insecticide formulations have also been used in the region (Blanco et al. 2014; Gutierrez-Moreno et al. 2020).

In Africa, few maize producers used chemical insecticides before FAW invaded (Ahissou et al. 2021a; 2021b; Rwomushana et al. 2018). The FAW invasion quickly spurred markedly increased use of many insecticides, including lindane, chlorpyrifos, carbamates, pyrethroids, neonicotinoids, fipronil, spinosyns, and avermectins (Ahissou et al. 2021b; Koffi et al. 2021b; Rwomushana et al. 2018; Van den Berg et al. 2021b).

Insecticide use in Asia and Oceania is also high against the recently introduced FAW with chlorpyrifos, pyrethroids, neonicotinoids, emamectin benzoate, spinetoram and chlorantraniliprole leading the usage (Kulye et al. 2021; Wan et al. 2021). The consequences of this intensive insecticide use mimic the problems reported in the Americas and more recently in Africa – insecticide resistance and non-target effects (Zhang et al. 2019; 2020; Wan et al. 2021). Insecticide overuse, and increased adoption of seed treatments and insecticide mixtures are taking place in Neotropical America and are likely to expand to these regions (Guedes et al. 2017; Oliveira et al. 2022; Wan et al. 2021). These practices are debatable and may potentially enhance the non-target impact of insecticides used against FAW inviting reductions in their use (Guedes et al. 2016; 2017; Tooker & Pearsons 2021).

5.8.2 Insecticide Resistance

The Arthropod Pesticide Resistance Database has reported resistance to 42 active ingredients and 182 cases of insecticide resistance in FAW (Gutierrez-Moreno et al. 2019; Mota-Sanchez & Wise 2021). The largest number of cases are from the Americas, where initial reports occurred in the 1960's. Local selection caused by intensive insecticide use is the primary driver of evolution of insecticide resistance. However, FAW is a migratory species in which resistance alleles can spread when new areas are invaded (Arias et al. 2019; Yainna et al. 2021; Nguyen et al. 2021).

In the US state of Florida, moderate (1-10x) to high levels (>100x) of resistance to organophosphates, carbamates and pyrethroids were detected by the 1990's (Yu 1991; 1992; Yu et al. 2003). Subsequent surveys in Brazil found resistance to organophosphates, pyrethroids (Carvalho et al. 2013; Diez-Rodríguez & Omoto 2001; Garlet et al. 2021a; 2021b), chitin synthesis inhibitors (do Nascimento et al. 2016; 2021), avermectins (Muraro et al. 2021), spinosyns (Lira et al. 2020; Okuma et al. 2018), oxadiazines (Kaiser et al. 2019), diamides (Bolzan et al. 2019), and Bt proteins (Farias et al. 2014; Omoto et al. 2016). As a result, mapping of areas where insecticide resistance occurs, use of novel insecticides, and insecticide rotation are important components of insecticide resistance management in Brazil (Barbosa et al. 2020; Burtet et al. 2017; do Nascimento et al. 2021).

In Puerto Rico, practical resistance (Tabashnik et al. 2014) of FAW has been detected to organophosphates, pyrethroids, carbamates, diamides, insect growth regulators, spinosyns (Gutierrez-Moreno et al. 2019), and Bt toxins (Storer et al. 2010; Gutierrez-Moreno et al. 2020). Because seed industry research is important in Puerto Rico, tolerance for pest damage is low there (Gutierrez-Moreno et al. 2019). A combination of ecological and operational factors makes a perfect storm for FAW resistance evolution in Puerto Rico, including high infestation, more than 10 armyworm generations per year, relative isolation, temperatures favorable for rapid insect development, and up to 29 sprays per season (Storer et al. 2012; Gutierrez-Moreno et al. 2019)

The potential for FAW movement to spread alleles conferring resistance to Bt toxins and other insecticides is a concern, especially as FAW in Africa and Asia share a common origin from the Eastern Hemisphere (Nagoshi et al. 2020b). Although some mutations conferring resistance to organophosphates and pyrethroids apparently spread from the Eastern Hemisphere to Australia (Nguyen et al. 2021), mutations conferring resistance to Bt toxins in Puerto Rico and Brazil were not detected in Africa (Van den Berg et al. 2021b).

Surveys from China and India document moderate to high levels of resistance to several classes of insecticide – from organophosphates to diamides (Kulye et al. 2021; Lv et al. 2021; Zhang et al. 2021a). Although more data are needed from Africa and the Middle East, the results from Asia and the apparent pattern of FAW invasion suggest insecticide resistance may occur throughout the present range of the species.

Enhanced detoxification is a mechanism of FAW resistance to organophosphates and pyrethroids in the US and Brazil (Carvalho et al. 2013; Yu 1992; Yu et al. 2003) and to chitin synthesis inhibitors in Brazil (do Nascimento et al. 2021). Recent studies provide molecular evidence of the likely involvement of cytochrome P450-dependent monooxygenases in insecticide resistance of FAW populations from across the globe (Gui et al. 2020; Zhang et al. 2020; Yainna et al. 2021). Altered acetylcholinesterase (AchE) is also associated with organophosphate and carbamate resistance (Carvalho et al. 2013; Chen & Palli 2022; Yainna et al. 2021). Selection for resistance in invaded areas was inferred from the higher frequency of resistance-associated AChE mutations and higher copy number of P450 genes in some invaded areas relative to native areas (Yainna et al. 2021). A ryanodine receptor target-site mutation (I4734M) was detected in diamide-resistant strain of FAW in Brazil (Boaventura et al. 2010). In China, resistance to diamide insecticides was low and not correlated with the two ryanodine receptor target-site mutations that were examined (Lv et al. 2021). In general, knowledge of the mechanisms of FAW insecticide resistance remains scant in recently invaded areas.

5.8.3 Non-target effects of insecticide use toward FAW natural enemies

Side effects of pesticides on natural enemies include lethal and a multitude of physiological and behavioral sublethal effects (Desneux et al. 2007). These effects are responsible of losses of key biocontrol services provided by natural enemies, either fortuitously present or artificially released (Lu et al. 2012). Insecticides applications can thus affect the suitability of FAW IPM programmes and make the control of this pest even more challenging, e.g., in case of selection of insecticide resistant FAW populations.

The toxicity of multiple active ingredients has been tested on various FAW natural enemies. Among studies on FAW egg parasitoids, *Tr. achaeae* exposed to eggs treated with various organophosphates, pyrethroids, carbamates and spinosad suffered high mortality levels and reduced fertility; while neonicotinoids, neem oil, cyromazine, lufenuron, chlorantraniliprole and *B. thuringiensis* showed little or no adverse effects (Fontes et al. 2018). Adults of the larval parasitoid *Cotesia flavipes* (Cameron) exposed to residues of synthetic insecticides and fed on contaminated sugary solutions suffered varying degrees of mortality, with organophosphates and carbamates being the most toxic (Akhtar et al. 2021). Zenner et al. (2006) showed that FAW larvae are more susceptible to chlorpyriphos, methomyl and cypermethrin when parasitized by the egg-larval FAW parasitoid *Chelonus insularis*. This hints that insecticide exposure through FAW larvae may reduce the chance of successful parasitoid development, even at low pesticide concentrations. Most of the parasitoids tested for the non-target impact of spinosad, including FAW parasitoids, suffered multiple side effects (Biondi et al. 2012a). Potentially important FAW predators, such as *Orius* spp., could be also negatively affected by exposure to avermectins, neem oils, insect growth regulators, pyrethroids and, to a lesser extent, to neonicotinoids; while chlorantraniliprole and *Bt* proved to be safe (Biondi et al. 2012b; Fernandes et al. 2016; Barros et al. 2018; Lin et al. 2020).

In field studies, earwig populations, including *Doru luteipes* (Scudder), are affected by organophosphates and spinosins (Méndez et al. 2002), but treatment with lufenuron did not threaten these predators (Frizzas et al. 2014). Coccinellids (e.g., *Harmonia axyridis* (Pallas) and *Coccinella undecimpunctata* (L.) and anthocorids (e.g., *Orius* spp.) are adversely affected by organophosphates and carbamates, pyrethroids and neonicotinoids, whereas field applications of modern insecticides (i.e., indoxacarb, chlorantraniliprole, sulfoxaflor and spirotetramat) appear to be more selective (Méndez et al. 2002; Musser & Shelton 2003; Galvan et al. 2005; Varenhorst and O'Neal 2012; Abd-Ella 2015; Fernandes et al. 2016; Tran et al. 2016; Vasileiadis et al. 2017; Machado et al. 2020). Neonicotinoids and pyrethroids were also reported reducing Chrysopidae (e.g., *Chrysoperla* spp.) populations (Abd-Ella 2015; Cruces, Peña, and De Clercq 2021; Machado et al. 2020). *Metarhizium rileyi* and SfMNPV were reported safe for *Orius* spp. (Vasileiadis et al. 2017) and other predators (Gómez et al. 2013; Barros et al. 2021) in maize. Araneae populations could be disturbed by broad-spectrum insecticides (e.g., pyrethroids, organophosphates, carbamates, fipronil and imidacloprid), but less so by anthranilic diamides (Larson et al. 2011; Sudhanan et al. 2017; Whalen et al. 2016; Yang et al. 2014).

There is a paucity of field studies assessing selectivity towards FAW parasitoids. Field trials stressed that methoxyfenozide is safe to *Tr. brassicae*, whereas indoxacarb, spinosin (emamectin benzoate) and beta-cyfluthrin reduce this parasitoid's survival (Hewa-Kapuge et al. 2003). Flubendiamide (an anthranilic diamide) was found to reduce FAW parasitism by *Chelonus bifoveolatus* and *Coccygidium luteum* (Ngangambe & Mwatawala 2020). Also, sprays of *M. anisopliae* and *B. bassiana* caused little effect on parasitism by *C. bifoveolatus*, whereas *M. anisopliae* reduced parasitism by *C. luteum*. The egg-larval endoparasitoid *C. insularis* was found to be more abundant on SfMNPV-treated areas than in those sprayed with chlorpyrifos (Armenta et al. 2003). *Beauveria bassiana* proved to be also effectively carried to lepidopteran pests by *Trichogramma* sp. without negatively impacting the carrying parasitoids (Wang et al. 2021).

To produce optimized IPM FAW packages that will prioritize non-chemical uses over chemical ones, the choice of insecticides to be included into FAW IPM packages should consider potential natural enemies naturally present or released for biological control in the crops (Huang et al. 2020c).

5.9 Resistant cultivars

5.9.1 Classical resistance selection

Host plant resistance is an important component of integrated pest management. In the period 1970s to 1990s, considerable effort was undertaken in the Americas to identify maize breeding lines with leaf and ear-feeding resistance to FAW (Wiseman & Davis, 1979; Williams et al. 1989). Development of the Davis 1-9 leaf damage rating scale (Davis et al. 1992) contributed significantly to this effort.

In the invaded range, conventional maize breeding for host resistance to FAW has also been initiated. Various international research centres and national research programs are presently screening maize inbred lines, pre-commercial and commercial hybrids, and improved open-pollinated varieties under artificial or natural FAW infestation to select breeding lines, perform crosses, and develop tolerant cultivars (Prasanna et al. 2021). Since 2017, the CIMMYT maize breeding program in Kenya has evaluated 1000s of maize breeding lines for resistance (Prasanna et al. 2021) and developed elite maize hybrids with tolerance to FAW damage (CIMMYT, 2020). Screening for FAW resistance in maize is ongoing (Kasoma et al. 2021b). Several quantitative trait loci, localised on chromosome 9, have been found associated with resistance to FAW in maize (see Kasoma et al. 2021a for a list and references) and are candidates for introgression into elite maize genotypes.

In Zambia, Kasoma et al. (2020) screened a set of 60 maize landraces, hybrids and open pollinated varieties of tropical maize and another set of 253 inbred lines, for resistance to FAW and for yield and yield-related traits. They found highly significant differences in leaf and ear damage induced by FAW as well as variations in other agronomic traits. Kasoma et al. (2021c) assessed the genetic diversity of 59 maize genotypes of diverse genetic background with variable resistance to FAW, using phenotypic traits and SNP-based DArT markers. Notable phenotypic variation was observed between and among populations for ear position, grain yield, and FAW induced leaf and ear damage. Morales et al. (2021) tested 6 maize cultivars used by smallholder farmers in Kenya but did not find high levels of resistance to FAW feeding. They did, however, detect differences in acceptance and preference when FAW larvae were given a choice between certain cultivars.

5.9.2 Transgenic crops

To help manage FAW, farmers have used maize and cotton genetically engineered to produce insecticidal proteins from the bacterium *Bacillus thuringiensis* (Bt). A recent review found that maize yield losses attributed to FAW were 13% for Bt maize without insecticides, 21% for non-Bt maize with insecticides, and 25% for unmanaged non-Bt maize (Overton et al. 2021). Most of the efficacy data reviewed came from Brazil and the United States, which together accounted for 67% of the 109 million hectares of Bt crops planted worldwide in 2019 (ISAAA 2019). Although FAW in South Africa has been reported to survive in large numbers on Bt maize (Botha et al. 2019), reduced damage caused by Bt-susceptible FAW larvae were reported under field-conditions (Van den Berg et al. 2021b). This success spurred consideration of expanded use of Bt maize in parts of Africa and Asia (Huang 2021; Van den Berg et al. 2021b).

In the Americas, however, FAW has rapidly evolved practical resistance to transgenic crops that produce Bt crystalline (Cry) proteins (Tabashnik & Carrière 2019, Huang 2021). Practical resistance is genetically based, field-evolved resistance that reduces the efficacy of a Bt crop and has practical implications for pest control (Tabashnik & Carrière 2019). FAW has evolved practical resistance to Cry1Ab maize in Brazil and to Cry1Fa maize in Argentina, Brazil, Puerto Rico, and the southeastern United States (Tabashnik & Carrière 2019). For the four cases of FAW practical resistance reviewed by Tabashnik & Carrière (2019), four years is the mean time from the first commercial planting of single-toxin Bt maize to the sampling of FAW populations providing evidence of resistance.

Growers have shifted from single-toxin Bt crops to crops that produce two or more Bt toxins targeting FAW. However, the benefits of such "pyramids" are greatly reduced when one or more of the Bt proteins is not highly effective against FAW because of field-evolved resistance, cross-resistance, or inherently low susceptibility of FAW (Carrière et al. 2015; Van den Berg et al. 2021b). Unfortunately, the several Cry1 proteins that are used in Bt crops are closely related and strong cross-resistance occurs (Van den Berg et al. 2021b). Fortunately, FAW resistance to Cry1Fa and Cry1A toxins does not cause strong cross-resistance to Cry2Ab, which is produced by some multi-toxin Bt maize and cotton cultivars (Van den Berg et al. 2021b). Nonetheless, during 2015–2016 in Brazil, "FAW control failure" was reported for late-planted Bt maize producing Cry1Fa + Cry1A.105 + Cry2Ab (Burtet et al. 2017).

The Bt vegetative insecticidal protein Vip3Aa produced by some Bt maize and cotton cultivars generally remains effective against FAW that are resistant to Cry proteins (Tabashnik & Carrière 2020). A lab-selected strain of FAW from the United States was reported to have >395-fold recessively inherited resistance to Vip3Aa (Yang et al. 2021b). In Brazil, the frequency of alleles conferring FAW resistance to Vip3Aa estimated from F2 screens increased from 0.0009 in 2013–2014 to 0.0033 in 2016–2017, which could be an early warning of resistance (Amaral et al. 2020, Van den Berg et al. 2021b).

The next generation of Bt maize features modified Cry1B + Cry1D proteins, which are both effective against FAW resistance to Cry1A.105 and Cry2Ab (Horikoshi et al.

2021). To promote sustainables use of Bt maize varieties, Van den Berg et al. (2021b) propose the development of Bt maize with a single cassette carrying linked genes encoding four different Bt proteins (Cry2Ab, Vip3Aa, and modified Cry1B and Cry1D). However, the key to long-term efficacy of any transgenic crop against FAW is using it in conjunction with other tactics as part of integrated pest management (Van den Berg et al. 2021b). A promising new tactic that has the potential to increase sustainability of Bt crops is to release susceptible, self-limiting FAW (Reavey et al. 2022).

5.9.3 Maize landraces and wild ancestors as resistance sources

Crop landraces and crop wild relatives are subjects of increasing research to uncover traits and strategies to improve stress tolerance in crops in the face of climate change. For example, crops may be exposed to novel pests following a rise in average temperatures, if the distributions of pests are expanded into areas beyond their historical distributions. In such cases, crops may lack defensive traits that could protect them against the novel pests (e.g., Köllner et al. 2008). The recent invasion of Africa and Asia by FAW poses a similar problem: Maize varieties in those areas, both commercial and traditional (i.e., landraces), likely are vulnerable to the pest because they lack a shared evolutionary history. Fresh research in Mexico and the American neotropics, where FAW and maize share an extended evolutionary history (see section 3 above), may provide valuable information for developing resistant cultivars and management strategies (de Lange et al. 2014). For example, in one series of studies Bernal et al. (2015) found that the infestation rate of Balsas teosinte growing within maize fields was 55% the rate for maize, FAW growth on teosinte was ~85% relative to maize, and parasitism and predation rates of FAW were respectively 4-fold and 3-fold greater on teosinte compared to maize (Takahashi et al. 2012; Bernal et al. 2015). In another study, the caterpillar defense gene wip1 was found to be induced at high levels in one geographic population of Balsas teosinte, but not in other populations nor in maize, and was associated with decreased growth and slower development of FAW larvae (Szczepaniec et al. 2013). These and similar studies (e.g., de Lange et al. 2016; 2020) point to the possibilities of improving maize cultivars for resistance to FAW by transferring genes for enhanced direct defence (e.g., wip1 transfer through genome editing) or indirect defence through the enhanced attraction of natural enemies. Other avenues of genetic improvement may be broader. For example, recent studies comparing resistance to western corn rootworm (*Diabrotica virgifera virgifera* Le Conte), a chewing root herbivore, among Balsas teosinte, maize landraces and modern cultivars showed that teosinte relies on induced defences and maize on constitutive defences (Fontes-Puebla & Bernal 2020; Fontes-Puebla et al. 2021). Overall, past and ongoing research on FAW resistance and tolerance in Balsas teosinte and maize landraces in Mexico and elsewhere in the American neotropics could be valuable for developing improved maize varieties and management strategies in newly invaded areas in Africa and Asia.

6 Conclusion and recommendations for future research

Despite the long history of damage by FAW and research in the Americas, several aspects of its ecology and management still need to be better understood to minimise its impact in invaded regions. Its management in the Americas relies mainly on transgenic crops and broad-spectrum chemical insecticides, but these options are considered undesirable and not sustainable in many invaded countries. Thus, the goal is to develop and implement sustainable IPM that is appropriate for each invaded region. Our specific recommendations for research to achieve this goal include the following:

- Pheromones that are presently available are not specific enough for monitoring FAW, especially in areas that are not yet invaded or in temperate areas where transient FAW occur. Region-specific pheromones should be identified, in particular from invasive populations at the edge of their distribution range.
- The spread of FAW has now been mapped using various models. However, for temperate countries in Europe, Asia, and Oceania, it will be important to model the seasonal spread and impact of migrating populations.
- High FAW populations and severe leaf damage do not necessarily result in severe yield losses. To build meaningful IPM strategies, it will be helpful to better understand the relationship between FAW infestation, leaf damage, ear damage and yield loss, and how these relationships vary with crop stage and agroecological conditions, including the abundance / efficacy of natural enemies.
- Methods for augmentative biological control with local parasitoids, predators, and entomopathogens should be developed in invaded areas, as well as agroecological approaches to enhance the effectiveness of natural enemies already present in the system. Their cost-effectiveness needs to be considered, considering the low value of the main crops affected by FAW.
- Classical biological control through the importation of parasitoids from the Americas should be considered even though FAW is a pest also in the Americas and many natural enemies have been found in the invaded regions. Indeed, CBC has no cost for farmers and even a reduction of population levels by a few percent may reduce the need of other, costly control methods.
- Agroecological approaches to FAW management should be given more attention, with specific studies in different agroecological zones in both the invaded and native ranges.

- The impact of chemical insecticides and other current control methods on natural enemies and the environment should be better assessed to improve IPM for FAW.
- Social studies on the impact of chemical insecticides on farmer health and the well-being of farming communities are also urgently required, especially in poorer developing countries where farmers rarely use protective clothing.
- Transgenic Bt maize is used extensively against FAW in its native range, but for various reasons, transgenic crops are not considered acceptable by most invaded countries. Sustainable use of Bt maize for managing FAW should be a priority research topic.
- Recent evidence of new introductions of foreign FAW into Africa emphasize the need for continued surveillance at entry points to limit the introduction of FAW populations with broader host range and resistance traits (Nagoshi et al. 2022).
- Socio-cultural studies are required to better understand how to develop culturally appropriate IPM recommendations and for improved communication of technologies.

Conflict of Interest

The authors declare no competing interests.

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