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Spodoptera frugiperda: Ecology, Evolution, and Management Options of an Invasive Species

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Abstract

The fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera, Noctuidae), is a well-known agricultural pest in its native range, North and South America, and has become a major invasive pest around the globe in the past decade. In this review, we provide an overview to update what is known about *S. frugiperda* in its native geographic ranges. This is followed by discussion of studies from the invaded areas to gain insights into *S. frugiperda*'s ecology, specifically its reproductive biology, host plant use, status of insecticide resistance alleles, and biocontrol methods in native and invasive regions. We show that reference to host strains is uninformative in the invasive populations because multidirectional introduction events likely underpinned its recent rapid spread. Given that recent genomic analyses show that FAW is much more diverse than was previously assumed, and natural selection forces likely differ geographically, region-specific approaches will be needed to control this global pest.

1. INTRODUCTION

1.1. Taxonomy

Given the significant economic losses and food security challenges caused by the recent habitat expansion of the fall armyworm (FAW), *Spodoptera frugiperda*, it is important to clarify contradictory findings relating to this lepidopteran pest's strain, species, and hybrid status. As the corn budworm moth, *Phalaena frugiperda*, it was first described in 1797 from specimens collected in Georgia, United States (118). It was redescribed by de Boisduval & Guenée (22) as *Laphygma macra* in 1852, and synonymized with *Spodoptera* by Zimmerman in 1958 (151). From the 1840s through the 1860s, damaging populations in corn in Kansas, Missouri, and Illinois were very low in the spring but expanded in the late summer and fall. As a result of this distribution, which was explained as being a result of larvae or pupae overwintering in the soil, C.V. Riley (State Entomologist of Missouri), who did not know that the species had already been described, named it *Prodenia autumnalis*, the fall armyworm (109).

FAW: fall armyworm, the Entomological Society of America's official name for *Spodoptera frugiperda* (J. E. Smith)

AFLP: amplified fragment length polymorphism

PCR-RFLP: polymerase chain reaction-restriction fragment length polymorphism

mt*COI*: maternally inherited mitochondrial (mt) *cytochrome oxidase subunit I* (*COI*) gene

***Tpi*:** *Triosephosphate Isomerase* gene on the Z chromosome

SSR: simple sequence repeat

SNP: single-nucleotide polymorphism

PLC: salivary phospholipase C; used by caterpillars against plant defense elicitors

C-strain: corn strain; original designation for the host strain found feeding on corn and other large grasses

R-strain: rice strain; original designation for the host strain found feeding on rice, pasture grasses, turf grasses, and other small grasses

1.2. Detection of Host Strains in the Native Range

In 1985, two strains of FAW were identified and named after the host plants (i.e., corn and rice strains) from which they were collected (98). These strains are morphologically similar, although there is an indication that host plant habitat affects wing morphology (13, 81). Various genetic markers have been used to better understand their genetic variation and evolutionary relationship, including allozymes (96); amplified fragment length polymorphism (AFLP) (70, 106); polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) (66); the maternally inherited mitochondrial *cytochrome oxidase subunit I* (mt*COI*) gene (64); the *Triosephosphate Isomerase* (*Tpi*) gene on the Z chromosome (82); simple sequence repeat (SSR) (i.e., microsatellite) loci (101); and more recently, genome-wide single-nucleotide polymorphism (SNP) markers and whole-genome resequencing (42, 108, 112, 124, 128, 150).

Soon after genetic differences were found between larvae collected from corn and those from bermudagrass or rice (96, 98), larval feeding studies were designed to test larval fitness from different plant hosts. While the first studies found developmental trend differences between the two strains on different host plants (133), further comparisons with larvae on bermudagrass and other grass species suggested more variable responses depending on season, artificial diets, and plants used (107).

Since host strains may also differ in their responses to constitutive plant defenses, the larvae's ability to metabolize the cyanide present in some pasture grasses (*Cynodon* spp.) (55) and salivary phospholipase C (PLC) activity levels (1) was also tested. Overall, only subtle differences between the two strains were identified in relation to host plant use, which has been confirmed by multiple studies (45, 58, 59). Therefore, these strains should not be called host strains, and we refer to them as C-strain and R-strain below. **Figure 1** outlines the basic biology of the FAW.

In addition to host plant differences, several prezygotic isolation barriers between the two strains have been investigated, including differential temporal patterns of female calling and copulation at night. In laboratory tests, the two strains were found to differ in the timing of female calling and copulation (51, 53, 97, 113, 114), with C-strain females being sexually active early at night and R-strain females late at night (but see 19, 110). Postzygotic isolation between the two strains has also been reported, with matings between C-strain females and R-strain males (CR matings) occurring significantly less than RC matings (27, 62, 110); hybrid RC females were found to be chaste, i.e., sexually completely inactive (62). Interestingly, 56–66% of all hybrids found in nature were shown to be RC hybrids (88, 90, 106). Thus, postzygotic isolation barriers seem to play a more important role than prezygotic isolation barriers (19, 110) and may explain

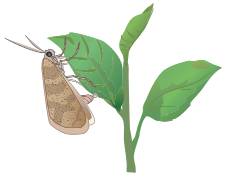
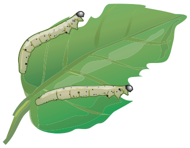
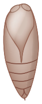
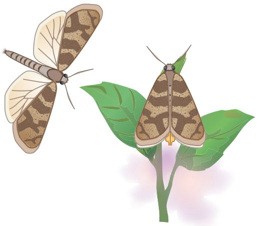
In native range	**Fall armyworm**	**In invasive ranges**
Egg clutches found on many plant species (1, 58, 136)	**Oviposition: egg clutches on plants** 	Egg clutches found in corn and sorghum fields, but also in other crops (19, 114, 122)
Two strains, C-strain and R-strain, with up to 2% genomic differences (50), although hybridization occurs between strains (10, 127)	**Larvae** 	No separate strains (127, 153)
No diapause, but adults migrate and remain active in (sub)tropical areas (70, 137).	**Pupae (diapause)** 	No diapause? Migration habits?
Sex pheromone components: Z9-14:OAc (major) (82, 132), Z7-12:OAc (2%) (21, 132, 133), Z11-16:OAc (132), Z9-12:OAc: function unclear) (133), E7-12:OAc (Brazil) (9)	**Sexual attraction** 	Sex pheromone components: Z9-14:OAc (major), Z7-12:OAc (minor) (54, 64, 74)
Postzygotic isolation between C- and R-strain (28, 65)	**Postzygotic isolation** 	Hybridization with, or postzygotic isolation, between locally occurring related *Spodoptera* species?

Figure 1

Basic biological differences in the life cycle of the fall armyworm between native and invasive populations.

the approximately 2% genomic divergence found between the two strains in their native range (26, 42). In addition to the C- and R-strains, Arias et al. (5) also reported two distinct C-strain clades in Brazil and Paraguay that diverged 0.65 Mya, which indicates that there are likely to be other genetically distinct native FAW populations.

1.3. Strain Hybridization in the Native Range

Whether assortative mating between the two strains occurs naturally across their native range is unclear (97, 99, 114). When the two strains were first identified, Prowell et al. (106) noted that as many as 16% of the collected individuals were hybrids, based on composite genotypes with mitochondrial DNA of one strain and esterase genotypes of the other. In laboratory choice tests, analyses of spermatophores also demonstrated common occurrences of interstrain matings where spermatophore mt*COI* markers were different from the mt*COI* markers of the females (72). Strain and hybrid identifications over the past two decades were predominantly based on two markers, the mt*COI* and the *Tpi* locus on the Z chromosome. However, since lepidopteran females are the heterogametic sex and possess only a single copy of the Z chromosome, a hybrid female or her offspring cannot be distinguished from a homozygous (i.e., nonhybrid) individual based on the *Tpi* marker or the nonrecombining mitochondrial genome (59). Analysis of whole-genome sequence data therefore offers a clearer picture of the level of hybridization between the two strains, and hybrids have now been identified from South America (5, 59, 124), Central America, the Caribbean, and North America (47, 112, 124).

1.4. Population Genetics in the Native Range

By 1913, it was known that the FAW had continuous generations in the tropics and subtropics (24). Later research suggested that outbreaks in the United States originated in Mexico and the West Indies and that the FAW overwinters in southern Texas; in southern Florida; and, in very warm winters, in the southern part of the Gulf Coast states (67, 134).

Genetic diversity of populations based on AFLP markers indicated significant gene flow, represented by high within-population variation and low between-population variation among North and South American populations (16, 69). However, local-scale isolation-by-distance between populations was detected in various South American populations (5, 9, 59). This highlights the difficulty of drawing general conclusions related to the FAW's propensity for long-distance migration, in which local and regional ecoclimatic factors are likely to also play important roles.

Seasonal migratory patterns of moths were inferred through haplotype ratios present in progenies of migrating populations (89) and through modeling-based genetic analysis (138, 139). These analyses showed that populations from Mexico, South America, and Trinidad and Tobago carried a haplotype ratio similar to that of moths from Texas (84, 91), while populations from Puerto Rico, the Dominican Republic, St. Kitts and Nevis, Dominica, and Barbados had haplotype ratios more similar to those of moths from Florida (84). These results thus suggest limited genetic exchange between Florida and South American FAW populations, as is also reported between distantly separated populations based on SSR markers (5, 101), although potential migrants were detected (101). However, lepidopteran SSR markers can be related to transposable elements (123) and could lead to misinterpretation of limited gene flow.

Based on 870 neutral and unlinked SNP markers throughout the genome, a principal component analysis grouped FAW populations from North America (Mississippi, Florida, Mexico), the Caribbean (Puerto Rico, Guadeloupe), and South America (French Guiana, Peru, Brazil) into five distinct populations that largely reflected their geographic regions (124) but not their strain identity, as was also reported by Schlum et al. (112). In line with the haplotype ratio findings (84, 91), Tay et al. (124) also showed that Guadeloupe and Puerto Rico FAW grouped with the Florida population, but separately from the Mississippi population. Furthermore, limited gene flow between North and South American populations (5, 9, 59) was detected, with one of the two Brazilian populations clustering with the Peruvian population (46, 143). In contrast, whole-genome SNP analysis (112) showed high gene flow between Caribbean and North and South American populations but also detected unique population clusters between Florida and Brazilian populations that suggested varying degrees of gene flow between the two continents.

2. INVASIONS OF FALL ARMYWORM

Invasion of the FAW into the Eastern Hemisphere and its resulting spread have been explained by two competing hypotheses, one positing a west-to-east spread and the other a complex of multiple introductions involving African and Asian origins. There are some indications that, since the mid-1960s, the FAW may have invaded the Eastern Hemisphere with increasing frequency. For example, adults that developed from larvae collected from crops in Israel in 1967 were identified as FAW (140), although trapping in the Jordan Valley in 1979 with a FAW pheromone lure did not capture any moths (145). In Germany, FAW-infected maize plants were collected and destroyed in August 1999 (57). In 2008, the FAW was reported to damage turfgrasses in parks surrounding Hanoi, Vietnam (136). Prior to February 2014, morphological identification by the USDA Identification Technology Program (ITP) of FAW-intercepted larvae entering US ports indicated that individuals were not only from native regions but also from countries such as Turkey, China, Indonesia, Israel, Micronesia, the Netherlands, and Thailand (39). However, as far as we know, in none of these cases are specimens available for molecular diagnostics or morphological reassessment.

ITP: United States Department of Agriculture Identification Technology Program

The FAW was officially reported in western Africa in early 2016 (41), throughout the sub-Saharan African nations by early 2018 (29, 32), and in the Middle East/Indian subcontinent by mid-2018 (36). Single-gene analysis of light-trapped specimens suggested that the FAW had spread from Myanmar into southern China's Yunnan Province by early December 2018 (122), with ensuing northward expansion into central China (141). Eastward expansion would lead to its detection in South Korea and Japan, and southward expansion through southeast Asia allowed it to reach Australia by early 2020 (92, 108, 125). Chronological reports showing it moving from Africa progressively across to Asia, together with population genetic analysis based on single markers, therefore suggested a rapid west-to-east spread of the FAW (29, 32).

2.1. Origins of Invasive Populations

The widely accepted west-to-east spread hypothesis of invasive FAW across the Old World was inferred from strain-specific partial single gene markers (85). Specifically, the invasion analysis based on the Z-linked *Tpi* marker identified predominantly C-strain moths, originating either from the eastern United States or the Greater Antilles (87). This finding concurred with findings from West Africa, where the invasive descendants of C-strain and hybrid genotypes contained a pheromone composition similar to that found in the United States (51). Further single-marker analysis of moths from South Africa, India, Myanmar, and southern China indicated genetic backgrounds similar to those from west Africa (83, 86). Genomic analysis that included FAW from Louisiana, South Africa, Ethiopia, and Kenya (47) was also used to support the idea that China's Yunnan and Guangxi populations originated from Africa, despite having a genomic signature that indicated multiple independent introductions within China and in Africa.

The complex multiple introductions hypothesis involving African and Asian origins is supported by other recent multigenetic and genomic analyses, which indicate multiple introductions (95, 108, 112, 124, 125), as well as by the east-to-west movements of the pest (124). For example, genome-wide SNP markers clustered FAW from Benin, some individuals from Uganda, and populations from India and Yunnan China together but excluded Malawian and various Ugandan individuals (46, 94, 95, 124), which had a southeast Asian origin (108) (**Figure 2**). Similarly, whole-genome sequence analysis of Kenyan (112) and Zambian (150) FAW also supported multiple introductions. Phylogenetic analysis showed that African populations were predominantly derived from distinct Chinese populations, while some Chinese individuals were closely related to US populations (47, 124).

Similarly, unique genomic signatures shared between Yunnan and southeast Asian FAW populations (108) do not support the origin of Yunnan population being Myanmar or long-distance movements via monsoon winds (149), but instead support the hypothesis of multiple introductions in southeast Asia (**Figure 2**). Resistance allele characterization (11, 46, 49, 68) and different insecticide responses between Queensland and western Australian FAW populations also supported

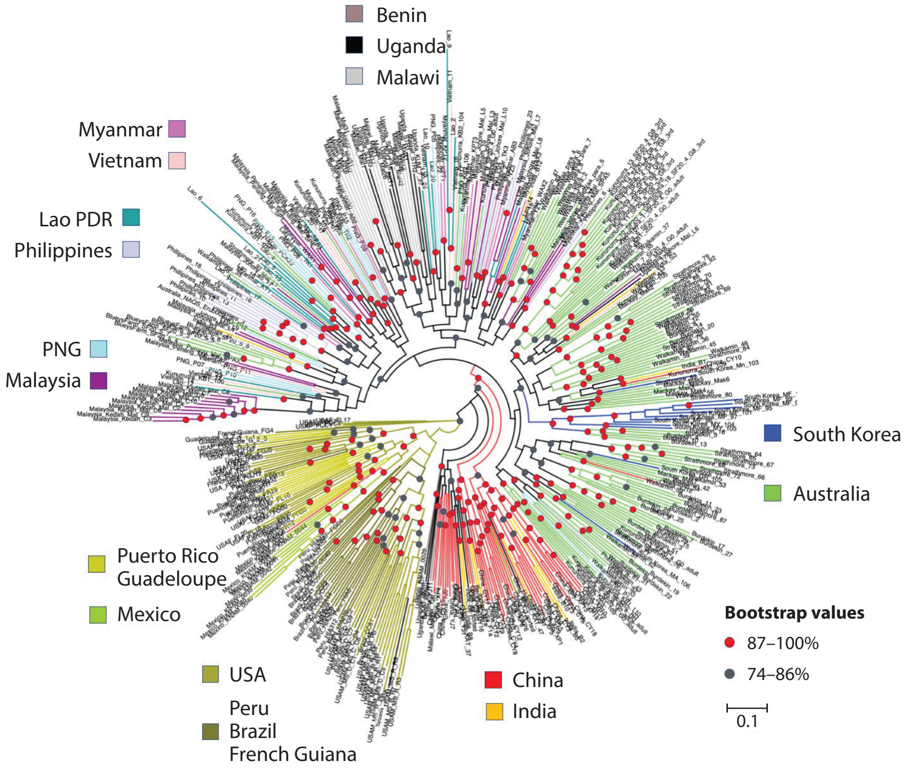


Figure 2

Maximum likelihood phylogeny of invasive (China, India, Australia, South Korea, Malaysia, Papua New Guinea, Philippines, Laos, Vietnam, Myanmar, Benin, Uganda, Malawi) and native [Puerto Rico, Guadeloupe, Mexico, United States (Florida, Mississippi), Peru, Brazil, French Guiana] populations. Fall armyworm populations are based on 870 neutral genome-wide single-nucleotide polymorphisms. Countries are indicated by branch colors. The derived state of African populations from southeast Asia is contrary to the axiom of west-to-east spread pattern. Evidence of multiple introductions can be seen from various populations, e.g., in Australia and Malaysia. Figure adapted with permission from Reference 108; CC BY-NC 4.0. Abbreviations: PDR, People's Democratic Republic; PNG, Papua New Guinea.

multiple non-African introductions into China, Indonesia, and northern Australia (108, 125). Understanding the degree of bidirectional gene flow between African, Asian, and Oceanian FAW, as well as genome diversity in countries such as Thailand, Cambodia, Indonesia, and many African and Asian countries, will require whole-genome analysis. Several of these countries may have had FAW introductions prior to 2016 (39).

2.2. Strain Differentiation in Invasive Populations?

Whether the two FAW strains have invaded other parts of the world has remained unclear. The confusion is in part due to disagreements between diagnostic markers, while usage of the terms strains, host-races, host forms, biotypes, and sibling and sister species to describe molecular diagnostics of the FAW has contributed to the confusion. Genetic analysis of Ugandan specimens documents both strains, with a higher genetic diversity in the C-strain than was previously reported (95). This higher genetic diversity in the C-strain in eastern Africa (e.g., Uganda, Malawi) reflected a southeast Asian–derived origin: FAW populations from Vietnam, Myanmar, Malaysia, and Laos have greater frequencies and diversity of C-strain mitochondrial genomes that are absent in a majority of Chinese FAW (47, 124, 150). Analyses based on higher density of nuclear markers and whole-genome analyses in southeast Asian FAW further showed a complex mixing of genomes when the strain types are considered (47, 126, 150). Interestingly, while whole-genome resequencing and genome-wide SNP analyses identified the majority of African, Asian, and Australian invasive populations as hybrids, some Chinese (47, 126), Malaysian (Kedah State) (47, 124, 150), and African (47) individuals were identified as having non-admixed genomes. Global invasive FAW populations thus consist predominantly of hybridized individuals but also contain non-admixed individuals, both of which should be identified via a whole-genome analysis approach. The binary thinking that there are two distinguishable FAW strains throughout the invasive range should thus be avoided.

Z9–14:OAc: (*Z*)-9-tetradecenyl acetate, the main component of the FAW sex pheromone

Z7–12:OAc: (*Z*)-7-dodecenyl acetate, a critical secondary component of the FAW sex pheromone

Z11–16:OAc: (*Z*)-11-hexadecenyl acetate, a minor component of the FAW sex pheromone

Z9–12:OAc: (*Z*)-9-dodecenyl acetate, a minor component of the FAW sex pheromone

E7–12:OAc: (*E*)-7-dodecenyl acetate, a minor component found in the FAW sex pheromone in South America

3. ECOLOGY

3.1. Mate Attraction in the Native Range

In addition to the host plant preference and performance studies, mating compatibility studies, and studies on variation in circadian rhythms mentioned in Section 1.2, variation in FAW mate attraction has been investigated throughout its native range. Mate attraction in the FAW occurs through a species-specific sex pheromone, which was identified in 1986 (129). The four main components are (*Z*)-9-tetradecenyl acetate (*Z*9–14:OAc), the main component; (*Z*)-7-dodecenyl acetate (*Z*7–12:OAc), the critical secondary sex pheromone component; and (*Z*)-11-hexadecenyl acetate (*Z*11–16:OAc) and *Z*9–12:OAc as minor components (see **Figure 1**). These components are used as lures in field trapping (79, 129, 130). In Brazil, an additional component, (*E*)-7-dodecenyl acetate (*E*7–12:OAc), was identified that increased male trapping in field tests (8).

Strain differences in female pheromone blends and attraction of males to females of different strains have been tested in several populations across the Americas. In field tests in Louisiana, 60% of males responded to same-strain females (97). However, in field tests in Florida, 68% of C-strain males responded to C-strain females, but 58% of R-strain males also responded to C-strain females (73). Identification of chemicals from the pheromone glands of the two strains in Colombia found nine compounds but no strain differences (12). Two other studies showed small differences in pheromone components between strains (44, 65). Follow-up field studies with lures with different blends showed that, in corn fields, more males of both strains responded to the C-strain blend than to the R-strain blend, while males of both strains in grass fields throughout North and South America were equally attracted to both blends (130, 131). Thus, differences in attraction based on pheromone blend between strains do not seem strong enough to cause assortative mating, although other factors such as differences in timing or means of pheromone emission might still cause assortative mating

3.2. Ecology in the Invasive Range

The ecology of FAW in the invasive ranges has been little investigated, as the focus of research has mostly been on trying to manage and control the pest. In this section, we summarize the ecological studies conducted with invasive FAW populations in relation to mate attraction, host use, and migration capabilities.

3.2.1. Mate attraction. Although many males were collected in commercial lure traps in West Africa (61, 71, 127), commercial FAW pheromone lures appear to be suboptimal in many invasive regions. This suggests that changes have occurred in the sexual communication of the FAW, either in the female sex pheromone or in the male response, possibly due to the predominantly hybrid nature of these populations. To date, only one study has been published on sex pheromones of moths; this studied moths from Africa and analyzed females collected as larvae from Benin and Nigeria (51). No significant differences were found between these populations and the Florida R-strain. However, male antennal responses showed significant differences, suggesting that males from different regions might respond differently.

3.2.2. Host plant use. In its invasive ranges, the FAW's use of host plants has been investigated to some extent (**Figure 1**). While maize has been the most widely damaged economic crop, other plants can also be attacked. For example, in Yangling, Shaanxi, China, FAW larvae were reported to develop fastest on maize but also developed well on other cash crops, especially wheat and, to a lesser extent, soybean, tomato, and cotton (137). On Chinese cabbage, the egg-hatching rate was low, with only 5.3% of larvae developing into egg-laying adults. Regardless, FAW larvae still fed voraciously on this plant and may use it as supplementary food during migration. In maize fields, competition may occur between the FAW and local pest species. For example, in laboratory feeding assays conducted in Yunnan, China, FAW larvae preyed on and outcompeted *Spodoptera litura* larvae on maize (119).

Host plant preference experiments have also been conducted in the FAW's invasive range, mostly to investigate the potential use of push-pull and intercropping management strategies. For example, testing oviposition preference on six grass species to determine the species' suitability as trap or pull plants showed that oviposition preference depended on plant size, although larvae mostly preferred maize (15). However, in no-choice oviposition tests, moths laid eggs on the grasses, indicating their potential usefulness as pull plants (15). As a repellent or push plant, *Desmodium intortum* was reported to significantly reduce numbers of FAW larvae on maize plants in Kenya, Uganda, and Tanzania (74). However, oviposition choice tests conducted in Kenya (111) also found that FAW laid similar number of eggs on *D. intortum* as on maize plants, and larvae could develop on *D. intortum* plants. In this region, *Brachiara* grasses were suggested as possible pull plants because FAW females oviposited similarly on these plants as on maize plants (111). Examples of intercropping experiments in Congo's Kashusha district also reported less frequent FAW attack on onion when intercropped with groundnut (17). Importantly, a population collected from maize fields in Zhejiang, China and established in the laboratory showed significant host plant adaptation (52). After 20 generations of selection on rice plants, larvae showed increased fitness (i.e., higher larval and pupal weight) and higher egg-laying rates on a rice plant host. This result suggests the potential for this pest to further impact agricultural productivity in China, as well as other Asian countries where rice is cultivated.

3.2.3. Migration capabilities. As mentioned above, the FAW is capable of long-distance migration. Population genomic studies of invasive populations suggest that long-distance movements occur frequently, either through natural migration and/or through anthropogenic activities (29, 32; see Section 2). In flight mill experiments, adult FAW developed from maize field–collected larvae in Yunnan, China could fly up to 120 km over five consecutive nights, with superior flight performance at 20–25°C and 60–90% relative humidity (38).

4. INSECTICIDE RESISTANCE IN FALL ARMYWORM

4.1. Insecticide Resistance in the Native Range

In native FAW populations, resistance to pyrethroids, carbamates, and organophosphates has been detected (14, 102); resistance to carbamates has been reported from Georgia, United States since the 1970s (146), and resistance to pyrethroids was reported in 1997 in a laboratory-maintained population in Brazil (25). More recently, resistance to novel classes of insecticidal compounds [i.e., spinosad, *Bacillus thuringiensis* (Bt) toxins] was also reported. For example, spinosad resistance was detected in Brazil (93) and Puerto Rico (50), while resistance to the Bt Cry1F toxin expressed in transgenic maize was also reported in Puerto Rico (121) and Brazil (31). In addition, resistance to diamides in Brazil (10) and the VIP3A toxin in Louisiana FAW populations (144) has been reported.

Bt: *Bacillus thuringiensis* toxins, including Cry1F and VIP3a, that have been genetically inserted into crop plants

Insecticides have been used to manage FAW populations since the early 1900s in the United States (67), which has led to the development of resistance to many insecticides. Monitoring for insecticide resistance frequency and response changes requires knowledge of baseline susceptibility levels. However, due to the long-term, early, and widespread use of insecticides on the FAW, baseline resistance levels are often unknown in target populations. Therefore, it is difficult to interpret how resistance levels have changed or evolved over time. The reported susceptible native FAW populations from North and South America (63, 147) represent valuable resources for monitoring insecticide response changes and for identification of the genetic basis underlying this resistance.

4.2. Insecticide Resistance in the Invasive Range

Research groups in Africa (46, 117), India (23, 63), China (46, 150), southeast Asia (11, 108), and Australia (92, 108, 125) have been investigating resistance status to various classes of insecticides in invasive FAW populations through bioassays, direct gene characterization via PCR and Sanger sequencing, and whole-genome resequencing. Unfortunately, the lack of consensus in bioassay approaches (e.g., chemical exposure methodologies, mortality rate scoring, insect life stages to be used, calculation of lethal dose) hinders meaningful comparisons between studies (23, 63).

Recently, insecticide resistance responses were compared between Indian invasive populations and a susceptible Brazilian native FAW population at spatial and temporal scales (63). These comparisons showed that responses to a range of insecticides have remained relatively constant between 2008 and 2019 and 2020. Changes in tolerance levels to some insecticides (e.g., chlorpyrifos and emamectin benzoate) were detected in some populations, although no genomic analysis was performed to rule out novel introduction events. In comparing differences in the response to methomyl among South African, Australian, and either susceptible or resistant Florida FAW populations (63, 147), Australian populations exhibited toxicity ratios within natural variability range, whereas high toxicity ratios were detected in the South African population (125). The characterization of resistance alleles supports the presence of unique FAW populations in southeast Asia, such as in Indonesia (11) and among different provinces in China (46, 68, 150). Notably, the same type of diamide resistance that was detected in Brazil (10) was also found in Guangzhou, China (68). Similarly, resistance to organophosphate and carbamate insecticides in native populations has been detected in populations from Hubei, China (49), but also in low frequency in Indonesia (11). These results indicate separate and potentially ongoing incursions of distinct New World FAW into the Old World.

Various FAW invasive populations exhibit unique resistance traits, and adoption of resistance management strategies developed from research on the assumed western African invasive bridgehead population (48) can lead to suboptimal outcomes. Understanding FAW introduction pathways and frequencies will help in monitoring future accidental introductions of novel resistance alleles and the ongoing management of this invasive pest, as well as in preparing for reciprocal introductions of undesirable genetic traits from the invasive range back to the native range.

5. OTHER MANAGEMENT STRATEGIES

5.1. Use of Sex Pheromone Lures in the Native Range

SfNPV: *S. frugiperda* nucleopolyhedrovirus; used in microbial control of the FAW

In its native range, pest management strategies against the FAW include the use of sex pheromones as lures for monitoring. Sex pheromones have also been used as mating disruptants (75, 120), whereby the air is permeated with pheromone point sources to make it difficult for males to locate females, either due to confusion or because communication is disrupted as a result of habituation on the part of the perceiving insect. Release of *Z*9–12:OAc in an area where virgin females were calling reduced male captures by 85% (77). Subsequent studies showed that release of (*Z*,*E*)-9,12-tetradecadienyl acetate, a chemical that is not part of the FAW's pheromone, reduced the number of mated females by 87% (76). Expanded field studies in corn fields showed that aerial application of *Z*9–14:OAc formulated in hollow fibers reduced matings by 86% and oviposition by 84% (78). Use of pheromones for mass trapping has also been suggested (75), but of all techniques that include pheromone lures, this technique has the lowest chance of success for the FAW because of its high dispersal rate, multiple matings, and outbreak populations (7).

5.2. Use of Sex Pheromone Lures in the Invasive Range

Sexual communication can quickly evolve in novel environments to minimize interactions and communication interference with endemic species (43). Even though the sex pheromone composition of populations in Benin and Nigeria did not seem to differ from that of the Florida R-strain, elevated antennal sensitivity toward *Z*7–12:OAc was found in African males (51). In Togo and Benin, locally designed traps were successfully used to trap male moths and could provide a less expensive resource for farmers (71, 127). In Zambia, pheromone traps with a yellow insecticide-treated screen were found to trap more FAW than those with a black insecticide-treated screen, although potential influencing factors such as cropping practices were not specifically investigated (40). These findings suggest a need for region-specific pheromone lures in the different invaded areas for timely FAW monitoring and management.

5.3. Biocontrol in the Native Range

The FAW in its native range is attacked by a large number of pathogens (bacteria, fungi, viruses), parasitoids (Diptera and Hymenoptera), and predators (Coleoptera, Dermaptera, Hemiptera, Hymenoptera) (6, 37, 80). Aside from the results of a few studies (54, 132), little is known about the impact of natural enemies in reducing populations in agricultural systems. For augmentative releases, egg parasitoids are the easiest of the natural enemies to rear in large numbers. In Brazil, a series of studies showed that release of the egg parasitoids *Telenomus remus* Nixon and *Trichogramma pretiosum* Riley has the potential to reduce field populations, and enough information has been gathered about the number of released individuals (34, 104), dispersal capacity (103), and costs (135) to allow the development of a *T. remus* release program. A release program of *T. pretiosum* in corn has also been developed using data on the number of FAW males caught in pheromone traps (33). The predatory earwig *Doru luteipes* Scudder is another natural enemy being considered for augmentative release in corn (100). The presence of at least one pair of *D. luteipes* per plant was enough to keep the FAW population under control and promote a 7% increase in corn production (18), although this approach relies on the cost effectiveness of rearing the predator.

Different types of viruses have also been identified and explored as potential biological control agents (56). The most promising viral candidates for biological control are the *S. frugiperda* nucleopolyhedrovirus (SfNPV) (105) and granuloviruses (20). The rerelease of the nucleopolyhedrovirus in a cotton production program caused high mortality of caterpillars and reduced damage to the reproductive plant structures (21).

5.4. Biocontrol in the Invasive Range

Although the FAW is native to the New World, many natural enemy species that target it have already been documented across sub-Saharan Africa (3, 28, 60, 94, 116) and Asia (35, 115, 148). Mass rearing of egg parasitoids for inoculative release has commenced in both Africa (2, 126) and Nepal (30). In India, up to 73% of FAW larvae were parasitized by endemic parasitoid wasps or infected with the naturally occurring entomopathogenic fungus *Metarhizium rileyi* (35). Fungi such as *M. rileyi* and *Beauveria bassiana* therefore have promise as effective biocontrol agents to complement integrative pest management strategies, although their efficacy in causing mortality in the FAW appeared to be strain specific. The efficacy of intrahost specificity of SfNPV against invading host populations requires further characterization, including via screening of naturally occurring field isolates from China, India, and Nigeria (56).

6. FALL ARMY WORM EVOLUTIONARY POTENTIAL

Genomic analyses have shown that FAW populations in both native and invasive ranges are genetically much more diverse than was previously assumed. In its native range, strain-specific chemosensory and detoxification genes against plant metabolites and insecticides have been identified (42). Such gene expansions likely contribute to adaptation to novel habitats and to the detection, identification, and utilization of diverse plant hosts as food sources and oviposition sites, as well as assisting in long-distance flight (42, 142, 150). In invasive populations, new mutations, such as gene translocation (150) and composition differences of transposable elements in the genomes (142, 150), seem to occur relatively frequently across the FAW's genome. In addition to the high genetic diversity found in many FAW populations, human-assisted long-distance movements of the FAW can reciprocate introductions of genotypes from invasive populations to native New World populations.

Natural selection forces exerted on FAW individuals and populations will likely differ from region to region, as interacting species, including natural enemies, may vary locally. Sympatrically occurring species in the native range have most likely evolved mechanisms to prevent cross-attraction. However, in invasive areas, introgression and hybridization may have occurred between the introduced and native species, as reported in other noctuid pests, resulting in novel genetic variants (4). As mentioned above, extensive hybridization has already been shown to occur between FAW strains in native and invasive areas, although hybridization between FAW and other *Spodoptera* and noctuid species in the invaded regions has not yet been discovered. The introductions of the FAW to all (sub)tropical regions of the world came with significant ecological and socioeconomic costs, but studying the ecology and evolution of this species also creates unprecedented opportunities in the age of genomics to understand adaptation and evolutionary potentials under real-world conditions.

7. CONCLUSIONS

In reviewing the literature, including the most recent genomic analyses, we can draw six important conclusions. First, the FAW does not consist of two distinguishable host strains in the invaded areas. Second, the spread of invasive FAW across the Old World likely involved both west-to-east and east-to-west introduction events, although specimen confirmation of multiple introductions before 2016 is needed. Third, some commercial pheromone lures are not effective in several invasive regions, which may be due to regional variation in male responses. Fourth, local host plant adaptation may occur relatively rapidly. Fifth, insecticide resistance responses are highly variable. Finally, biocontrol is likely to be most effective with endemic (egg) parasitoids, viruses, and entomopathogenic fungi.

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