

A Review of the Scientific Literature on the Use of Reproductive Pheromones in the Management of *Spodoptera frugiperda* (Lepidoptera: Noctuidae)¹

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Abstract The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is native to tropical and subtropical areas of the Americas but has recently invaded and established in several African and Asian countries, including India. It successfully oviposits and feeds on a variety of host plants, but its feeding damage to maize, *Zea mays* L., is of great concern in its native and expanded ranges. Conventional insecticides are the usual means of managing the pest, despite the adverse impacts of these chemistries on nontarget species, as well as human and environmental health. Botanicals, biological agents, cultural practices, host plant resistance, and genetically modified hosts also have been explored for management, as has the use of reproductive pheromones for management, monitoring, and decision making. We conducted a review of available scientific literature on the use of reproductive pheromones for monitoring, mass trapping, disrupting mating, and decision making in the management of *S. frugiperda*. Assembling this information in one location will facilitate additional research with pheromone-based management strategies and tactics, especially within expanded ranges of the pest.

Key Words *Spodoptera frugiperda*, reproductive pheromone, insect pest management

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a migratory insect that is native to the tropical and subtropical regions of the Americas. Until recently, the pest had remained restricted to the Western Hemisphere, but it has now successfully expanded its range to Africa and Asia. In 2016, it was first reported causing significant damage to maize, *Zea mays* L., in Africa (Goergen et al. 2016), and has since spread to approximately 44 countries on the continent (Prasanna et al. 2018, Rwomushana et al. 2018). Subsequent to its invasion of Africa, it was reported from India in December 2018, China and Southeast Asia in June 2019, and Australia in early 2020 (FAO 2019, DPI 2020). It is considered as a serious threat to maize production in these areas of its expanded range.

Management tactics for this pest are primarily directed to the larval stage that feeds on foliage and other structures of host plants. Those tactics include application of conventional chemical insecticides and botanicals, cultural practices,

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and biological control agents, which Assefa and Ayalew (2019) recently reviewed, as well as host plant resistance and transgenics recently reviewed by Prasanna et al. (2018). Herein, we present an overview of the pheromone-mediated management techniques used against *S. frugiperda*. Pheromones are used as monitoring, mass trapping, mating disruption, and decision-making tools in insect pest management (IPM). Their use in fall armyworm IPM has been studied, but the results of these have not heretofore been annotated and compiled in a review to serve as a resource for additional research and development of pheromone use in fall armyworm IPM.

Pest Status

Spodoptera frugiperda is polyphagous. Montezano et al. (2018) reported 353 larval host plant species representing 76 families with the highest number of host plants belonging to family Poaceae (106), followed by Asteraceae and Fabaceae (31 each). Several economically important crop plants are among these hosts, including maize, rice (*Oryza sativa* L.), sugarcane (*Saccharum officinarum* L.), wheat (*Triticum aestivum* L.), and a variety of vegetables. Of particular note is yield losses caused by the fall armyworm to cotton (*Gossypium hirsutum* L.) in Brazil and maize worldwide (Cruz et al. 1999).

In maize, fall armyworm larvae attack and damage growth stages 1–7 (i.e., leaf development to fruit development; Meier 2001). They defoliate and can kill young plants, damage the foliage in the whorl stage that can result in yield losses, and feed on ears that can result in reduced grain quality and yield (Capinera 2017). Detecting an infestation before populations reach a level that causes economic damage is the key to its management in maize and other crops. If detected too late, resulting damage could lead to yield reductions (Capinera 2017, Rwomushana et al. 2018). The Centre for Agriculture and Biosciences International (CABI) estimated that, in 12 maize-producing countries, the fall armyworm without proper management can cause maize yield losses ranging from 4.1 to 17.7 million t/yr. This is equivalent to an estimated loss between US\$1.1 and US\$4.7 billion annually.

In India, this pest has devastated nearly 1,700 ha of maize since its first report in May 2018 at Karnataka (Ganiger et al. 2018). Crop losses are reported from 10 states with percentage plant infestations ranging from 9.0 to 62.5% at various locations (Shylesha et al. 2018). Larvae have caused 34 to 73% damage (Cruz et al. 2012). Chemical pesticides are routinely used to control pest infestations. Costa et al. (2005) concluded that two applications of insecticides are needed to totally control *S. frugiperda* infestations in maize and sorghum (*Sorghum bicolor* [L.] Moench), irrespective of the damage levels. They proposed that the first application should be at 19 d after plant emergence (e.g., vegetative growth stage V4 with 4 leaves completely expanded), followed by a second application at 47 d after emergence, irrespective of pest density. However, indiscriminate use and application insecticides pose dangers to workers, nontarget organisms, and environmental integrity (Hunt et al. 1999, Tinoco-Ojanguren and Halperin 1998). Varying degrees of resistance to several insecticides also have been detected (Pacheco-Covarrubias 1993).

Pheromone Use in Fall Armyworm Management

Insect behavior is mediated by semiochemicals. Sex pheromones are intraspecific compounds regularly used by noctuid males to seek and locate females who disperse pre-reproductive pheromonal cues (Achiraman and Archunan 2002, 2005; Buda et al. 2012; Cardé and Minks 1997; Rajanarayanan and Archunan 2011; Rasmussen et al. 1997). Lepidopteran female moths typically produce species-specific sex pheromones in a pheromone gland to attract males over long distances (Cardé and Baker 1984, Cardé and Haynes 2004, Cardé and Minks 1997, Tamaki 1985). Because moths are nocturnal, a reliable sexual communication system between females and males is essential for the mating and reproduction of a species (Cardé and Haynes 2004, Löfstedt 1990). Sex pheromones might also be used to manage populations of lepidopterans. Herein, we provide a review of available scientific literature on the potential use of pheromones for *S. frugiperda* management. Those tactics include monitoring, mass trapping, and mating disruption.

Components of the fall armyworm sex pheromone were identified in previous investigations (Descoins et al. 1988, Malo et al. 2002, Meagher 2001, Meagher and Mitchell 1998, Warthen and Jacobson 1967). In a laboratory bioassay, Sekul and Sparks (1967) reported a mating response was induced in fall armyworm males to monitor the isolation and identification of the sex pheromone, (Z)-9-tetradecen-1-ol acetate (Z9-14:Ac), from fall armyworm females. However, subsequent tests showed that this compound was an ineffective lure for fall armyworm males in the field (Mitchell and Doolittle 1976, Sparks 1980). However, mating disruption tests showed that this compound reduced mating among fall armyworms when it was allowed to evaporate into the atmosphere (Mitchell and McLaughlin 1982). A second compound, (Z)-9-dodecen-1-ol acetate (Z9-12:Ac), was isolated and identified from fall armyworm females (Sekul and Sparks 1976) and, when used either alone or in a blend with Z9-14:Ac, was proven to be a good practical lure for fall armyworm males when used in sticky traps (Jones and Sparks 1979, Mitchell 1979). However, relatively large quantities (e.g., 5–10 mg on a rubber septum) of Z9-12:Ac were required for it to be effective, and the baits were effective in the field for only 1 to 2 wk (Mitchell et al. 1983). Sparks (1980) reported that two additional compounds were isolated from fall armyworm ovipositors; however, he did not reveal their identity and stated that they did not improve the effectiveness of Z9-12:Ac as a lure.

Monitoring. The fall armyworm sex pheromone was reported as a mixture of (Z)-9-tetradecen-1-ol acetate ((Z)-9-4:Ac), (Z)-7-dodecen-1-ol acetate ((Z)-7-12:Ac), (Z)-9-dodecen-1-ol acetate ((Z)-9-12:Ac), and (Z)-11-hexadecen-1-ol acetate ((Z)-11-16:Ac) in the ratio of 81:0.5:0.5:18 (Tumlinson et al. 1986). These four components have been artificially formulated, and this blend has been quite effective in monitoring populations of *S. frugiperda* in the United States and the Caribbean Basin (Mitchell et al. 1985). Commercially available fall armyworm sex pheromones have been shown to be a useful tool for monitoring fall armyworm males (Adams et al. 1989, Gross and Carpenter 1991, Mitchell et al. 1989).

Pheromone traps are amenable to monitoring because they are species specific, require little maintenance, and can be operated by nonentomologists (Wall 1990).

Their main limitations rest with the interpretation of the catches, particularly the relationship of trap-catch to population density. Monitoring fall armyworm populations with pheromone traps has been very successful in determining the timing and number of pesticide applications (Adams et al. 1989; Cruz et al. 2012; Malo et al. 2001, 2004). In some cases, the four-component blend of the pheromone was replaced by a mixture of Z9-14:OAc (99.42%) and Z7-12:OAc (0.58%) without losing the effectiveness of the blend as a lure (Mitchell et al. 1985). The use of this formulation in several commercial dispensing systems (e.g., rubber septa, microtubules, polyvials, plastic laminates, and polyethylene tubes) has revealed its usefulness for survey purposes.

Monitoring using trap captures can provide a basis for decision making in management of the fall armyworm. In Brazil, Cruz (1995) noted that management of *S. frugiperda* is largely by the application of chemical insecticides against larval stages, usually without the consideration of the environmental consequences. Using pheromone traps to monitor fall armyworm adult activity provided an effective means of determining the number of pesticide applications necessary to control the larval infestations in maize (Cruz et al. 2010b). A delay in the timing of an insecticide application decreased insecticide effectiveness in reducing larval infestations and did not significantly reduce larval feeding damage. Consequently, the relationship between maize yield and the time when a conventional insecticide is applied to control *S. frugiperda* larvae was linear and negative. Hence, adequate timing of application of a chemical insecticide based on adult captures in pheromone traps can reduce the degree of pest-mediated plant damage and protect maize yield. Cruz et al. (2010a) concluded that when larval infestation occurs shortly after maize seedling emergence, which commonly occurs in Brazil, the efficiency of the insecticide and the maize grain yield is directly and inversely related to insecticide application time, respectively. They, furthermore, concluded that the application of insecticide is determined by three criteria: (1) the number of trap-caught moths in a Delta-type trap with a commercial sex pheromone lure placed soon after plant emergence in the center of the crop target area, (2) the percentage of plants exhibiting pinhole-type damage (10% or 20%), and (3) the percentage of plants exhibiting shot hole-type damage (10% or 20%) compared with a check plot without any control measures. They found that, compared with other approaches, calculating the number of moths caught using traps is the most effective approach to determine the insecticide application on maize to control the fall armyworm infestation. We also found that Spinosad, in combination with pheromone traps, resulted in 490% larval mortality, whereas control plots experienced a yield reduction of 39% owing to fall armyworm larval damage (M.M. and J.S.K., unpubl. data).

Mass trapping. Mass trapping technique uses species-specific chemical lures that attract and confine insects to traps where they die. The density and efficacy of the traps and the attractant power of the lures should be sufficient to catch high levels of insects to reduce the adult populations and thus subsequent economic damage to crops. This technique has been used to control a variety of agricultural, orchard, and forest pests. More than 200 reports, cited from 1970 to 2005, are of the use of mass trapping of lepidopteran pests; yet, only a few studies have focused on *Spodoptera* spp. (El-Sayed et al. 2006). For example, mass trapping of fall armyworm and *S. sunia* Guenée in Costa Rican melon fields was implemented in

1992 to maintain low pest populations and reduce expensive applications of *B. thuringiensis* for pest management (Andrade et al. 2000). The pheromone was deployed in 4–5 traps/ha to more than 2,000 ha of melon fields, resulting in a lowering of the number of *B. thuringiensis* applications by 30–70%. In experiments conducted for optimization of these treatments, the binary combination of Z7-12: OAc and Z9-14: OAc was found to be at least 109 times more attractive than other commercial lures (Andrade et al. 2000).

Mating disruption. As a management tactic, mating disruption aims to disrupt the intraspecific chemical communication thereby interrupting normal mating behavior. Theoretically, this is accomplished by inundating an area with synthetic sex pheromone, thereby causing confusion in mate-seeking to reduce the insect's probability of successful mating and reproduction (Cardé and Minks 1995). Such disruption can be achieved using both attractive and nonattractive pheromone blends. The area in which mating disruption is being used for pest management has increased almost exponentially since the 1990s. In 2010, that crop area had increased to 770,000 ha worldwide (Ioriatti et al. 2011, Witzgall et al. 2010).

One must be aware of the constraints of the technique to use it most effectively. Gut et al. (2004) provided a detailed description of such constraints. The success of mating disruption for a particular pest is impacted by biological and ecological factors (e.g., pest's host specificity, dispersal capacity, and population density), male response to pheromones (e.g., whether males are susceptible to adaptation or habituation), chemical characteristics of the pheromone (e.g., evaporation rate and propensity to adhere to surfaces), and the physical environment (e.g., effects of environmental conditions, such as heat and wind, plot size and shape, and site topography). Taking these factors into account, researchers can choose the most effective mating disruption formulations and application techniques based on the target insect and treatment location.

Limitations

Weather parameters. Environment can greatly affect the size of the trap catch by influencing both the activity of the insect and the relative performance of the trap. The interpretation of trap catch data is often difficult because of confounding effects of the environment and the interaction between insect activity and trap performance (Dent and Pawar 1988). If a consistent relationship is found to exist between trap catches and weather parameters, pheromone traps can be used to indicate when a field should be scouted more intensively to determine the need to initiate management measures. Prasannakumar et al. (2011) reported a significant difference in *S. litura* (F.) moth catches across different weeks. The trap catches lowered the damage caused by the insect. However, the performance of the pheromone traps and lures and the activity of the pest were influenced by several weather-related factors, especially maximum and minimum temperature, evaporation, and wind speed, which had a positive effect on the trap catches and percent defoliation caused by the pest. Basavaraj et al. (2013) found that pheromone trap catches of *Heliothis armigera* (Hübner) were negatively correlated with minimum temperature ($r = -0.671$) and morning relative humidity ($r = -0.491$) of the corresponding week. Multiple linear regression equations revealed that the weather

parameters of corresponding week influenced the moth catches in traps containing *S. litura* and *H. armigera* lures to 25.7% and 50.6%, respectively.

Strain variation. *Spodoptera frugiperda* is a migratory, polyphagous pest of a variety of crops throughout the Nearctic and Neotropical Western Hemisphere (Luginbill 1928, Sparks 1979). The species is composed of two morphologically identical strains that are defined by their host plant preferences (Nagoshi and Meagher 2004a, b). One strain prefers corn and sorghum (corn strain) and the other prefers rice and forage grasses (*Cynodon* spp.; Pashley 1986, Pashley et al. 1985). The two strains also can be distinguished by genetic markers (Levy et al. 2002, Nagoshi and Meagher 2003, Nagoshi et al. 2006). Previous studies have shown that, in agricultural habitats, pheromone trapping routinely attracts males of both strains, although the proportion varies on the basis of the dominant plant type, indicating that the strains overlap substantially in their distribution and are mutually attracted to a common pheromone source (Meagher and Nagoshi 2004).

The pheromone composition of the two strains differs significantly. Corn strain females contained significantly higher amounts of the second most abundant pheromone compound Z11-16:Ac (m) and significantly lower amounts of most other compounds compared with rice strain females. When females were injected with polybutadiene acrylonitrile (PBAN) before their glands were extracted, the differences between the pheromones of the two strains were less pronounced but still statistically significant. The pheromone composition of hybrid females showed a maternal inheritance of the major component Z9-14:Ac (M) and of Z11-16:Ac (m). Most other compounds also showed an inheritance indicating genetic dominance of the corn strain. Swamy et al. (2018) and Nagoshi et al. (2019) reported that the samples collected from wild population consisted of more than 90% of "R" strain and primarily fed on maize. Srinivasan et al. (2018) reviewed strain variation in African pest population and raised the question whether the rice strain on maize and the maize strain on maize maintained reproductive isolation or mated with each other when they are found in the same location. Hence, for the most effective use of pheromones, it is necessary to identify the strains, their pheromone composition, and the responses of male fall armyworm moths to pheromone blends resembling those of maize- and rice-strain females in major maize-producing locations of Africa where the pest is already present.

Geographical variation. Blends that proved successful in trapping male fall armyworm moths in North America and Europe performed poorly when tested in Brazil, Costa Rica (Andrade et al. 2000), and Mexico (Malo et al. 2001). Moth sex pheromones are species-specific communication systems for mate location and would be under intense stabilizing selection when selection pressures are similar for all populations (Hansson et al. 1990). However, significant intraspecific geographic variation in the pheromone composition of insects, especially moths, has previously been reported (Andrade et al. 2000, Anglade et al. 1984, Batista-Pereira et al. 2006, El-Sayed et al. 2003, Hansson et al. 1990, Lofstedt 1990, Lofstedt et al. 1986, Miller et al. 1997, Toth et al. 1992). These are probably the result of varied selection pressures acting on allopatric populations of the same species. Thus, the failure to effectively capture Brazilian male fall armyworm moths with European and North American lures might be attributed to the geographic variability in the sex pheromone. Furthermore, the two morphologically indistinguishable strains of fall

armyworm (Levy et al. 2002; Pashley 1986; Pashley et al. 1985, 1992) also occur in Brazil (Busato et al. 2002).

Conclusion

The female-produced sex pheromone of *S. frugiperda* is commercially available in several countries. Pheromones have been a useful tool for monitoring male populations. Knowledge of when and where adult pests are active and abundant provides a sensitive early-warning system to enable field sampling and/or control measures to be initiated at the appropriate time. Mass trapping of insect using pheromones is an effective, environmentally friendly, and relatively inexpensive means of suppressing a specific pest population. It is an effective and ecologically acceptable means of control for the *S. frugiperda*. Most control measures against *S. frugiperda*, when adopted, involve the spraying of chemical insecticides, usually without consideration of the environmental consequences. The timing of insecticide application is a key factor in determining its efficiency. Based on the number of adult pests caught in pheromone trap with *S. frugiperda* lure, insecticide application becomes effective, thereby facilitating economic usage of inputs in the management of fall armyworm. Further ecologic implications could include the conservation of natural enemies with minimum disturbance to the ecosystem leading to a sustainable crop production.

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