ABSTRACT. The fall armyworm, Spodoptera frugiperda (J. E. Smith), is a sporadic pest with a diverse host range. This insect occasionally causes damage to cotton across the United States from the Rocky Mountains to the East Coast. Fall armyworm has been problematic in cotton due to its overall tolerance to many insecticide use strategies and difficulty in finding and surveying field infestations with sampling protocols. A review of insect biology, description of life stages, behavior and host strain identification, injury to cotton, and potential management options for the southeastern United States are presented.

Key Words: Spodoptera frugiperda, Gossypium hirsutum, cotton, transgenic cotton, insecticide

The fall armyworm, Spodoptera frugiperda (J. E. Smith), has been classified as a sporadic pest due to its migratory behavior. This species does not enter diapause, so it migrates from warmer climates such as southern Florida, Caribbean Islands, southern Texas, Mexico, and coastal areas of southern Georgia, Alabama, Mississippi, and Louisiana, northward across the United States annually (Luginbill 1928, Sparks 1979, Knipling 1980, Ashley et al. 1989, Adamczyk 1998). Fall armyworm movement each year generally creates sporadic problems across multiple crops, including cotton, Gossypium hirsutum (L.). Fall armyworm outbreaks and subsequent damage can be unpredictable. When outbreaks do occur, the severity of the problem is compounded by the ability of fall armyworm to damage a range of vegetative to reproductive plant structures, creating the opportunity to cause devastating crop losses.

Insect Biology

The fall armyworm has several generations per year, with the life cycle consisting of egg, six to seven larval instars, pupa, and adult. In areas of the southern United States, six or more generations per year may occur (Luginbill 1928). Completion of the life cycle usually takes about 4 wk in Southern cotton production regions, but can take as long as 12 wk during periods of low temperatures in the spring and fall (Vickery 1929). Eggs are generally laid on the abaxial (underside) surface of leaves; however, when oviposition frequency in a cotton field is high, females will oviposit eggs on all plant structures (Luginbill 1928, Sparks 1979, Ali 1989). The most preferred location for oviposition is on leaves emerging directly from the main stem in the middle to lower portion of the plant canopy (Ali 1989).

Upon eclosion, neonates consume the egg mass from which they hatched. Larvae then disperse in all directions, beginning to feed on vegetative tissue. Later instars prefer to feed on reproductive structures such as squares (flower buds) and bolls. Larval feeding and adult activity most frequently occurs at night, but can occur in late evening and early morning. Number of instars can range from six to seven depending on environmental conditions and availability of food. The final instar will consume a greater quantity of food than all previous instars combined (Luginbill 1928). The length of time for larval development (hatching to pupation) varies based on temperature and environmental conditions, but can range from 11 to 50 d (Luginbill 1928, Hogg et al. 1982). At 25°C larval development on cotton takes 22 d (Pitre and Hogg 1983).

Larvae fall from the plant and burrow into soil to a depth of one to three inches in the soil, remain in a prepupal state for 2–4 d, and pupate there for ~7–10 d (Luginbill 1928, Pitre and Hogg 1983). Depth of pupation is dependent upon factors such as soil texture, soil moisture, and soil temperature (Sparks 1979). As moths emerge from the soil, they can mate locally or migrate up to 300 miles before mating and ovipositing (Ashley et al. 1989). The North American geographical range of fall armyworm exceeds the boundaries of the U.S. cotton production areas and spans areas from the Rocky Mountains to the East Coast and as far north as Canada.

Description of Life Stages

Egg. The egg of the fall armyworm is “oblate-spheroidal” (0.39 mm in height, 0.47 mm in diameter; Luginbill 1928). Freshly oviposited eggs are initially greenish gray in color, and become progressively darker with age. Approximately 12 h after deposition, eggs appear brown, and become nearly black just prior to larval eclosion (Fig. 1A–C; Luginbill 1928). Eggs will, at times, be covered with a “downy” material (dense covering of scales) from the moth. Oviposition can be initiated during the early evening hours. Eggs are laid in masses ranging in size from just a few to hundreds and will usually hatch within 4 d under optimal conditions (Dew 1913, Luginbill 1928, Sparks 1979).

Larva. When first instars eclose (L1), larvae are colored off-white to yellow with black head capsules, and small black spots from which primary setae protrude (Fig. 2A and B). Larvae darken as they feed and appear greenish in color (Luginbill 1928). The proceeding two larval instars (L2–L3) are similar in color to earlier instars just after molting from the preceding instar, but typically darken just prior to molting to the proceeding instar. The three final instars (L4–L6) are typically dark in color, with varying color patterns depending on their diet and other factors (Figs. 3–5). The larva displays a prominent inverted “Y” on the head capsule (Fig. 6). The head capsule is traditionally dark in color, ranging from brown to black. Later instars (L4–L6) lack primary setae and are generally smooth (Oliver and Chapin 1981). Older larvae may range from light green to brown or even black in color. Markings on the larvae can include a noncontinuous white line in the mid-dorsal area, as well as yellow and red “flecking” on the venter (abdomen). Larvae also have a distinct pattern of four “dots” on the eighth abdominal segment (Fig. 7). Fall armyworm larvae possess tooth-like projections on their mandibles. The pupal case has an orange-brown appearance, typical of most Noctuids (Fig. 8), and turning darker as it ages. Larval length ranges from 1.68 mm for first instars to 34.15 mm for sixth instars. Head capsule width ranges
from 0.314 mm for first instars to 2.78 mm for sixth instars (Luginbill 1928).

**Adult.** Fall armyworm adults (moths) have a wing span of about 1.5 inches (3.81 cm). The upper portion of the forewings are a mottled dark gray, with a distinctive white spot near the dorsal tip, or apex, of the wing, while the lower portion of the forewings is a light gray to brown color (Fig. 9; Oliver and Chapin 1981). The hind wings appear light gray to white. Male adults are often confused with yellowstriped armyworms, Spodoptera ornithogalli (Gueneé). Yellowstriped armyworm adults have crescent-shaped markings on the forewings resulting in more contrast in color shades compared to fall armyworm male forewings. Fall armyworm female adults also may be confused with beet armyworms, Spodoptera exigua (Hübner). Beet armyworm adult forewings have a paler ground color with a pale round orbicular spot,
while female fall armyworm adult forewings have an oval dark-centered orbicular spot (Todd and Poole 1980). Fall armyworm moths have filiform (threadlike) antennae common in Noctuids. These moths are generally most active at night (Oliver and Chapin 1981).

Behavior and Host Strains

The behavior of fall armyworm is complicated due to the existence of two separate, though morphologically identical, strains. These strains are referred to as “host specific” reflecting their host plant preferences. They are commonly referred to as the rice-strain (R-strain) and
corn-strain (C-strain; Quisenberry 1991, Nagoshi and Meagher 2004). Pashley (1986) initially classified fall armyworm populations being composed of sibling species, or strains. Fall armyworms of the R-strain prefer rice, *Oryza sativa* (L.), and bermudagrass, *Cyndon dactylon* (L.) Pers. and other Graminaceae, whereas the C-strain prefers cotton and corn, *Zea mays* L.

Carbon isotope ratios in adults have indicated that the C-strain represents the majority of the fall armyworm subpopulation in a cotton environment. The C-strain develops in substantial numbers compared to the R-strain (Nagoshi et al. 2007). Interstrain mating can occur, but variability exists in mating preference. R-strain females prefer to accept C-strain males, resulting in mixed populations, but C-strain females and R-strain males appear to be reproductively incompatible (Whitford 1988, Quisenberry 1991).

Genetic markers and allozyme variants are used to distinguish the two strains (Nagoshi and Meagher 2004). Differences between these two strains have a profound effect on crop protection strategies due to variation in several life history characteristics between the two strains. Differences in larval development on host plants, mating behavior, use of food resources, resistance to insecticides, and variation in susceptibility to plants expressing *Bacillus thuringiensis* (Bt) proteins can influence management tactics (Veenstra 1994, Nagoshi and Meagher 2004).

**Non-Cotton Crop Hosts**

Fall armyworm is a generalist pest on a variety of plants, being reported on >80 species in 23 families (Pashley 1988). A number of these plant species include crops such as corn; sorghum, *Sorghum bicolor* (L.); forage grasses; turf grasses; rice; cotton; and peanut, *Arachis hypogaea* (L.). However, this species shows preferences for grasses such as corn, sorghum, and bermudagrass, which are C₄ plants, as opposed to C₃ plants such as cotton or soybean, *Glycine max* (L.) Merr. (Luginbill 1928, Buntin 1986, Wittwer 1995, McCarty and Miller 2002, Lewter et al. 2006, Nagoshi et al. 2007).

**Injury to Cotton**

Early instars (L1–L3 stages) are found in the lower-to-mid levels of the plant canopy, where they feed on foliage (Cook et al. 2004). Larvae in the first few instars “skeletonize” (partially feed on) leaves near the egg mass from which they eclosed (Fig. 10). Early in the cotton-growing season, later instars have the potential to destroy terminals on cotton seedlings (Leigh et al. 1996). Older instars (L4–L6 stages) are usually present within the lower regions of the plant canopy, feeding on fruiting structures (Cook et al. 2004). Larger larvae feed internally in fruiting structures making successful chemical control more difficult. This problem is exacerbated due to increased tolerance to insecticides during later larval instars (Cook et al. 2004). Cotton bolls at any age are susceptible to fall
Management Strategies in Cotton

Overview. The fall armyworm can be a very destructive pest during agricultural cropping seasons due to its wide host range and geographical distribution (Knipping 1980). Density-dependent biological factors are likely negated by the migratory nature of the pest, allowing it to escape many predators, parasitoids, and entomopathogens. A suppression program implemented in specific overwintering areas could potentially reduce the fall armyworm problem in the southern United States.

Monitoring for fall armyworm populations can be a helpful tool in assessing populations. Colored traps have been evaluated for collecting fall armyworm moths to determine the effectiveness of various colors as visual cues for moth capture. The standard bucket trap with a green canopy, yellow funnel, and white bucket was the most effective at attracting fall armyworm moths to determine the effectiveness of various colors for moth capture. The standard bucket trap with a green canopy, yellow funnel, and white bucket was the most effective at accomplishing this goal (Meagher 2001).

Currently there is little information available concerning fall armyworm sampling and monitoring techniques related to management strategies. Recommendations for initiating the use of a control strategy are limited to “treat when egg masses or small larvae appear on plants” (Beuzelin et al. 2014). Sampling for fall armyworm infestations in cotton is generally accepted as those recommendations used for heliothines (tobacco budworm, Heliothis virescens (F.), and bollworm, Helicoverpa zea (Boddie)), where cotton fruiting structures are evaluated. Initiation of a management tactic is warranted using triggers of pest populations in at least three ways: 1) optimization of naturally occurring diseases, 2) introduction and colonization of pathogens into insect populations as natural regulatory agents, and 3) repeated applications of pathogens as microbial insecticides (Gardner and Fuxa 1980). Several microbial pathogens have been studied in hopes of utilizing them to control fall armyworm populations. Viruses demonstrate limited efficacy against fall armyworm, but are not temporally effective, allowing for significant damage prior to insect mortality (Sparks 1986). Inconsistent results have been documented in field studies evaluating the use of entomogenous pathogens to suppress fall armyworm on corn and cabbage. Fall armyworm-specific Bt isolates have not been developed for commercial spray formulations (Sparks 1986), but the Cry1F Bt protein is generally considered to be more toxic to fall armyworm than other Cry proteins (Tindall et al. 2006).

Current literature does not describe predators that attack fall armyworm. Many predators attack fall armyworm eggs and larvae, but there is no summary available to describe these species (Lewis and Nordlund 1980, Sparks 1986). While predators have an effect on fall armyworm survival and development, their role is largely undermined by parasitoids, which are more efficient in affecting fall armyworm populations. Previous attempts to utilize fall armyworm parasitoids generally have been unsuccessful (Gross and Pair 1986, Sparks 1986).

Conventional Chemical Insecticide Use Strategies. Fall armyworm control usually has been accomplished incidentally with foliar insecticide applications used to control heliothines (Table 1). However, fall armyworm larvae generally are not discovered until they are late instars, and producers prefer to manage an infestation with a single insecticide application. Successful fall armyworm control usually necessitates the use of insecticides at the upper range of their labeled rates (Adamczyk and Sumerford 2000). However, once a fall armyworm population becomes established in a field, two applications are often needed for successful management (Sullivan et al. 1999). Dispersion of fall armyworm larvae lower in the plant canopy makes them more difficult to control. This problem is due to the difficulty in insecticide applications penetrating the plant canopy to the location of larvae (Adamczyk et al. 1997, 1999; Cook et al. 2004). Fall armyworm has developed resistance to several classes of insecticides, including pyrethroids (cypermethrin, fenvalerate, fluvalinate, and permethrin), organophosphates (chlorpyrifos, methyl parathion, diazinon, thiodicarb, and profenofos (Table 1). Fall armyworm larvae are likely negated by the migratory nature of the pest, allowing it to escape many predators, parasitoids, and entomopathogens. A suppression program implemented in specific overwintering areas could potentially reduce the fall armyworm problem in the southern United States. Fall armyworm sampling and monitoring techniques related to management strategies are limited to “treat when egg masses or small larvae appear on plants” (Beuzelin et al. 2014). Sampling for fall armyworm infestations in cotton is generally accepted as those recommendations used for heliothines (tobacco budworm, Heliothis virescens (F.), and bollworm, Helicoverpa zea (Boddie)), where cotton fruiting structures are evaluated. Initiation of a management tactic is warranted using triggers of pest populations in at least three ways: 1) optimization of naturally occurring diseases, 2) introduction and colonization of pathogens into insect populations as natural regulatory agents, and 3) repeated applications of pathogens as microbial insecticides (Gardner and Fuxa 1980). Several microbial pathogens have been studied in hopes of utilizing them to control fall armyworm populations. Viruses demonstrate limited efficacy against fall armyworm, but are not temporally effective, allowing for significant damage prior to insect mortality (Sparks 1986). Inconsistent results have been documented in field studies evaluating the use of entomogenous pathogens to suppress fall armyworm on corn and cabbage. Fall armyworm-specific Bt isolates have not been developed for commercial spray formulations (Sparks 1986), but the Cry1F Bt protein is generally considered to be more toxic to fall armyworm than other Cry proteins (Tindall et al. 2006).

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<table>
<thead>
<tr>
<th>Active ingredient</th>
<th>Trade name</th>
<th>IRAC MoA classification$</th>
<th>Rate per acre</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorantraniliprole benzoxathion</td>
<td>Prevathon 0.43SC</td>
<td>28</td>
<td>9.2–11.3 fl. oz</td>
</tr>
<tr>
<td>Emamectin benzoate</td>
<td>Denim 0.16EC</td>
<td>6</td>
<td>8–12 fl. oz</td>
</tr>
<tr>
<td>Flu bendiamide</td>
<td>Belt 4SC</td>
<td>28</td>
<td>2–3 fl. oz</td>
</tr>
<tr>
<td>Indoxacarb</td>
<td>Steward 1.25SC</td>
<td>22A</td>
<td>9.2–11.3 fl. oz</td>
</tr>
<tr>
<td>Methomyl</td>
<td>Lannate 2.4LV, Lannate 90SP</td>
<td>1A</td>
<td>1.5–2.25 pt, 0.5–0.75 lb</td>
</tr>
<tr>
<td>Methoxyfenozide</td>
<td>Intrepid 2F</td>
<td>18</td>
<td>4–10 fl. oz</td>
</tr>
<tr>
<td>Novaluron</td>
<td>Diamond/ Mayhem 0.83EC</td>
<td>15</td>
<td>6–12 fl. oz</td>
</tr>
<tr>
<td>Profenofos</td>
<td>Curacron 8E</td>
<td>1B</td>
<td>0.75–1.0 pt</td>
</tr>
<tr>
<td>Spinosad</td>
<td>Tracer 4SC</td>
<td>5</td>
<td>2.144–2.88 fl. oz</td>
</tr>
<tr>
<td>Thiodicarb</td>
<td>Larvin 3.2F</td>
<td>1A</td>
<td>1.5–2.25 pt</td>
</tr>
</tbody>
</table>

Adapted from Carson et al. (2014) and Beuzelin et al. (2014). $ IRAC MoA, Insecticide Resistance Action Committee mode of action classification (http://www.irac-online.org); 1A, 1B, acetylcholinesterase inhibitors; 5, nicotinic acetylcholine receptor allosteric activators; 6, chloride channel activators; 15, inhibitors of chitin biosynthesis, type 0; 18, ecysdane receptor agonists; 22A, voltage-dependent sodium channel blockers; 28, ryanodine receptor modulators.

Biological Control. There are 53 species of parasites, representing 43 genera and 10 families that attack fall armyworm globally (Ashley 1979, Sparks 1986). Entomogenous pathogens can suppress fall armyworm populations in at least three ways: 1) optimization of naturally occurring diseases, 2) introduction and colonization of pathogens into insect populations as natural regulatory agents, and 3) repeated applications of pathogens as microbial insecticides (Gardner and Fuxa 1980).

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malathion, and trichlorfon), and carbamates (methomyl, carbaryl, and thiodicarb; Wood et al. 1981, Yu 1992, Adamczyk et al. 1999, Al-Sarar et al. 2006, Whalon et al. 2008). In addition, common insecticides most recently registered are increasingly target-specific, further reducing incidental fall armyworm control when treating for other non-Lepidopteran pests.

Limited field research exists on control of fall armyworm with many of the newly registered insecticides. Research is needed to determine effective control rates with new insecticides specific to fall armyworm. In laboratory studies evaluating field-treated cotton plant structures, fall armyworm mortality was generally greater with new insecticides (chlorantraniliprole, flubendiamide, and spinetoram) compared to traditional insecticides (lambda-cyhalothrin and novachlor) when applied at full rates to non-Bt cotton (Hardke et al. 2014). In 2005, Dow AgroSciences released a similar technology in their WideStrike varieties. WideStrike varieties produce the same Cry1Ac Bt endotoxin in both Bollgard and Bollgard II, but also produce a Cry1F endotoxin (Adamczyk and Gore 2004, Adamczyk and Mahaffey 2007, Siebert et al. 2007, Naranjo et al. 2008). In field trials WideStrike exhibited significantly fewer abscised bolls than non-Bt cotton, while no significant differences were observed for damaged bracts, larval-penetrated bolls, or number of fall armyworm larvae. In laboratory experiments, larval mortality on WideStrike tissue was significantly greater than the non-Bt treatment (Tindall et al. 2006). It will become increasingly important to monitor the effects of this technology on fall armyworm, as there are already reports of unexpected fall armyworm survival on Cry1F corn in the southeastern United States and in Puerto Rico (Huang 2014). Shifts in fall armyworm susceptibility to Cry1F, coupled with its limited susceptibility to Cry1Ac, may create potentially serious management issues in the future.

Bollgard III (Monsanto) and WideStrike 3 (Dow AgroSciences) are currently under development and will include the vegetative insecticidal protein, Vip3A. In 2014, Bayer CropScience released TwinLink varieties. TwinLink cotton produces Cry1Ab and Cry2Ae endotoxins. Also under development, TwinLink Plus combines the Cry1Ab and Cry2Ac proteins with Vip3A. Laboratory assays have examined fall armyworm larvae fed squares and flowers of cotton expressing Vip3A and Cry1Ab proteins (Hardke et al. 2009). In these assays, no larvae were capable of surviving on cotton tissue expressing the Vip3A protein. Fall armyworm larvae fed leaf tissue from WideStrike 3 and TwinLink Plus cotton had higher levels of mortality compared to non-Bt cotton, but did not significantly differ from WideStrike, TwinLink, or Bollgard II (Williams et al. 2014). These new technologies have the potential to improve fall armyworm management in Southern cotton. As with many conventional chemical control strategies, fall armyworm susceptibility varies among Bt technologies used in cotton varieties. Therefore, each technology should be scouted and managed based upon expected results and real-time field observations.

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