The Fall Armyworm, **Spodoptera frugiperda** (J.E. Smith)[1]: A Review F.B. Peairs and J. L. Saunders [2,3].

A. Taxonomy.

The genus **Spodoptera**, a group of armyworms, includes serious worldwide pests of maize (Ortega 1974) and other crops (Lamb 1974). The genus was erected in 1852 by Guenee (cited in Luginbill 192 8) and, after the revision of Zimmerman (1958), includes species formerly in the genus **Laphygma.** Important species include **S. exempta** (Walker), the African armyworm, **S. exigua** (Hubner), the beet armyworm, and **S. frugiperda** (J.E. Smith), the fall armyworm. The distribution of **S. exempta** is South-east Asia, Australia and Africa. **S. exigua** is found in Africa, Asia, Australia and North America. **S. frugiperda** is found only in the Americas. Keys to the mature larvae of the North American species were published by Levy and Habeck (1976).

The insect was first described in 1797 as **Phaleana frugiperda** (Smith and Abbot 1797, cited in Luginbill 192 8). In 1852 , Guenee (cited in Luginbill 1928) placed **frugiperda** in the genus **Laphygma.** Although several other names were proposed, **Laphygma frugiperda** (S. and A.) was accepted until Zimmerman (1958) synonimized **Laphygma** and **Spodoptera.**

The larvae of the fall armyworm are distinguished among noctuid pests by a white inverted Y on the head capsule and longer, more prominent black hairs arising from black tubercules. The adults appear like cutworm moths, but have whitish spots at the tips of the front wings (Metcalf, Flint and Metcalf 1964). All life stages have been figured by Etcheverry (1957).

1/ Lepidoptera, Noctuidae

2/ The review of the literature was completed January 30, 1977, with some additions being made during 1978. The review is limited to papers reporting original results. Because of their number, only some of the more recent chemical control papers have been cited.

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B. Distribution.

Luginbill (192 8) stated that, apart from the Gulf States and Florida, all U.S. records of the fall armyworm (FAW) were due to summer migration from tropical and subtropical areas. The extent of this migration depended on the weather. Cold wet springs often preceded severe outbreaks in the southern states. In 1912 , all states east of the Rocky mountains, excluding North Dakota, and parts of Canada reported this insect. A september, 1973 infestation in Sault Ste Marie, Ontario probably came from Mississippi (Rose **et al.** 1975). The insect was permanent in small parts of Florida and Texas, but could survive mild winters in all of Florida, and larger part of Texas, and southern Louisiana (Snow and Copeland 1969). Trapping results in Florida indicated that the FAW could survive winter temperatures greater than 15.5°C (Tingle and Mitchell 1977). In Mexico, the fall armyworm was most important in the states of Guerrero, Michoacan, Morelos, Oaxaca and Veracruz and the territories in Yucatan (Sifuentes **et al.** 1969). Southern distribution was to northern Argentina and Chile (Ortega 1974).

C. Host Plants.

Luginbill (1928) reported the FAW from over 60 kinds of fruits, vegetables, grasses and weeds. Vickery 1929 observed the FAW on 16 different crops and grasses. Maize and sorghum and other grasses were preferred, but cotton, cabbage, alfalfa, peanuts, beans and soybeans were also attacked.

D. Life History.

This is, unless otherwise indicated, a composite of the observations presented by Luginbill (1928) and Vickery (1920) Quantitative observations are in Table 1. Oviposition was indiscriminate on hosts, non-hosts or even buildings, the round eggs were deposited in flattened, irregular masses, often composed of several layers of eggs and covered with hairs or scales from the female. The color of the masses varied from pink to dark gray. Newly hatched larvae consumed the egg shells and then dispersed. These larvae were positively phototactic and negatively geotactic. These tropisms were reversed in older larvae which fed in the whorl of maize plants

(Greene and Morril 1970). First-instar larvae were starved for 2 0 to 35 hours without subsequently affecting their life cycle. Older instars were thigmotactic (Morrill and Greene 1973b). In Florida, on the hybrid Dixie 18, 1st–instar larvae were found throughout the upper parts of pretassel plants, while older larvae were found in the whorl and in folded leaves. Larval numbers decreased after tasseling. Larvae on the ears had moved from the tassel (Morrill and Greene 1973a). The FAW completed 6 larval instars and then normally pupated in the soil, although it can pupate in the plant (Burkhardt 1953). The adults were nocturnal and fed on nectar.

One to 2 generations can occur per year where the insect does not overwinter. In Brownsville, Texas, Vickery (192 9) estimated 9 to 11 generations per year. Six generations occurred per year in the Gulf States (Luginbill 1950). In Cuba, 11.5 generations per year predicted, based on a temperature threshold of 12 .29°C (Blahutiak 1970b).

E. Damage and Economic Importance.

Damage is from larval feeding. The lst 3 instars were skeletonizers, while the last 3 ate entire portions of the leaf. First-instar larvae ate about 2 1mm^2 of crabgrass, while the last instar ate about 10,000mm^2 more than the other instars combined (Luginbill 192 8). In maize, apart from defoliating the plant and killing the young plants, the larvae gouged or burrowed into the stalks and ear shanks, causing stalk breakage and ear drop and fed in the ears (Burkhardt 1953). Tassels and silks were attacked (Morrill and Greene 1974).

Yield–loss estimates are scarce for the fall armyworm. Yield increases in maize in Mexico from insecticides applied against *S. frugiperda* were as much as 1 to 2 metric tons per hectare, under experimental conditions (Sifuentes *et al.* 1969, Alvarado R. 1975). In Florida, infesting with up to 20 2nd–instar larvae per plant at different growth stages failed to produce yield loss (Morrill and Greene 1974). Defoliation was less then 30 per cent and no plants were killed. Tassel feeding did not interfere with pollination. In one field with chewed–silk damage, 26 per cent of the ears showed incomplete pollination, with up to one–third of the kernels missing. Hynes (1924) believed that the FAW did not prevent a good maize crop in Trinidad. In the sorghum hybrid RS610, under natural infestation in Oklahoma, Henderson **et al.** (1966) measured yield reductions of 5.4, 10.5 and 19.4 per cent over 3 seasons, due mainly to smaller kernels. The loss was 27.2 per cent, due to smaller and fewer kernels when **Diatraea grandiosella** Dyer (Pyralidae) also attacked the plants.

F. Control.

1. Natural control.

Little is known about the role of abiotic factors in the control of the fall armyworm. Vickery (192 9) emphasized the importance of temperature. On St. Croix, U.S. Virgin Islands, the number of trapped adults increased with the onset of the rainy season (Snow **et al.** 1968).

2. Biological control.

Both Luginbill (1928) and Vickery (1929) gave lists, relative importance and some descriptions of the natural enemies of **S. frugiperda.** The common vertebrate insectivores such as lizards, toads and birds were important. Swainson's hawk, **Buteo swainsonii** (Bonaparte) (Falconiformes) ate an average of 8 larvae per minute during 5-minute observations during an infestation in Texas (Littlefiedl 1973). In Florida, FAW larvae were found in the stomachs of 25.2 per cent of 85 Maynard's red-winged blackbird, **Agelaius phoenicius floridanus** ( ) ( ) examined (Genung **et al.** 1976). Insect predators included **Calosoma** spp. (Carabidae) and **Podisus maculiventris** (Say) (Pentatomidae). **Calosoma** was the most important natural enemy during an outbreak in Virginia (Hofmaster and Greenwood 1949). Hair and scales protected egg masses from **Coleomegilla** sp. and **Cycloneda** sp. (Coccinellidae) feeding in the laboratory (Szumkowski 1952). Competition in the ears of maize with the corn earworm, **Heliothis zea** (Boddie) (Noctuidae) caused FAW mortality in Georgia (Wiseman and McMillian 1969).

The parasitic insects included the Hymenoptera **Ophion bilineata** Say (Ichneumonidae), **Chelonus texanus** Cresson, **Meteorus laphygmae** Viereck, **Apanteles marginiventris** Cresson

(Braconidae). **Trichogramma minutum** Riley (Trichogrammatidae), **Euplectrus comstockeii** Howard, and **E. platyhypenae** Howard (Eulophidae). The important Diptera were the tachinids **Archytas piliventris** Van der Wulp and **Winthemia quadripustulata** (F.). Luginbill stated that the tachinids accounted for most of the FAW mortality, while Vickery stated that **C. texanus** was most important. The laboratory biology of **E. platyhypenae** has been described (Wall and Berberet 1974). Host preference tests showed the fall armyworm to be a suitable host for **Campoletis perdistinctus** (Viereck) (Ichneumonidae) (Lingren **et al.** 1970) and **Talenomus remus** Nixon (Scelionidae) (Wojick **et al.** 1976). Total parasitism in large collections of fall armyworm larvae was determined by dissection (Burrell 1966).

Beauveria globulifera (Speg.) (Fungi Imperfecti) attacked the FAW in Texas (Vickery 1929). A nuclear polyhedrosis virus (NPV) disease of the fall armyworm has been reported (Champan and Glaser 1915). Thirty–seven per cent of the larvae in a collection from Mississippi died from this disease (Allen 1921). A granulosis virus disease was found in larvae from Colombia (Steinhaus 1957). The granulosis virus attacked the fat body and killed the larvae slowly, while the NPV attacked several tissues and killed the larvae quickly (Hamm 1968). The baculoviruses from 3 species of **Spodoptera** were compared (Harrap **et al.** 1977). The virus of **S. littoralis** appeared the least related. The DNA of the **S. frugiperda** NPV was compared to that of **Trichoplusia ni** (Hubner) (Noctuidae) (Summers and Anderson 1972). When 4 **Spodoptera** NPV were compared for genome size and nucleotide sequence homology, that of **S. littoralis** again appeared the least related (Kelly 1977). Resistance in the fall armyworm to the NPV was due to a single gene or a few genes with no dominance (Reichlderfer and Benton 1974). Treating the virus with 3-methylcolanthrene increased virulence 9 times (Reichelderfer and Benton 1973). The virus replicated on FAW cell cultures (Goodwin **et al.** 1970) and the infection process has been described (Knudson and Harrap 1976). Methods for culturing FAW cells and producing the NPV have been described (Gardiner and Stockdale 1975, Vaughn 1976). To aid in diagnosing diseased larvae, the osmolality of the haemolymph of healthy larvae has been determined (Adams and Wilcox 1973).

The NPVs of the corn earworm and the fall armyworm were as effective in combination as DDT on sweet corn in Florida (Young and Hamm 1966). Late–whorl or early–tassel treatment with the NPVs was the most effective, by preventing large, difficult–to–kill larvae from moving to the silks from the whorl at tassel emergence. Larvae that moved to the silks contaminated them with NPV (Hamm and Young 1971).

3. Chemical control.

a. Field studies.

Methomyl, leptophos and tetrachlorvinphos were effective against FAW on sweet corn in Florida. A combination of methomyl and chlordimeform was most effective (Janes 1975). Permethryn (AmbushR) showed contact ovicidal activity equal to that of chlordimeform had less ovicidal activity against the FAW than against several other cotton pests. (Wolfenbarger **et al.** 1974). In the territory of Quintana Roo, Mexico, chlorpyriphos, mephosfolan and monocrotophos were best in increasing yield in maize (Alvarado R. 1975). Harrell **et al.** (1977) compared 4 experimental insecticides, menocrotophos and methomyl applied conventionally and in ULV against FAW on late–planted sweet corn in Florida. Except with methomyl, ULV applications were more effective. The experimentals were not as effective as methomyl or monocrotophos. Numerous other chemical control studies have been reported.

b. Laboratory studies.

An arrestant–feeding stimulant, an extract of maize leaves, failed to increase FAW feeding and therefore insecticide ingestion. The extract did show promise with the corn earworm (Starks **et al.** 1967). Azasteroids were effective in killing or inhibiting developmen when applied to larvae on artificial diet (Svoboda **et al.** 1972).

Uptake of telodrin residues by the fall armyworm was reported (Cox and Bowman 1965). Lethal dosages in the integument ranged from 5.86 to 6.05 ppm. Internally the values were about 3.50 ppm. In last–instar larvae, the lethal dosages could not be correlated with total lipid content, but it was directly correlated with unsaturated fat content. There was no detectable metabolism of telodrin in any of the instars studied.

4. Autocidal control.

Tepa fed to the adults in microgram quantities induced sterility in both sexes (Young and Cox 1965). Males sterilized by tepa could not compete effectively with normal males for females (Young **et al.** 1968). Mating a normal female first with a sterile male and then with a fertile male produced fertile eggs. Egg viability was reduced by 50 per cent by reversing this order (Snow **et al.** 1970). Ten per cent of the tepa persisted in treated moths after 24 hours (Cox **et al.** 1967). **Trichogramma** fasciatum **(Perkins) was reared for 5 generations on eggs from** tepa–sterilized adults (Young and Hamm 1967). Techniques were developed to field–collect adults for sterilization and to feed tepa to large numbers of moths (Harrell **et al.** 1966, Young **et al.** 1969).

Exposing 6–day old pupae to gamma radiation gave 100 per cent mortality in the F_1 generation. Females were more sensitive to irradiation, while male mating activity was reduced (Noblet **et al.** 1969). Adults irradiated as pupae had reduced flying ability (Shepard **et al.** 1968). Irradiating newly emerged adults did not affect lifespan, the ability to search for a mate or the ability to copulate. Competitiveness of the males was reduced by 50 per cent (Snow **et al.** 1972).

5. Host–plant resistance.

Resistance or screening for resistance to the FAW was reported for Bermuda grass (Leuck **et al.** 1968), pearl millet (Leuck **et al.** 1968), peanut (Leuck and Skinner 1971) and grain sorghum (McMillian and Starks 1967). The effects of resistance on the development of **S. frugiperda** has been reported for Bermuda grass (Leuck and Skinner 1970), peanut (Leuck and Skinner 1971) and pearl millet (Leuck 1970). Leuck and Perkins (1972) suggested a method to estimate population reduction due to resistance based on pupal weights.

Wiseman **et al.** (1966) found differences among maize seedlings in the greenhouse. The most resistant were FAW No.1, selected from Antigua 2D x (B10 x B14), and Texas Experimental Hybrid 6417. In North Carolina, resistance in sweet corn was largely due to vigor and tolerance. The insect preferred succulent, healthy plant tissue, but did not distinguish among varieties beyond these characters (Brett and Bastida 1963). Based on an unusual type of feeding at the junction of the leaf sheath and the node in Kansas, the varieties Cuba Honduras 46–J and ETO Amarillo were most resistant (Wiseman **et al.** (1967). Larvae of the fall armysorm strongly preferred excized leaves of maize over those of its near relative, **Tripsacum dactyloides.** Transferring genes from this species into maize might provide useful levels of resistance in maize (Wiseman **et al.** 1967).

Genetic control of resistance to **S. frugiperda** in maize was reported from Georgia (Widstrom **et al.** 1972). Additive genetic effects were highly significant. A program of recurrent selection based on selfed–progeny performance to accumulate genes for resistance until useful levels were attained was recommended. In Mississippi, studies of 4 FAW –resistant lines inbred from Antigua Gpo 2 also indicated the importance of general combining ability in FAW resistance (Williams **et al.** 1978).

Wiseman **et al.** (1966) presented an 11–class rating scale designed to detect small differences in resistance among maize seedlings. They used artificial infestation with lst-instar larvae. Second-instar larvae were used in Florida (Morril and Greene 1974). Chemically separated eggs suspended in a dilute agar solution were used (McMillian and Wiseman 1972), but the technique was not suitable for infesting plants in the field */. Egg masses have been used in other crops (Leuck **et al.** 1968).

The effect of crop fertilizers on resistance and susceptibility in Antigua Gpo 2, Antigua FAW Selection 130-60-90 No./Am was measured on excized leaves in choice situations (Wiseman **et al.** 1973b). Treatments containing nitrogen were the most susceptible. Treatments receiving foliar applications of zinc showed antibiosis and nonpreference reactions. Nitrogen–containing treatments were more susceptible in tests with potted plants. Mortality was highest on phosphorus and potassium–treated plants and lowest on nonfertilized plants (Wiseman **et al.** 1973a). Feeding preferences were affected by foliar sparys containing 14 trace elements,

*/ Wiseman, B. R., N.W. Widstrom and and W. McMillian. 1976. Techniques for evaluating plant resistance in corn to corn earworm and fall armyworm. Second National Biennial Host Plant Resistance Workshop, Tucson, Arizona, 18–19, February.

including sulphur, copper, iron and zinc (Leuck **et al.** 1974). An organic compound extracted from Chinaberry leaves deterred feeding, retarded development and increased mortality when applied to seedlings in the greenhouse (McMillian **et al.** 1969).

G. Feeding Behaviour.

Larvae preferred sorghum, followed in order by maize, tomato, cotton, tobacco and chinaberry (McMillian and Starks 1966). Young maize kernels were preferred over maize silks, sorghum leaves and tomato fruits. Sugar content influenced the choice. The larvae preferred the extracts of young kernels over silks, 4–week old leaves and mature kernels. In a test of extracts of parts of different maize inbreds, larvae preferred leaves more than silks and kernels, but there were significant differences among different inbreds for the same part (McMillian **et al.** 1967). Fourth-instar larvae gained more weight on diets containing younger rather than older leaves or kernels. A greater percentage of kernels than leaves was retained by the larvae (Wiseman **et al.** 1970). When lyophilized young kernels, silks, mature kernels and leaves were compared for per cent retention and 9–day larval weight, retention was highest for kernels and lowest for leaves. Larval weight was highest on the leaves (McMillian **et al.** 1966). Inbreds varied in retention of their lyophilized plant parts by the fall armyworm (Starks **et al.** 1967).

H. Mass Rearing.

The fall armyworm was reared in the greenhouse on sorghum (Bailey and Chada 1968), lima bean, cowpea, grain sorghum, millet and maize (Roberts 1965). Larvae from these different crops responded differently to topical applications of endrin and carbaryl. The fall armyworm has also been reared in the greenhouse on a sequence of maize seedlings and meridic diet (Revelo and Raun 1964). Procedures for rearing the insect using meridic diets have been described (Bailey and Chada 1968, Bowling 1967, Burton 1967 and Burton and Perkins 1972). Automated machinery for infesting diets was developed (Burton and Cox 1966, Harrell **et al.** 1968). Larvae which had been on diet for 15–17 generations damaged sorghum as much as 2nd–to–4th generation larvae (Mayo 1972).

I. Physiology and Behavior.

Both males and females were sexually active in the laboratory for 5 nights, with males copulating once per night and the females once or occasionally twice. Copulation would last for approximately 1 hour. Mating activity started 2 hours after dark and lasted 4 to 6 hours (Young **et al.** 1968). Pigmentation of the ductus ejaculatorius simplex was used to determine male reproductive status (Snow and Carlysle 1967). An ultrastructural study of the sperm within the spermathecae of several lepidopterous pests reveled that only the FAW eupyrene (nucleate) sperm lacked an intrasheath rod. Fall armyworm pyrene (anucleate) sperm were similar to the others (Riemann and Gassner 1973).

A sex pheromone in **S. frugiperda** was demonstrated (Sekul and Cox 1965), identified as **cis**–9–tetradecen–1–ol and synthesized (Sekul and Sparks 1967, Jacobson and Harding 1968). The female months, which emerged a day before the male, started producing the phermone 18 hours after emergence and peaked at about 48 hours when about 50 per cent of the males were receptive (Sekul and Cox 1967). This compound was moderately attractive in field tests in Florida, but **cis**–9–dodecen–1–ol–acetate, also isolated from the FAW, was more attractive (Mitchel and Doolittle 1976). The latter disrupted pheromone communications In Florida (Mitchel **et al.** 1974). An isomer mixture of 9,12 – tetradecadien–1–ol–acetate reduced trap catpures and mating (Mitchell **et al.** 1976).

Traps baited with virgin females in Florida caught males all night, with peaks at 2400 and 0300 hours (Mitchell **et al** 1974). Counts of larvae in the whorls of corn plants were a better indication of population peaks than trap captures (Greene **et al.** 1971). In Florida, sampling egg masses was most efficient when the egg mass outline was looked for in the sampler's shadow rather than when entire plants were examined **in situ** or removed from the field and examined (Waddill 1977). Female baited traps also captured males of **Elasmopalpus lignosellus** (Zeller) (Pyralidae) and **Heliophana mitis** (Grote) (Noctuidae) (Ganyard and Brady 1972). Electric grid traps and sticky traps were the best for use with pheromone (Tingle and Mitchell 1975).

Exposure to a blacklight doubled carbon dioxide release and affected circadian rhythms of CO_2 release in adult males (Levengood 1969). Infrared radiation at 337 um was attractive to adults and reduced vigor and mating potential (Eldumiati and Levengood 1972). Adults were not affected, however, when exposed to a laser source of 337 um radiation (Turner **et al.** 1977).

Flight behavior in **S. frugiperda** was analyzed (Callahan 1965). Increased wingbeat frequency increased body temperatures more efficiently in males than in females (Elder and Davis 1967). Lipid utilization during flight was measured (Handel 1974), Nayar and Handel 1971). Carbohydrates were also used directly for flight energy (Handel and Nayar 1972).

The histology of the compound eyes was compared to that of **S. exigua** (Agee 1975). The morphology and histology of the gut canal and salivary glands of **Heliothis virescens** (F.), **S. ornithigalli** (Guenee) (Noctuidae) were compared (Che Chi **et al.** 1975).

The amount of liquid imbibed by an adult female was dependent on the amount of fat body depletion and the reproductive status of the moth (Callahan 1961).

J. Conclusions.

Knowledge of all aspects of this insect's biology is incomplete, making it difficult to recommend future studies. As economic entomologists, however, we would like to point out some areas in which more knowledge would be of immediate use.

The yield relationships of the FAW with its many crop hosts have yet to be studied, with the exceptions of maize and sorghum which have not been studied in detail. This would provide a sounder basis for rational control decisions. In addition, the relationships of the fall armyworm with its several weed hosts and the relationships of FAW populations in these weeds with nearby crops are unknown, but in our experience quite important. Several host–plant resistance studies have been reported, mostly in maize, but agronomically acceptable resistant varieties are still lacking.

Work on natural control is incomplete. Very little is known about abiotic factors affecting this insect which might be used in predicting population trends. Parasites, predators and diseases have been studied at a few locations. Given the wide geographic range of this pest, its biological control complex probably varies widely also. There may be much potential for interchange of effective parasites, predators or diseases.

There remains much to be done in the study of the fall armyworm, but we think work on the problems mentioned could make some immediate and practical contributions to the understanding of this species and its control.

Table 1. Quantitative Observations on Fall Armyworm Life History

Sources	Eggs per Female	Egg Masses per female	Eggs per Mass	Egg Period (Days)	Larval Period (Days)	Pupal Period (Days)	Adult Longevity (Days)
Bailey and Chada (1968) (meridic diet, 26.7°C)	868	–	–	3.0	15.9	10.2	7.5
Blahutiak (1970a) (meridic diet, 26°C, 80 o/o RH)	–	–	50 to 500 200 a/	–	–	–	–
Blahutiak (1970c) (meridic diet, 26°C, 80 o/o RH)	–	–	–	–	14.12 b/ 18.62 c/ 23.12 d/		
Bowling (1967) (meridic diet, 26.7°C, 85–90 o/o RH)	696	–	–	3.5	19.2	12.0	–
Burton and Perkins (1972) (wheat-soy diet)	1900	–	–	–	13.45	–	–
Hinds and Dew (1915) (field conditions)	–	–	60 to 500	3	14	10	–
Hynes (1942) (field conditions)	1313 to 4963	6.5	207 to 749	2 to 3	14 to 25	8 to 11	5.1 e/ 6.3 f/
Luginbill (1928) (field conditions)	747 to 2142	1 to 13 6-7 a/	44 to 593 243 a/	2 to 10	10.9 to 49.4	6 to 27	6 to 23
Randolfph and Wagner (1966) (meridic diet, 26.7°C,15L: 9D)	1281.3	8.6	–	2.21	14.65	7.86	8.78 e/ 9.26 f/
Vickery (1929) (maize leaves)	1024	0 to 13 7 a/	9 to 400	3.0 (25°C) 11.0 (15.5°C) 18.0 11.1°C)	12 (26.7°C) 25 to 28 (21;1°C)	7 to 8 (27.7°C) 34 (16.1°C) 55 (11.1 to 13.3°C)	

a/ mean
b/ maize
c/ millet
d/ guinea grass
e/ male
f/ female