

INSECT RESEARCH AND CONTROL

Susceptibility of Fall Armyworm Collected from Different Plant Hosts to Selected Insecticides and Transgenic Bt Cotton

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INTERPRETIVE SUMMARY

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a destructive pest of cotton throughout the western hemisphere. Two strains have been identified according to their host preference: a corn-associated strain that feeds primarily on corn, and a rice-associated strain that feeds primarily on forage grasses and rice. The determination of which strain feeds on cotton has not been fully characterized. The importance of fall armyworm as a pest in cotton and the difficulties experienced in controlling this pest with insecticides emphasizes the need to determine differences in insecticide susceptibility between host strains. Our objective was to determine the relative susceptibility of fall armyworms collected from field corn, bermudagrass, and browntop millet to selected cotton insecticides and the δ -endotoxin present in transgenic Bt cotton.

The fall armyworm is considered a sporadic, but serious late-season pest on cotton and many insecticide efficacy studies have been conducted. Fall armyworm populations often originate on corn and various grasses prior to migrating to cotton. Researchers often use fall armyworm larvae collected from rice, various forage grasses, or corn when evaluating cotton insecticides, because these larvae are readily available. Previous research has shown that differences in fall armyworm insecticide susceptibility could be associated with host specific strains. Other agronomically important insects, such

as the tobacco budworm and cotton bollworm, differ in susceptibility to various cotton insecticides. Therefore, susceptibility differences among fall armyworm host-associated strains needs to be addressed before insecticide recommendations on cotton are considered.

Fall armyworm colonies were collected from field corn, bermudagrass, and browntop millet. Technical grade insecticides, cypermethrin (Ammo; FMC Corp.), methyl parathion (Methyl; ChemService), and methomyl, (Lannate; E. I. DuPont de Nemours Co.) were topically applied to larvae in laboratory tests. Mortality was assessed after 48 h. Fall armyworm colonies collected from field corn and bermudagrass were reared in the laboratory on normal and transgenic Bt cotton leaves. Percent mortality was recorded at 2, 4, 6, and 12 d after initial infestation on the cottons.

Do fall armyworms collected from different plant hosts exhibit different susceptibilities to selected cotton insecticides and the δ -endotoxin in transgenic Bt cotton?

Larvae of the fall armyworm collected from bermudagrass and browntop millet were significantly more susceptible to cypermethrin, methyl parathion, methomyl, and transgenic Bt cotton than larvae collected from field corn. These data show that differences in insecticide susceptibility were associated with fall armyworms collected from different hosts. Thus, fall armyworm management strategies on cotton need to consider the origin of the population that eventually infests cotton. It is possible that a rate of insecticide to control fall armyworms on cotton may control populations that originally migrated from various forage grasses, but not populations that originally migrated from corn. Because the two strains cannot be identified with the naked eye, certain techniques, such as using genetic markers, need to be further developed to distinguish between strains. If positive identification of strains is

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associated with differences in insecticide susceptibility, then treating the two strains as separate species that have different susceptibilities to insecticides, such as with tobacco budworm and bollworm control on cotton, may be a valid way to ensure that an effective rate of insecticide is used to control both fall armyworm host-associated strains on cotton.

ABSTRACT

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is a destructive pest of many agricultural crops throughout the southern USA. Populations of the fall armyworm that feed on different plant species can be classified as genetically differentiated host-associated strains: a corn (*Zea mays* L.)-associated strain that feeds primarily on corn and a rice (*Oryza sativa* L.)-associated strain that feeds primarily on forage grasses and rice. Although details are limited, differences in susceptibility to insecticides have been reported between the two fall armyworm host-associated strains. Our objective was to determine the relative susceptibilities of fall armyworms collected from different hosts to common cotton insecticides and transgenic *Bacillus thuringiensis* Berliner (Bt) cotton. Technical grade insecticides including cypermethrin {(I)-cyano-3-phenoxybenzyl (I)-*cis*, *trans*-3-(2,2-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate}, methyl parathion {O,O-dimethyl O-(4-nitrophenyl) phosphorothioate}, and methomyl {S-methyl N-[(methylcarbamoyl)oxy] thioacetimidate} were applied topically to third instars collected from field corn and various forage grasses. Fall armyworms collected from forage grasses were significantly more susceptible to all insecticides tested than any of the collections from field corn. In a separate experiment, neonate larvae originally collected from bermudagrass and field corn were fed on conventional and transgenic Bt cotton. Fall armyworms collected from bermudagrass were significantly more susceptible to Bt cotton than larvae collected from field corn. Our data show that differences in larval susceptibility to commonly used cotton insecticides and transgenic Bt cotton appear to be related to the host-associated strains of the fall armyworm. Therefore, future management of this pest on cotton may need to address the susceptibility of fall armyworm host-associated strains before insecticide recommendations on cotton are considered.

The fall armyworm is a destructive pest of corn, cotton (*Gossypium hirsutum* L.), rice, and forage grasses throughout the western hemisphere (Sparks, 1979). Populations of the fall armyworm

that feed on different plant species can be classified as genetically differentiated host-associated strains: a corn-associated strain that feeds primarily on corn and a rice-associated strain that feeds primarily on forage grasses and rice (Pashley et al., 1985). Both host-associated strains are broadly sympatric (Pashley, 1986), and reproductive isolating mechanisms and incompatibility have been reported between the strains (Pashley and Martin, 1987; Pashley et al., 1992). Because the strains are morphologically identical, genetic markers are required to distinguish them.

Before host-associated strains of the fall armyworm were characterized, differences in susceptibility of fall armyworm larvae to insecticides were categorized based on host plant influences rather than behavioral and physiological differences attributed to reproductively isolated host strains (Wood et al., 1981). Larvae reared on bermudagrass [*Cynodon dactylon* (L.)], and millet [*Pennisetum glaucum* (L.)], were more susceptible to carbaryl and permethrin than larvae reared on corn, cotton, or soybean [*Glycine max* (L.) Merr.] (Wood et al., 1981). Pashley et al. (1987) were the first to show that differences in insecticide susceptibility could be associated with the two fall armyworm host-associated strains. Larvae of the rice-associated strain were about three and five times more susceptible to diazinon {O,O-diethyl O-[6-methyl-2-(1-methylethyl)-4-pyrimidinyl] phosphorothioate} and carbaryl (1-naphthyl methylcarbamate), respectively, than larvae of the corn-associated strain. Some evidence suggests that physiological factors, such as the activity of detoxifying enzymes [i.e., mixed-function oxidase], may play an important part in host plant adaptation of fall armyworm host-associated strains (Veenstra et al., 1995).

With the advent of transformation technology, the question of whether fall armyworm host-associated strains may differ in their susceptibility to the δ -endotoxin present in transgenic crops such as *B. thuringiensis* Berliner (Bt) cotton arises. Other agronomically important Lepidoptera, such as the tobacco budworm, *Heliothis virescens* (F.); cotton bollworm, *Helicoverpa zea* (Boddie); and pink bollworm, *Pectinophora gossypiella* (Saunders), differ in their susceptibility to the δ -endotoxin found in foliar Bt products (MacIntosh et al., 1990) as well as transgenic Bt cotton (Jenkins et al., 1992; Wilson et al., 1992; Halcomb et al., 1996).

Because the fall armyworm is considered a sporadic but serious pest on cotton as well as other agronomically important crops (Young, 1979), many insecticide efficacy studies have been conducted (Combs and Chambers, 1979; Leeper, 1979; Smith, 1985; Mink and Luttrell, 1989; Nyouki et al., 1996). Because of ease and availability of making collections, researchers often use larvae collected from rice, various forage grasses (Nyouki et al., 1996), or corn (Mink and Luttrell, 1989) when examining insecticides registered for cotton. Our objective was to determine the relative susceptibilities of fall armyworms collected from different hosts.

MATERIALS AND METHODS

Insects

A laboratory reference strain (LAB-REF) collected from field corn and verified using genetic markers to be the corn-associated strain was provided by H. W. Fescemyer, Department of Entomology, Clemson University. All field colonies of the fall armyworm were collected from field corn (BENHUR, BRNV, and ST. JOSEPH colonies), bermudagrass (WINNCRASS colony), or the forage grass, browntop millet [*Brachiaria ramosa* (L.) Staph] (MILLET colony). Approximately 200 larvae were collected from each host (Table 1). Prior to topical bioassays, larvae were reared for at least one generation on artificial diet, to minimize disease and eliminate parasitoids, according to the methods described in Perkins (1979) as modified by the use of a soybean/wheat [*Triticum aestivum* (L.)] mericid diet (King and Hartley, 1985).

Topical Bioassay

Technical grade insecticides dissolved in acetone were applied topically (1.0 μ L total volume) to the dorsal region of the thorax of third instar fall armyworms weighing 30 to 45 mg using a Hamilton microsyringe with repeating ratchet dispenser. The insecticides tested included a pyrethroid (FMC Corp., Princeton, NJ); an organophosphate, methyl parathion (ChemService, West Chester, PA); and a carbamate, methomyl {*S*-methyl *N*-[(methylcarbamoyl)oxy] thioacetimidate} (E. I. DuPont de Nemours Co., Wilmintgon, DE). Treated larvae were held on artificial diet in an

environmental chamber (14:10 [light:dark] cycle, 27 ± 1 °C, $70 \pm 10\%$ RH). Mortality was assessed after 48 h and defined as the inability of larvae to make coordinated movements within 10 s of prodding. Except for the methomyl treatment of one of the collections from field corn (BRNV), the same generation/colony was used for each insecticide. Acetone-treated larvae were used as controls, and mortality in the insecticide treatments was adjusted for control mortality using Abbott's formula (Abbott, 1925). Control mortality never exceeded 5%. Data were analyzed by probit analysis using POLO-PC (LeOra Software, 1987). Toxicity ratios (TR) were calculated by dividing the LD50 of a field colony by that of LAB-REF. Confidence limits (C. L., 95%) for toxicity ratios were estimated using the method described in Robertson and Preisler (1992). LD50 values for an insecticide and colony and were considered significantly different if their 95% confidence limits did not overlap.

Transgenic Bt Cotton Bioassay

Mortality was compared between fall armyworm colonies fed a transgenic Bt cotton cultivar expressing the *cryIA* (c) gene (cv. NuCOTN 33^B) and its conventional parental cultivar not expressing the *cryIA* (c) gene (cv. DP 5415). Neonate larvae from the field corn colony, BRNV, (F₃ generation) and the bermudagrass colony, WINNCRASS, (F₁ generation) were placed inside 9.2-cm diam. plastic petri dishes with 9.0-cm diam. filter paper discs (moistened daily to prevent leaf desiccation) and covered to prevent escapes (BRNV: 5 larvae/dish and 20 dishes/cultivar; WINNCRASS: 5 larvae/dish and 40 dishes/cultivar). Because fall armyworm larvae are usually distributed low in the plant canopy (Ali et al., 1990), larvae confined within the dishes were fed whole leaves that were selected from the lower one-third of field-grown plants of the same age (Northeast Research Station, Macon Ridge Location, Winnsboro, LA). Leaves were changed every 48 h. To prevent cannibalism, after 96 h larvae were placed into individual 5.7-cm diameter plastic petri dishes with a moistened 5.5-cm diameter filter paper disc and reared as described above. Dishes were kept in a growth chamber (14:10 [light:dark] cycle, 27 ± 1 °C) throughout larval development. Larval mortality at 2, 4, 6, and 12 d after exposure were recorded for each cultivar. To minimize the possible fitness differences associated with larvae from two

Table 1. Host, date, number collected, and site of fall armyworm collections.

Colony	Host	No. collected	Collection site/Date
LAB-REF	Field corn	-----	Reference corn strain- in culture for . 30 generations
BRNV	Field corn	. 200	Brownsville, TX, 7-8 May 1996
BENHUR	Field corn	. 200	Baton Rouge, LA, 25 June 1996
ST. JOSEPH	Field corn	. 200	St. Joseph, LA, 8 Aug. 1996
WINN GRASS	Bermudagrass	. 200	Winnsboro, LA, 3 July 1996
MILLET	Browntop millet	. 200	Winnsboro, LA; 16 Sept .1996

Table 2. Susceptibility of three collections of fall armyworm from corn, two collections from various grasses and a laboratory-reference corn strain after 48 hours of exposure to selected insecticides.

	Source‡	GEN§	n¶	LD50	95% C. L.		Slope, SE	TR# 95% C.L.	C ²
				µg/larva	Low	High			
CYP†	LABR	-----	160	0.151	0.140	0.161	13.6 ± 2.46	-----	0.79
	BRNV	F ₂	270	0.199	0.187	0.216	7.0 ± 1.17	1.32 (1.20 - 1.45)	3.07
	BENH	F ₂	90	0.359	0.281	0.537	3.2 ± 0.71	2.38 (1.77 - 3.20)	1.27
	STJO	F ₂	170	0.050	0.040	0.063	2.4 ± 0.35	0.33 (0.26 - 0.42)	2.17
	WINN	F ₂	240	0.003	0.002	0.004	2.0 ± 0.38	0.02 (0.02 - 0.03)	0.40
	MILL	F ₂	110	0.019	0.010	0.034	1.3 ± 0.21	0.13 (0.07 - 0.22)	1.72
MPA	LABR	-----	275	2.115	1.717	2.725	3.3 ± 0.38	-----	7.18
	BRNV	F ₃	210	1.225	0.982	1.442	3.3 ± 0.57	0.58 (0.46 - 0.73)	2.07
	BENH	F ₃	80	2.984	2.396	3.895	3.8 ± 0.81	1.41 (1.08 - 1.84)	1.73
	STJO††	F ₃	200	0.445	0.115	1.159	1.5 ± 0.18	0.21 (0.15 - 0.30)	20.63‡‡
	WINN	F ₃	244	0.018	0.011	0.026	3.5 ± 0.59	0.01 (0.01 - 0.02)	3.46
	MILL	F ₃	160	0.026	0.019	0.035	2.5 ± 0.40	0.01 (0.01 - 0.02)	0.67
MET	LABR	-----	150	1.679	1.018	3.711	1.1 ± 0.26	-----	1.73
	BRNV	F ₆	160	0.916	0.307	1.723	1.3 ± 0.26	0.55 (0.21 - 1.44)	0.61
	BENH	F ₄	210	59.486	41.271	99.276	1.4 ± 0.27	35.43 (17.54 - 71.59)	0.57
	STJO	F ₄	160	5.586	3.070	14.695	1.2 ± 0.20	3.33 (1.32 - 8.42)	0.45
	WINN	F ₄	125	0.455	0.181	0.977	0.8 ± 0.16	0.27 (0.14 - 0.50)	1.97
	MILL	F ₄	100	0.447	0.316	0.524	5.3 ± 1.66	0.27 (0.10 - 0.71)	0.01

† CYP, MPA and MET are cypermethrin, methyl parathion and methomyl, respectively.

‡ LABR, BRNV, BENH, STJO, WINN, MILL are LAB-REF (field corn), BRNV (field corn), BENHUR (field corn), ST. JOSEPH (field corn), WINN GRASS (bermudagrass), MILLET (browntop millet) collections.

§ GEN is generation tested.

¶ n = Number of larvae tested.

TR = Toxicity ratio (LD50 field strains/LD50 LAB-REF).

†† 90% C. L. is 90% confidence level.

‡‡ Significant C².

different generations, WINNGRASS and BRNV were reared for 8 to 10 generations in the laboratory on artificial diet prior to repeating the experiment as described above except for replacing NuCOTN 33^B with ‘NuCOTN 35^B’ (which also expresses the *cryIA* (c) insecticidal protein) and DP 5415 with ‘DP 5690’ (parental cultivar of NuCOTN 35^B). This allowed the use of cotton plants of approximately the same size and age as in the initial experiment. Mortality frequencies were generated using the FREQ procedure (SAS Institute, 1985) and were analyzed using Cochran-Mantel-Haenszel statistics (Landis et al., 1978).

RESULTS AND DISCUSSION

Topical Bioassay

Susceptibility of third instar fall armyworm to all insecticidal classes was significantly greater, based on LD50 values, for the colonies from bermudagrass and browntop millet (WINNGRASS and MILLET, respectively) compared with the laboratory colony (LAB-REF) and colonies collected from field corn (BENHUR, BRNV, and ST. JOSEPH), with the exception of the methomyl treatment of BRNV (Tables 1 and 2). However, the F₆ generation from BRNV was treated with methomyl, whereas the F₄ generations of the other colonies were treated with methomyl. Thus, differences in BRNV susceptibility to methomyl in comparison with other colonies may have been due to differences in generation tested rather than host-associated or host strain-specific differences. Fall armyworm collected from bermudagrass (WINNGRASS) and browntop millet (MILLET) were up to 50, 118, and 4 times more susceptible than LAB-REF to cypermethrin, methyl parathion, and methomyl, respectively. In addition, toxicity ratios (LD50 field strains/LD50 LAB-REF) for WINNGRASS and MILLET were significantly lower than BENHUR, BRNV, and ST. JOSEPH (Table 2).

The LD50's for fall armyworm larvae from ST. JOSEPH were significantly lower for cypermethrin and numerically lower for methyl parathion compared to all other colonies from field corn. Only 90% confidence limits and a significant chi-square were reported for the ST. JOSEPH colony treated with methyl parathion. Plotting the dosage-mortality line for this colony revealed an inflection in the

Table 3. Percent mortality of fall armyworm larvae fed DP5415 and NuCOTN33^B at 2, 4, 6, and 12 d after exposure (DAE).

Colony (source)	Percent mortality	
	DP 5415	NuCOTN 33 ^B
2 DAE		
BRNV† (field corn)	10.0	11.0
WINNGRASS‡ (Bermudagrass)	24.0	57.0
	<i>P</i>	
	0.004	0.001
4 DAE		
BRNV	10.0	13.0
WINNGRASS	27.5	61.5
	<i>P</i>	
	0.001	0.001
6 DAE		
BRNV	25.0	34.0
WINNGRASS	32.5	64.0
	<i>P</i>	
	0.182	0.001
12 DAE		
BRNV	26.0	49.0
WINNGRASS	64.5	96.5
	<i>P</i>	
	0.001	0.001

Percent mortality transformed to mortality frequencies and analyzed by each variety using the FREQ procedure (SAS Institute, 1985) with Cochran-Mantel-Haenszel statistics (*P* = 0.05) (Landis et al., 1978).

† F₃ generation tested; 100 larvae tested.

‡ F₁ generation tested; 200 larvae tested.

LD50 line, suggesting that multiple phenotypes were present in the ST. JOSEPH colony (data not shown). Larval densities of the rice-associated strain on various grasses peaks in late summer (Pashley, 1988a), and both host-associated strains can easily be reared on each other's host plants in the laboratory (Pashley, 1988b) and in the field (Pashley, 1986), suggesting that because the ST. JOSEPH colony was collected from field corn late in the growing season, both host-associated strains may have been collected from this site and are present in this colony. The reason(s) for the high methomyl LD50 of the BENHUR colony is not known.

These data show insecticide susceptibility differences between fall armyworm larvae collected

Table 4. Percent mortality of fall armyworm larvae fed DP 5690 and NuCOTN 35^B at 2 and 4 d after exposure (DAE).

Colony (source)	Percent mortality	
	DP 5690	NuCOTN 35 ^B
	2 DAE	
BRNV [†] (field corn)	13.0	27.0
WINNCRASS [‡] (Bermudagrass)	21.0	44.0
	<i>P</i>	
	0.133	0.012
	4 DAE	
BRNV	16.0	31.0
WINNCRASS	23.0	51.0
	<i>P</i>	
	0.213	0.004

Percent mortality transformed to mortality frequencies and analyzed by each variety using the FREQ procedure (SAS Institute, 1985) with Cochran-Mantel-Haenszel statistics ($P = 0.05$) (Landis et al., 1978).

[†] F₁₀ generation tested; 100 larvae tested.

[‡] F₈ generation tested; 100 larvae tested.

from field corn and forage grasses. To show genetic differences between the fall armyworm host-plant-associated strains, we used the method described in Lu and Adang (1996). We found 29 of 36 WINNCRASS larvae tested (80.6%) had the mitochondrial DNA pattern indicative of a rice-associated strain, while 12 of 12 BRNV larvae tested (100%) had the pattern indicative of a corn-associated strain. Current genetic markers to distinguish fall armyworm host-associated strains are sex-linked (Adamczyk et al., 1996), or in the case of mitochondrial DNA, maternally inherited (Lu and Adang, 1996). Therefore, the ability to detect the extent of intraspecific-strain matings is severely hindered without the use of an autosomal or nuclear marker. However, the topical bioassay described here, using either cypermethrin or methyl parathion, may be a reliable method to distinguish or corroborate verification of fall armyworm host-associated strains, although further testing of our method is needed.

Transgenic Bt Cotton Bioassay

Mortality data for fall armyworm larvae collected from field corn (BRNV) or bermudagrass

(WINNCRASS) when fed on transgenic Bt cotton foliage (NuCOTN 33^B) or its conventional parental cultivar (DP 5415) are given in Table 3. When analyzed by cotton cultivar for both colonies, larval mortality for the bermudagrass colony fed on transgenic Bt cotton and conventional cotton was significantly greater than the colony from field corn at 2, 4, and 12 days after exposure.

Similar trends in Bt susceptibility were observed when the experiment was repeated with larvae from BRNV and WINNCRASS colonies reared on artificial diet for 8 to 10 generations (Table 4). When analyzed by cultivar for both colonies, mortality for the bermudagrass colony fed on transgenic Bt cotton was significantly greater than the mortality of the colony from field corn at 2 and 4 days after exposure. No significant differences in mortality on conventional cotton were observed between fall armyworm colonies.

CONCLUSIONS

Fall armyworm larvae collected from bermudagrass (F₁ generation) were more susceptible to the δ -endotoxin present in transgenic Bt cotton than fall armyworm larvae collected from field corn (F₃ generation). This trend also was observed after larvae were reared for 8 to 10 generations in the laboratory, indicating susceptibility differences to Bt between the two colonies may be due to intrinsic host strain differences, such as those discussed in Veenstra et al. (1995). Further studies have shown that the bermudagrass colony (WINNCRASS) is >3.5X more susceptible to the δ -endotoxin present in a diet overlay bioassay of foliar Bt (Javelin® WG, Sandoz Agro, Inc., Des Plaines, IL) than the laboratory reference colony (LAB-REF) (Adamczyk, 1997, unpublished data). Veenstra et al. (1995) reported that food consumption and utilization in the fall armyworm is host strain-specific. Larvae of the corn-associated strain performed better than larvae of the rice-associated strain. The corn-associated strain was more efficient in converting digested food into biomass than the rice-associated strain when fed corn. The data in the present study indicate that larvae collected from corn may survive better on conventional cotton than larvae collected from bermudagrass.

Differences in larval susceptibility to commonly used cotton insecticides and transgenic Bt cotton appear to be related to the host-associated strains of

fall armyworm. Fall armyworms on cotton may consist of a mixture of corn and rice-associated strains, although the strain status of fall armyworm on cotton has not been fully characterized (Pashley, 1986). Therefore, future management of this pest on cotton needs to address the susceptibility of fall armyworm host-associated strains. If only the corn-associated strain uses cotton as a food source, fall armyworms collected from rice or various forage grasses may bias insecticide bioassay results towards foliar cotton insecticides and transgenic Bt cotton susceptibility. Because host-associated strains are common in many Lepidoptera (Pashley et al., 1990; see Sperling, 1994 for a recent review), variation in susceptibility of other lepidopteran species to a particular insecticide may be related to intraspecific host strain differences rather than simply natural variation.

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REFERENCES

- Abbott, W.S. 1925. A method of computing the effectiveness of an insecticide. *J. Econ. Entomol.* 18: 265–267.
- Adamczyk, J.J., Jr., J.F. Silvain, and D. Pashley Prowell. 1996. Intra- and interspecific DNA variation in a sodium channel intron in *Spodoptera* (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 89:812–821.
- Ali, A., R.G. Luttrell, and J.C. Schneider. 1990. Feeding sites and distribution of fall armyworm (Lepidoptera: Noctuidae) larvae on cotton. *Environ. Entomol.* 19: 1060–1067.
- Combs, R.L., and H.W. Chambers. 1979. Comparison of toxicity of insecticides to larvae of a laboratory strain of fall armyworm to those collected from cotton and corn in central Mississippi. *J. Ga. Entomol. Soc.* 14: 8-11.
- Halcomb, J.L., J.H. Benedict, B. Cook, and D.R. Ring. 1996. Survival and growth of bollworm and tobacco budworm on nontransgenic and transgenic cotton expressing a CryI insecticidal protein (Lepidoptera: Noctuidae). *Environ. Entomol.* 25:250–255.
- Jenkins, J.N., W.L. Parrott, and J.C. McCarty, Jr. 1992. Effects of *Bacillus thuringiensis* genes in cotton on resistance to lepidopterous insects. p. 606. *In* D.J. Herber and D.A. Richter (ed.) Proc. Beltwide Cotton Conf., Nashville, TN. 6–10 Jan. 1992. Natl. Cotton Council Am., Memphis, TN.
- King, E.G., and G.G. Hartley. 1985. *Diatraea saccharalis*. p. 265–270. *In* P. Singh and R.F. Moore (ed.) Handbook of insect rearing. Vol. 2. Elsevier, Amsterdam.
- Landis, R.J., E.R. Heyman, and G.C. Koch. 1978. Average partial association in three-way contingency tables. *Int. Stat. Rev.* 46:237–254.
- Leeper, J.R. 1979. Monitoring fall armyworm for susceptibility/resistance to methomyl. *Fla. Entomol.* 67:339–342.
- LeOra Software. 1987. POLO-PC a user's guide to Probit or Logit analysis. LeOra Software, Berkeley, CA.
- Lu, Y.J., and M.J. Adang. 1996. Distinguishing fall armyworm (Lepidoptera: Noctuidae) strains using a diagnostic mitochondrial DNA marker. *Fla. Entomol.* 79: 48–55.
- MacIntosh, S.C., T.B. Stone, S.R. Sims, P.L. Hunst, J.T. Greenplate, P.G. Marrone, F.J. Perlak, D.F. Fischhoff, and R.L. Fuchs. 1990. Specificity and efficacy of purified *Bacillus thuringiensis* proteins against agronomically important insects. *J. Invert. Pathol.* 56:258–266.
- Mink, J.S., and R.G. Luttrell. 1989. Mortality of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) eggs, larvae and adults exposed to several insecticides on cotton. *J. Entomol. Sci.* 24: 563–571.
- Nyouki, F.F.R., J.R. Fuxa, and A.R. Richter. 1996. Spore-toxin interactions and sublethal effects of *Bacillus thuringiensis* in *Spodoptera frugiperda* and *Pseudoplusia includens* (Lepidoptera: Noctuidae). *J. Entomol. Sci.* 31: 52–62.
- Pashley, D.P. 1986. Host-associated genetic differentiation in fall armyworm: A sibling species complex? *Ann. Entomol. Soc. Am.* 79: 898–904.
- Pashley, D.P. 1988a. Current status of fall armyworm host strains. *Fla. Entomol.* 71: 227–234.
- Pashley, D.P. 1988b. Quantitative genetics, development, and physiological adaptation in host strains of fall armyworm. *Evolution* 42:227–233.
- Pashley, D.P., and J.A. Martin. 1987. Reproductive incompatibility between host strains of the fall armyworm

- (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 80:731–733.
- Pashley, D.P., A.M. Hammond, and T.N. Hardy. 1992. Reproductive isolating mechanisms in fall armyworm host strains (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 85:400–405.
- Pashley, D.P., T.N. Hardy, A.M. Hammond, and J.A. Mihm. 1990. Genetic evidence for sibling species within the sugarcane borer (Lepidoptera: Pyralidae). *Ann. Entomol. Soc. Am.* 83:1048–1053.
- Pashley, D.P., S.J. Johnson, and A.N. Sparks, Jr. 1985. Genetic population structure of migratory moths: The fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 78:756–762.
- Pashley, D.P., T.S. Sparks, S.S. Quisenberry, T. Jamjanya, and P. Dowd. 1987. Two fall armyworm strains feed on corn, rice and bermudagrass. *La. Agric.* 30: 8–9.
- Perkins, W.D. 1979. Laboratory rearing of the fall armyworm. *Fla. Entomol.* 62: 87–91.
- Robertson, J.L., and H.K. Preisler. 1992. Pesticide bioassays with arthropods. CRC Press, London.
- SAS Institute. 1985. *Statistics*. 5th ed. Cary, NC.
- Smith, R.H. 1985. Fall and beet armyworm control. p. 134–136. *In* T.C. Nelson (ed.) *Proc. Beltwide Cotton Prod. Res. Conf.*, New Orleans, LA. 6–11 Jan. 1985. Natl. Cotton Council Am., Memphis, TN.
- Sparks, A.N. 1979. A review of the biology of the fall armyworm. *Fla. Entomol.* 62: 82–87.
- Sperling, F.A.H. 1994. Sex-linked genes and species differences in Lepidoptera. *Can. Entomol.* 126: 807–818.
- Veenstra, K.H., D.P. Pashley, and J.A. Ottea. 1995. Host-plant adaptation in fall armyworm host strains: Comparison of food consumption, utilization, and detoxification enzyme activities. *Ann. Entomol. Soc. Am.* 88:80–91.
- Wilson, F.D., H.M. Flint, W.R. Deaton, D.A. Fischhoff, F.J. Perlak, T.A. Armstrong, R.L. Fuchs, S.A. Berberich, N.J. Parks, and B.R. Stapp. 1992. Resistance of cotton lines containing a *Bacillus thuringiensis* toxin to pink bollworm (Lepidoptera: Noctuidae) larvae. *J. Econ. Entomol.* 76:219–222.
- Wood, K.A., B.H. Wilson, and J.B. Graves. 1981. Influence of host plant on the susceptibility of the fall armyworm to insecticides. *J. Econ. Entomol.* 74:96–98.
- Young, J.R. 1979. Fall armyworm: Control with insecticides. *Fla. Entomol.* 62:130–133.