

CURRENT STATUS OF FALL ARMYWORM HOST STRAINS

DOROTHY P. PASHLEY
Department of Entomology
Louisiana State University
Baton Rouge, Louisiana 70803

ABSTRACT

Research on two host strains of the fall armyworm (FAW), *Spodoptera frugiperda* [J. E. Smith], is reviewed. They differ at allozyme loci and mtDNA restriction enzyme profiles, in their development on a variety of plants, and in their resistance to insecticides. Data on interstrain matings indicate unidirectional incompatibilities in the laboratory and strong preferences among males for females of their own strain in nature. Further study is required to clarify precise strain affinities for the long list of FAW host records. Information on phenologies and geographic distributions is presented but clearly in need of in-depth study. Those studying FAW are recommended to collect from a single host, to keep host records with laboratory colonies, to replenish colonies with individuals from the same host, and to establish a set of voucher specimens for each collection or study.

RESUMEN

Se revisa el estudio sobre dos tipos de hospederos del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith). Ellos difieren en el loci de alozyme y en la restricción del mtDNA de las enzimas, en su desarrollo en varios tipos de plantas, y en su resistencia a insecticidas. Datos sobre cruce de razas indican incompatibilidades no-direccionales en el laboratorio, y una gran preferencia entre los machos hacia hembras de su propia raza bajo condiciones naturales. Se requiere un estudio adicional para aclarar las afinidades de las razas hacia la larga lista de hospederos del gusano cogollero. Se presenta información sobre la fenología y distribución geográfica, pero está claramente necesitada de un estudio a fondo. Se recomienda a aquellos que estudian el gusano cogollero, que lo coleccionen de un solo hospedero, que mantengan un registro del hospedero de las colonias de laboratorio, que reemplacen las colonias con individuos del mismo hospedero, y que establezcan un grupo de especímenes justificante de cada colección o estudio.

The fall armyworm (FAW), *Spodoptera frugiperda* [J. E. Smith], has been subdivided recently into two strains on the basis of genetic differentiation associated with larval host plants (Pashley et al. 1985, Pashley 1986). One strain feeds primarily on corn (*Zea mays* L.) and the other on rice (*Oryza sativa* L.) and various forage and native grasses. The strains may represent one of three types of taxa. They may be biotypes in which genetic differences are due to a selectively-mediated polymorphism within a single randomly-mating species. They may be host races in the initial stages of speciation in which interbreeding is reduced due to host preference differences (Diehl & Bush 1984). Lastly, they may be sibling species that are either capable of hybridizing to a limited degree or completely reproductively isolated.

In this paper, I review research relevant to the status of these strains, elaborating on some of the more problematic areas. I also emphasize the impact that these taxa have on our current thinking about FAW biology and end with some recommendations for those studying FAW.

RELEVANT BACKGROUND ON FAW BIOLOGY

FAW has been reported on more than 80 plant species in 23 families (Table 1). It is primarily regarded, however, as a pest of grasses (Poaceae). The two host strains appear to utilize different sets of hosts (Fig. 1). The corn strain feeds primarily on corn, cotton (*Gossypium hirsutum* L.), and sorghum (*Sorghum vulgare* Pers.), but occasionally will feed on other plants either growing in proximity to primary hosts (such as signal grass, *Brachiaria platyphylla* (Nash), [LA 8/85 in Fig. 1]), or in isolation (LA(BH) 8/85 in Fig. 1). The rice strain has been reported on rice, signal, bermudagrass (*Cynodon dactylon* [Pers.]), and Johnson grass (*Sorghum halepense* [Pers.]). It has been suggested that early season FAW feed on corn and then shift to forage grasses after corn is harvested in the south (Morrill 1978). Genetic data do not support this hypothesis.

TABLE 1. HOST PLANT RECORDS FOR FAW. PLANT FAMILIES ARRANGED PHYLOGENETICALLY, SPECIES ALPHABETICALLY. SPECIES INTRODUCED TO THE WESTERN HEMISPHERE INDICATED BY AN ASTERISK. ALL REFERENCES FROM LUGINBILL (1928) UNLESS FOOTNOTED.

<u>FAMILY</u>	<u>SPECIES</u>
1. Chenopodiaceae	<i>Chenopodium album</i> L.* (lambs quarters); <i>Spinacia oleracea</i> L.* (spinach); <i>Beta vulgaris</i> L.* (sugar beets)
2. Amaranthaceae	<i>Amaranthus</i> spp. including <i>spinosus</i> L. ^a (pigweed)
3. Portulacaceae	<i>Portulaca oleracea</i> L.* (purslane)
4. Polygonaceae	<i>Fagopyrum esculentum</i> Moench* (buckwheat)
5. Malvaceae	<i>Althaea rosea</i> Cav.* (hollyhock); <i>Gossypium hirsutum</i> L. (upland cotton)
6. Violaceae	<i>Viola</i> spp. (violets)
7. Caricaceae	<i>Carica papaya</i> L. ^b (papaya)
8. Cucurbitaceae	<i>Citrullus vulgaris</i> Schrad.* (watermelon); <i>Cucumis sativus</i> L.* (cucumber); <i>Cucurbita pepo</i> L. ^c (pumpkin)
9. Brassicaceae	<i>Brassica napobrassica</i> Mill.* (rutabaga); <i>B. oleracea</i> L.* (cabbage, kale); <i>B. rapa</i> L.* (turnip)
10. Rosaceae	<i>Fragaria chiloensis</i> Duchesne (strawberry); <i>Prunus persica</i> Batsch* (peach); <i>Malus pumila</i> Mill.* (apple)
11. Fabaceae	<i>Arachis hypogaea</i> L. (peanut); <i>Cajanus cajan</i> Millsp.* (pigeon pea); <i>Cicer arietinum</i> (L.)* (chick pea); <i>Glycine max</i> Merr.* (soybean); <i>Medicago sativa</i> L.* (alfalfa); <i>Pisum sativum</i> L.* (pea); <i>Pueraria lobata</i> Ohwi* (kudzu); <i>Stizolobium deeringianum</i> Bort.* (velvet bean); <i>Trifolium pratense</i> L.* (red clover); <i>T. repens</i> L.* (white clover); <i>Vigna unguiculata</i> Walpers* (cowpea)
12. Myrtaceae	<i>Eucalyptus camaldulensis</i> Dehuh.* ^b
13. Vitaceae	<i>Vitis</i> spp. (grape)
14. Rutaceae	<i>Citrus aurantium</i> L.* (seville orange)
15. Apocynaceae	<i>Plumeria rubra</i> L. ^d
16. Solanaceae	<i>Capsicum</i> spp. ^b (red peppers); <i>Lycopersicon esculentum</i> Mill. (tomato); <i>Nicotiana tabacum</i> L. (tobacco); <i>Solanum tuberosum</i> L. (potato)
17. Convolvulaceae	<i>Ipomoea</i> spp. (wild morning glory)
18. Asteraceae	<i>Lactuca sativa</i> L.* ^e (lettuce); <i>Xanthium italicum</i> Moretti (cocklebur)
19. Cyperaceae	<i>Cyperus rotundus</i> L.* (nut-grass)
20. Poaceae	<i>Agrostis hyemalis</i> (Walt.) (spring bentgrass); <i>A. stolonifera</i> L. (redtop bentgrass); <i>Andropogon virginicus</i> L. (broomsedge); <i>Avena sativa</i> L.* (oats); <i>Axonopus affinis</i> Chase (carpet grass);

TABLE 1. (Continued)

FAMILY	SPECIES
	<i>Brachiaria platyphylla</i> (Nash) ^f (signal grass); <i>Cenchrus tribuloides</i> L. (sandspur grass); <i>Chloris gayana</i> Kunth* (Rhodes grass); <i>Cynodon dactylon</i> (Pers.)* (bermudagrass); <i>Dactyloctenium aegyptium</i> (Beauv.)* (crowfoot grass); <i>Digitaria sanguinalis</i> (Scop.)* (crabgrass); <i>Hordeum vulgare</i> L.* (barley); <i>Oryza sativa</i> L.* (rice); <i>Panicum maximum</i> Jacq.* (guinea grass); <i>P. miliaceum</i> L.* (broomcorn millet); <i>P. purpurascens</i> Raddi ^g (paragrass); <i>P. texanum</i> Buckl. (Texas millet); <i>Penisetum glaucum</i> (R. Br.)* (pearl millet); <i>P. purpureum</i> Schum.* ^h (Napier grass); <i>Phleum pratense</i> L.* (timothy grass); <i>Poa pratensis</i> L.* (Kentucky bluegrass); <i>Saccharum officinarum</i> L.* (sugarcane); <i>Secale cereale</i> L.* (rye); <i>Sorghum sudanense</i> Hitch.* (sudan grass); <i>S. vulgare</i> Pers.* (sorghum); <i>S. halepense</i> (Pers.)* (Johnson grass); <i>Triticum aestivum</i> L.* (wheat); <i>Zea mays</i> L. (corn); <i>Z. mexicana</i> Reeves & Mangelsdorf (teosinte)
21. Liliaceae	<i>Allium cepa</i> L.* (onion); <i>A. sativum</i> L.* ^e (garlic); <i>Asparagus officinalis</i> L.* (asparagus)
22. Iridaceae	<i>Gladiolus</i> spp.* ^b
23. Pinaceae	<i>Pinus caribaea</i> Morelet ⁱ (Caribbean or slash pine)

^aChereguino & Menendez 1975; ^bBruner et al. 1975; ^cPretto 1970; ^dSantiago-Blay 1983; ^eMcGuire & Crandall 1967; ^fD. P. Pashley, pers. obs.; ^gAshley et al. 1983; ^hPiedra 1974; ⁱHowell 1979

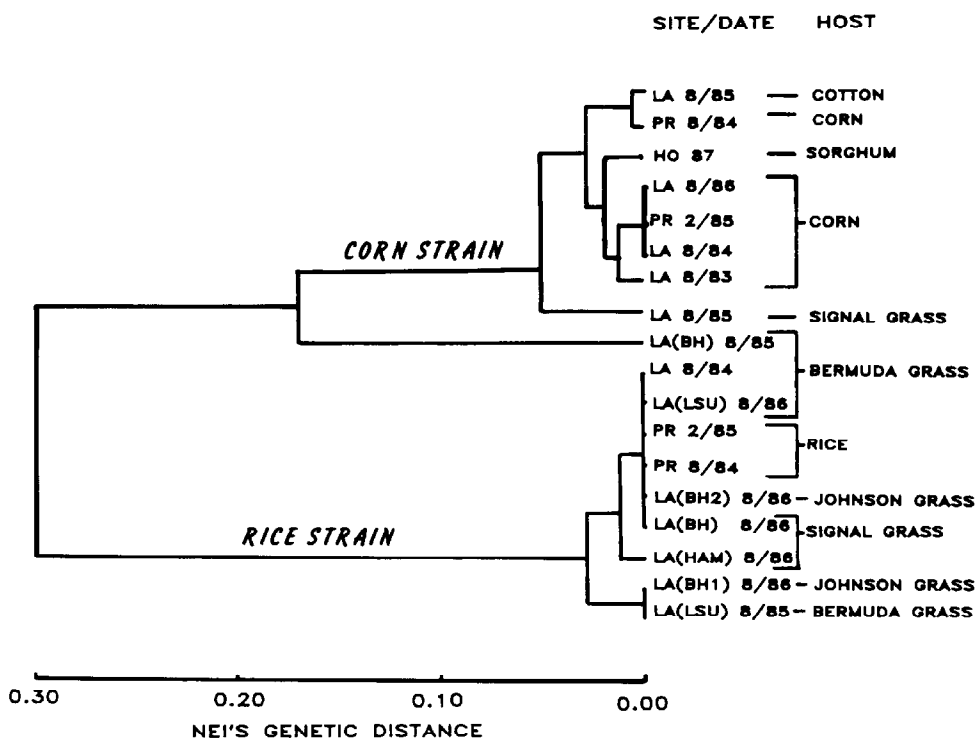


Fig. 1. Genetic relationships among wild FAW collected from different host plants. Genetic distances are based on three polymorphic loci used to separate strains (esterase, hydroxybutyrate dehydrogenase, and peptidase). PR = Puerto Rico, LA = Louisiana (sites in parentheses are different locations in LA), HO = Honduras.

Data on the phenology of strains in Louisiana indicate that the rice strain is present throughout much of the year (D. P. Pashley, T. N. Hardy & A. M. Hammond, unpublished data). Populations remain at low density on various grasses until a rapid buildup that generally occurs in late summer. Corn strain individuals are also present from at least late spring through December but densities peak in early to mid-summer prior to corn harvest. At present it is unclear where these individuals spend the rest of summer. They may migrate northward following developing corn, shift to some other locally available host, die because no hosts are available, or, although unlikely, enter some sort of summer aestivation.

The geographic distribution of the corn strain is well documented (Pashley et al. 1985, Pashley 1986). It occurs throughout much of the western hemisphere, generally in most places where corn is grown (Fig. 2). Less is known about the distribution of the rice strain because very little sampling has been done on hosts other than corn. It occurs sympatrically with the corn strain, often in neighboring fields, in Puerto Rico, southern Florida, Georgia, and Louisiana. Reported attacks on forage grasses throughout much of Latin America are more than likely due to the presence of the rice strain. Future collaboration with scientists from these localities will allow a more precise characterization of the rice strain's range.

RESEARCH ON STRAIN DIFFERENCES

Populations of FAW sampled from corn exhibit significant differences at five allozyme loci from populations collected from rice or bermudagrass (Pashley 1986). Cross-rearing experiments in which larvae were reared on their own and the other strain's host indicated that differences were not due to different selective regimes of the host environment (Pashley 1986).

Although it is possible to use genotypes from multiple allozymes to type individuals to strain with a high degree of accuracy, there are no diagnostic loci. Because of that, an independent genetic marker has recently been examined for use in strain identification. Mitochondrial DNA (mtDNA) has been isolated from individuals of each strain and restriction enzyme patterns at 35 enzymes have been examined (D. P. Pashley, unpublished data). Preliminary data indicate that major strain differences exist at two restriction enzymes (Table 2), and possibly at two others (MboI and MboII; D. P. Pashley, unpublished data). Like the allozyme data, genotypes are strongly associated with hosts; the small amount of overlap (e.g., 2 rice collected individuals with AA and 2 corn collected individuals with BB in Table 2) is probably due to a small number of individuals within each strain that use the other strain's host. Further analysis and geographic sampling are required to determine if differences in mtDNA are diagnostic. Host-associated differences at these two very independent markers (allozymes and mtDNA) are strong evidence for the existence of sibling species.

Many developmental differences have been reported between the strains (Pashley et al. 1987a, Pashley 1988, Whitford et al. 1988). Rates of development and pupal weights tend to differ consistently. The only adult character that differs significantly is preoviposition period (D. P. Pashley, T. N. Hardy & A. M. Hammond, unpublished data). In addition, the rice strain appears to be physiologically adapted to its hosts. It performs well on bermudagrass and rice but poorly on corn, whereas the corn strain is less influenced by larval host. The rice strain is probably the more specialized of the two strains.

Reproductive incompatibilities have been reported in interstrain matings performed in the laboratory (Pashley & Martin 1987). Rice strain females mated successfully with corn strain males but matings in the reciprocal cross (corn females with rice males) did not occur. In backcrosses using individuals from the successful cross, only F₁ hybrid



Fig. 2. Collection sites of FAW strains. Circles indicate locations where the corn strain has been collected. Stars indicate locations where both corn and rice strains coexist.

males mated with parentals while F_1 hybrid females would not. In a subsequent study (Whitford et al. 1988), strains successfully mated in both directions. In the two experiments reported by Pashley & Martin (1987), material was relatively freshly collected (first and second lab generations in one case and fourth and fifth in the other). Whitford et al. (1988) used colonies at least three years old. Incompatibilities may be due to behavioral characteristics that are altered during the selection process that accompanies colonization. Future studies should focus on newly collected material to clarify this discrepancy.

TABLE 2. MTDNA GENOTYPES AT TWO RESTRICTION ENZYMES (*HinfI* AND *BstNI*, INDIVIDUALLY, AND COMPOSITE TWO-ENZYME GENOTYPES) IN INDIVIDUAL FAW COLLECTED ON RICE ($N = 15$) AND CORN ($N = 18$) IN PUERTO RICO IN JAN. 1985. THE LOW OVERLAP (COMPOSITE GENOTYPE BB ON CORN AND AA ON RICE) IS PROBABLY DUE TO INDIVIDUALS OF ONE STRAIN FEEDING ON THE HOST OF THE OTHER STRAIN.

	<u>HinfI</u>		<u>BstNI</u>				<u>HinfI/BstNI</u>			
	A	B	A	B	C	D	AA	AC	AD	BB
Corn	16	2	14	2	1	1	14	1	1	2
Rice	2	13	2	13	0	0	2	0	0	13

The detection of incompatibilities in laboratory mating studies is informative because it probably reflects conditions in nature (particularly when intrastain breeding is routinely successful under laboratory conditions). However, when taxa are interfertile in a laboratory environment, it cannot be assumed that mating occurs in nature (Mayr 1970, Diehl & Bush 1984). Therefore, definitive tests of interbreeding must involve studies of cross-attraction and mating in the field. Preliminary data from several ongoing studies suggest that although males are attracted preferentially to females of their own strain, some cross-attraction occurs. In Louisiana and Georgia, females of each strain have been placed in traps and captured males identified to strain using electrophoresis. In Louisiana, most rice strain males (119/166 = 72%) were attracted to rice strain females and most corn strain males (12/16 = 75%) were attracted to corn females (D. P. Pashley, A. M. Hammond & T. N. Hardy, unpublished data). Sample sizes are smaller in Georgia but roughly the same percentages, 75% fidelity for the rice strain and 86% for the corn strain, were observed (J. E. Carpenter & D. P. Pashley, unpublished data). Similarities between these separate studies suggest that either a phomonal or calling time difference facilitates assortative mating within strains. Current efforts are being focused on the analysis of captured field-mated pairs and observations at mating tables to determine if the attraction of males to females of the opposite strain actually results in interstrain mating (J. E. Carpenter & D. P. Pashley, unpublished data).

Data have been gathered or studies initiated on several other features of the biology of the two strains. They have been reported to exhibit differences in resistance to several insecticides (Pashley et al. 1987b) and differences in survival and development on selections of bermudagrass (Pashley et al. 1987a). Morphological differences at traits in both larval and adult stages have been detected (A. M. Hammond, unpublished data; D. P. Pashley & E. R. Taylor, unpublished). So far, however, no differences have been found in pheromone chemistry (A. M. Hammond & H. Fescmeyer, unpublished data).

PROBABLE TAXONOMIC STATUS OF FAW STRAINS

Differences have been detected between strains at almost every character examined to date. It is unlikely that selective regimes on the two hosts could be maintaining differences at all of these independent characters. The strains are probably not interbreeding to a large degree or differences would quickly disappear. Therefore, these taxa are not biotypes and represent either host races or sibling species. Because the life history characteristics of FAW are not in any way similar to those proposed for host races (Bush 1975a, 1975b), they are probably sibling species. When studies of reproductive isolation in nature are complete, the correct taxonomic status of FAW host strains will be resolved.

RECOMMENDATIONS

It should be clear that much is yet to be learned about the biology of these two host-associated strains. Their taxonomic status is only a technical point. Differences exhibited at many different traits should cause those involved in research on these taxa to be extremely cautious. Material for study should be collected from a single host plant species and records of those collections should be kept with laboratory colonies. Colonies should not be replenished with collections from other hosts. Voucher specimens should be set aside for every collection made in the event that morphological differences can eventually be used for strain identification. If there is access to an ultra-cold (-70°C) freezer, a sample should be frozen for electrophoretic analysis, if necessary. If these suggestions are followed, research results will not be invalidated if the strains are concluded to be separate species.

ACKNOWLEDGMENTS

Research on FAW biology was supported by USDA Grant 86-CRCR-1-2027. The manuscript was improved by comments from David Pashley and Bruce McPheron.

REFERENCES CITED

- ASHLEY, T. R., C. S. BARFIELD, V. H. WADDILL, AND E. R. MITCHELL. 1983. Parasitization of fall armyworm larvae on volunteer corn, Bermuda grass, and paragrass. *Florida Entomol.* 66: 267-271.
- BRUNER, S., L. SCARAMUZZA, AND A. OTERA. 1975. Catalogo de los insectos que atacan a las plantas economicas de Cuba. Academia de Ciencias de Cuba. La Habana, Cuba. 393 pp.
- BUSH, G. L. 1975a. Modes of animal speciation. *Annu. Rev. Ecol. Syst.* 6: 334-364.
- BUSH, G. L. 1975b. Sympatric speciation in phytophagous parasitic insects. pp. 187-206. *In* P. W. Price (ed.), *Evolutionary strategies of parasitic insects and mites*. Plenum, New York.
- CHEREGUINO, R. S., AND A. L. MENENDEZ. 1975. Biología y hábitos del gusano cogollero (*Spodoptera frugiperda*) en El Salvador. Memoria de la XXI Reunion de PCCMCA. San Salvador, El Salvador. pp. 251-261.
- DIEHL, S. R., AND G. L. BUSH. 1984. An evolutionary and applied perspective of insect biotypes. *Annu. Rev. Entomol.* 29: 471-504.
- HOWELL, H. N. 1979. Fall armyworm (*Spodoptera frugiperda*) in a pine (*Pinus*) nursery in Honduras, C. A. *Ceiba* 22: 35-37.
- LUGINBILL, P. 1928. The fall armyworm. USDA Tech. Bull. No. 34. 92 pp.
- MAYR, E. 1970. Populations, species, and evolution. Harvard Univ. Press, Cambridge, Mass.
- MCGUIRE, J. U., AND B. S. CRANDALL. 1967. Survey of insect pests and plant diseases of selected crops of Mexico, Central America, and Panama. USDA/U.S. Agency for International Development, Washington, D.C. 157 pp.
- MORRILL, W. L. 1978. Georgia grasslands: reservoirs for beneficial and destructive insects. *Georgia Agr. Res.* (spring issue): 25-28.
- 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. 1988. Quantitative genetics, development and physiological adaptation in sympatric host strains of fall armyworm. *Evolution* 42: 93-102.
- PASHLEY, D. P., S. J. JOHNSON, AND A. N. SPARKS. 1985. Genetic population structure of migratory moths: the fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. America* 78: 756-762.
- PASHLEY, D. P., AND J. A. MARTIN. 1987. Reproductive incompatibility between host strains of fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. America* 80: 731-733.

- PASHLEY, D. P., S. S. QUISENBERRY, AND T. JAMJANYA. 1987a. Impact of fall armyworm (Lepidoptera: Noctuidae) host strains on the evaluation of Bermuda grass resistance. *J. Econ. Entomol.* 80: 1127-1130.
- PASHLEY, D. P., T. C. SPARKS, S. S. QUISENBERRY, T. JAMJANYA, AND P. DOWD. 1987b. Two fall armyworm strains feed on corn, rice and Bermuda grass. *Louisiana Agriculture* 30: 8-9.
- PIEDRA, F. 1974. Effects of different forage diets on the biology of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Cuban J. Agric.* 8: 99-103.
- PRETTO, M. R. 1970. Evaluacion de dos insecticidas para el control del gusano taladrador del cuello del maiz, *Spodoptera frugiperda*. *Boletin Num. 9. MAG Panama.* 13 pp.
- SANTIAGO-BLAY, J. A. 1983. *Plumeria rubra*: A new host plant record of the fall armyworm (Lepidoptera: Noctuidae) in Puerto Rico. *Florida Entomol.* 66: 359.
- WHITFORD, F., S. S. QUISENBERRY, T. J. RILEY, AND J. W. LEE. 1988. Mating compatibility, ovipositional preference, and larval development of two electrophoretically differentiated fall armyworm colonies. *Florida Entomol.* 71: 234-243.

OVIPOSITION PREFERENCE, MATING COMPATIBILITY, AND DEVELOPMENT OF TWO FALL ARMYWORM STRAINS

F. WHITFORD, S. S. QUISENBERRY, T. J. RILEY, AND J. W. LEE

Department of Entomology
Louisiana Agricultural Experiment Station
Louisiana State University Agricultural Center
Baton Rouge, Louisiana 70803

ABSTRACT

Host strains (corn and rice) of the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), were evaluated for oviposition preference, mating compatibility, and development on artificial diet and four plant species. Both strains oviposited a greater percentage of egg masses on corn (*Zea mays* L.), sorghum (*Sorghum bicolor* [L.] Moench.), and bermudagrass (*Cynodon dactylon* [L.] Pers.) than on centipedegrass (*Eremochola ophiuroides* [Munro] Hack). The corn strain oviposited preferentially on corn and sorghum, while the rice strain preferred bermudagrass. The number of fertile intrastrain and interstrain pairs ranged from 77 to 100%. Egg hatch was extremely high for all crosses (>80%). The F₁ (rice ♀ x corn ♂) interhybrid cross had fewer pairs mating and a decreased number of egg masses per female than the F₁ (corn ♀ x rice ♂) interhybrid cross. The corn and rice strain progeny had similar larval weights and survivorship, but the two strains differed significantly in pupal weights and rates of development on modified pinto bean diet. The corn strain developed equally well on corn, bermudagrass and sorghum, whereas the rice strain developed best on bermudagrass. On these hosts the corn strain had significantly heavier larvae and pupae than rice strain feeding on the same hosts. A discussion is provided that delineates problem areas associated with bermudagrass/FAW resistance studies.

RESUMEN

Se evaluaron razas hospederas (maíz y arroz) del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith), sobre su preferencia oviposicional, compatibilidad de apareamiento, y su desarrollo en dieta artificial y en cuatro especies de plantas. Ambas