FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) HOST STRAIN REPRODUCTIVE COMPATIBILITY

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ABSTRACT

The reproductive compatibility between fall armyworm, *Spodoptera frugiperda* (J. E. Smith), host strains (corn and rice) and the impact of colony age on reproductive potential were evaluated. Incompatibilities in interstrain matings were not observed and strains successfully mated in both directions. The number of fertile intrastrain and interstrain females ranged from 50 to 100% and 80 to 100%, respectively. Egg mass numbers were greater when colony age of corn females was older (25+ yr). Colony age of corn or rice males in the intrastrain and interstrain matings was less important in the number of egg masses produced than colony age of the corn females. In contrast, the number of egg masses oviposited was greater when colony age of rice females was younger (< yr and 1 yr). Regardless of strain, the younger the colony age the greater the number of viable eggs. Fewer viable eggs were produced as the period of colonization was extended, particularly period of colonization of females.

RESUMEN

Se evaluó la compatibilidad reproductiva entre el cogollero, *Spodotera frugiperda* (J. E. Smith), las líneas del hospedero (maíz y arroz), y el impacto de la edad de la colonia en el potencial reproductivo. No se observaron incompatibilidades en el apareamiento de razas entrecruzadas, y las razas se aparearon con exito en ambas direcciones. El numero de entrerazas fertiles y hembras entrerazadas varió desde 50 a el 100% y de 80 al 100% respectivamente. El número de posturas de huevos ovipositadas fue mayor cuando la colonia de las hembras criadas en maíz alcanzó mayor edad (25+ años). La edad de la colonia de machos criados en maíz o arroz fue menos importante que la edad de las hembras criadas en maíz en los apareamientos entre raciales e inter-raciales en lo relacionado con el numero de posturas producidas . En contraste, el numero de posturas fue mayor cuando la edad de la colonia de hembras criadas en arroz, era mas joven (< año y 1 año). Entre mas joven fue la colonia, mas grande fue el número de huevos producidos, sin que importara la raza. En la misma proporción que la edad de la colonia aumentaba se produjeron menos huevos viables, particularmente en el periodo de colonizacion de hembras.

Two strains (corn and rice) of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), have been identified (Pashley et al. 1985, Pashley 1986) that differ at allozyme loci (Pashley 1986) and in their mitochondrial DNA (mtDNA) restriction enzyme profiles (Pashley 1989). Numerous biological differences have been detected since their discovery. Physiological (i.e., development) differences exist between strains reared on each other's host plants (Pashley 1988a, Whitford et al. 1988), on artificial diets (Quisenberry & Whitford 1988, Whitford et al. 1988), and on selected bermudagrass genotypes (Lynch et al. 1983, Pashley et al. 1987a b, Quisenberry & Whitford 1988). Pashley et al. (1987b) also reported dissimilarity between strains in insecticidal resistance. In addition, ovipositional preferences were found to differ (Whitford et al. 1988).

Studies of interstrain hybridization and compatibility have been conducted to ascertain the taxonomic status of the strains. Pashley & Martin (1987) reported undirectional reproductive incompatibilities in interstrain matings. In no choice matings, rice females mated with corn males but corn females did not mate with rice males. Furthermore, F_1 hybrid females did not mate but males did. However, Whitford et al. (1988) found strains successfully mated in both directions. Pashley (1988) suggested the reproductive compatibilities reported by Whitford et al. (1988) may be due to altered behavioral characteristics that accompanies the selection process of colonization. Pashley & Martin (1987) used first and second or fourth and fifth generation fall armyworm while Whitford et al. (1988) used colonies at least 3 yr-old.

The objectives of this study were to determine the reproductive compatibility between fall armyworm host strains and to evaluate the impact of colony age on reproductive potential.

Materials and Methods

Six fall armyworm laboratory colonies were used. Colonies were previously identified electrophoretically as the corn and rice strains (Mason et al. 1987, Pashley et al. 1987a, D. P. Pashley unpublished). Corn strain 1 (C1) and corn strain 2 (C2) colonies were field collected from corn and maintained in the laboratory for 3 generations and 1 yr, respectively. Corn strain 3 (C3) was originally collected on bermudagrass but was supplemented with larvae from an unidentified (probably corn) source (Burton 1967, Perkins 1979) and maintained in the laboratory for 25+ yr. Rice strain 1 (R1), rice strain 2 (R2), and rice strain 3 (R3) colonies were field collected from bermudagrass and maintained in the laboratory for 2 generations, 1 yr, and 4+ yr, respectively. C2 was obtained from the USDA-ARS, Crop Science Research Laboratory, Mississippi State, Mississippi, and the C3 from the USDA-ARS, Insect Biology and Population Management Research Laboratory, Tifton, Georgia. Colonies were maintained individually according to procedures by Perkins (1979) at 26.7 ± 0.5°C, 14:10 (L:D) photoperiod, and > 50% relative humidity. Larvae were reared on a modified pinto bean diet (Quisenberry & Whitford 1988).

Pupae from the corn and rice strain colonies were sexed and placed individually in polystyrene cups (29.7 ml) and capped with a waxed lid which had an attached pad of moistened cellulose wadding (2.54 × 2.54 cm). At emergence, intrastrain and interstrain pairs of virgin adults were placed in oviposition containers (1.89 liter) containing vermiculite and an ovipositional substrate (cheesecloth top). Each container was provided a wicked polystyrene cup (29.7 ml) containing adult diet (honey-beer-ascorbic acid). Ovipositional containers were checked daily and egg masses removed when present for a total of 4 ovipositional days per mated female. Egg masses were held individually until hatch at 26.7 ± 0.5°C, 14:10 (L:D) photoperiod, and > 50% relative humidity. Females were dissected after successful oviposition or death for the presence of spermatophores to determine if mating had occurred.

The experiment was arranged in a completely randomized design with 36 total mating types and 10 replicates per mating type, for a total of 360 individual pairings. All possible combinations of colony mating types were examined. Data were subjected to analysis of variance and significant ($P < 0.05$) means separated by least-squares means (SAS Institute 1985).

Results

The colonies used in this study were identified electrophoretically as different fall armyworm strains (corn or rice). The influence of colony age on reproductive compatibility (i.e., number of egg masses oviposited and number of females with spermatophores) varied between strains and according to mating type (significant strain by colony age interaction; $P < 0.003$) and required that data be analyzed within each strain by mating type (Table 1).

The crossing results indicated the strains successfully mated in both directions (Table 1). Dissections of females showed that spermatophores had been transferred in 80-100% of the matings, except for intrastrain (C2 ♀ × C2 ♂) corn matings where only 50% of the females had spermatophores.

The number of egg masses oviposited by females in corn matings was greater when the colony age of females was older (25+ yr). Thus, the colony age of corn females was more important in the number of egg masses produced than colony age of corn or rice

TABLE 1. FALL ARMYWORM INTRASTRAIN AND INTERSTRAIN REPRODUCTIVE COMPATIBILITY.

Strain	Colony age	Cross ♀ ♂	No. of pairs	No. egg masses	No. with Spermatophores
Corn	25+ Yr × 25+ Yr	C3 × C3	10	11.4 a	10 a
	25+ Yr × 1 Yr	C3 × C2	10	10.9 a	10 a
	1 Yr × 25+ Yr	C2 × C3	10	10.0 a	10 a
	25+ Yr × < Yr	C3 × C1	10	8.3 ab	10 a
	1 Yr × < Yr	C2 × C1	10	5.2 bc	8 b
	< Yr × 1 Yr	C1 × C2	10	3.2 c	9 ab
	< Yr × < Yr	C1 × C1	10	2.5 c	8 b
	< Yr × 25+ Yr	C1 × C3	10	2.4 c	8 b
	1 Yr × 1 Yr	C2 × C2	10	1.9 c	5 c
Corn hybrid	25+ Yr × 1 Yr	C3 × R2	10	13.0 a	10 a
	25+ Yr × < Yr	C3 × R1	10	12.1 a	10a
	25+ Yr × 4+ Yr	C3 × R3	10	11.2 a	9 ab
	1 Yr × < Yr	C2 × R1	10	5.2 b	10 a
	1 Yr × 4+ Yr	C2 × R3	10	4.1 b	9 ab
	1 Yr × 1 Yr	C2 × R2	10	3.9 b	9 a
	< Yr × 1 Yr	C1 × R2	10	2.8 b	10 ab
	< Yr ×4+ Yr	C1 × R3	10	2.8 b	9 a
	< Yr × < Yr	C1 × R1	10	2.4 b	8 b
Rice	1 Yr × 1 Yr	R2 × R2	9	12.3 a	10 a
	1 Yr × 4+ Yr	R2 × R3	10	9.2 ab	10 a
	1 Yr × < Yr	R2 × R1	10	8.6 ab	10 a
	< Yr × 1 Yr	R1 × R2	10	6.1 b	10 a
	4+ Yr × 1 Yr	R3 × R2	10	5.8 b	10 a
	4+ Yr × < Yr	R3 × R1	10	5.7 b	10 a
	< Yr × < Yr	R1 × R1	10	5.4 b	10 a
	4+ Yr × 4 Yr	R3 × R3	10	5.3 b	10 a
	< Yr × 4 Yr	R1 × R3	10	5.3 b	10 a
Rice hybrid	1 Yr × 25+ Yr	R2 × C3	10	10.9 a	10 a
	1 Yr × 1 Yr	R2 × C2	10	9.7 ab	10 a
	1 Yr × < Yr	R2 × C1	10	9.1 ab	10 a
	< Yr × 25+ Yr	R1 × C3	10	6.6 bc	10 a
	4+ Yr × 25+ Yr	R3 × C3	10	4.8 c	10 a
	< Yr × 1 Yr	R1 × C2	10	4.5 c	10 a
	< Yr × < Yr	R1 × C1	10	4.4 c	9 a
	4+ Yr × < Yr	R3 × C1	10	4.4 c	10 a
	4+ Yr × 1 Yr	R3 × C2	10	3.4 c	10 a

Means within a column (strain or hybrid by length of colonization) followed by the same letter are not significantly different ($P > 0.05$); least-squares means test).

males in matings. In contrast, the number of egg masses produced by rice female matings was greater when female colony age was younger (< yr and 1 yr).

Colony age significantly influenced the number of viable eggs produced (Table 2). The younger the colony age, regardless of strain, the greater the number of viable eggs and thus, reproductive potential. Conversely, the older the colony age of the female the fewer the number of viable eggs.

Discussion

Incompatibilities reported in interstrain matings by Pashley & Martin (1987) were not found in this study (Table 1). Results are in agreement with Whitford et al. (1988) who found strains successfully mated in both directions. Colony age did not affect repro-

TABLE 2. EFFECT OF COLONY AGE ON FALL ARMYWORM EGG VIABILITY.

Colony age	Cross ♀ ♂	No. of pairs	No. viable eggs
< Yr × 1 Yr	C1 × C2	40	391 a
	C1 × R2		
	R1 × R2		
	R1 × C2		
< Yr × < Yr	C1 × C1	40	375 a
	C1 × R1		
	R1 × R1		
	R1 × C1		
1 Yr × < Yr	C2 × C1	40	331 a
	C2 × R1		
	R2 × R1		
	R2 × C1		
< Yr × 25+/4+ Yr	C1 × C3	40	310 ab
	C1 × R3		
	R1 × R3		
	R1 × C3		
1 Yr × 25+/4+ Yr	C2 × C3	40	259 abc
	C2 × R3		
	R2 × R3		
	R2 × C3		
1 Yr × 1 Yr	C2 × C2	39	199 bc
	C2 × R2		
	R2 × R2		
	R2 × C2		
25+/4+ Yr × 1 Yr	C3 × C2	40	169 bc
	C3 × R2		
	R3 × R2		
	R3 × C2		
25+/4+ Yr × < Yr	C3 × C1	40	151 c
	C3 × R1		
	R3 × R1		
	R3 × C1		
25+/4+ Yr × 25+/4+ Yr	C3 × C3	40	121 c
	C3 × R3		
	R3 × R3		
	R3 × C3		

Means followed by the same letter are not significantly different (P > 0.05; least-squares means test).

ductive compatibility as suggested by Pashley (1988); however, colony age, particularly of females, had a significant impact on the number of viable eggs produced. Extended colonization of fall armyworms resulted in production of fewer viable eggs (Table 2).

The corn and rice fall armyworm strains differ in a number of physiological (Lynch et al. 1983, Pashley et al. 1987a b, Pashley 1988, Quisenberry & Whitford 1988, Whitford et al. 1988) and behavioral (Whitford et al. 1988) traits; however, the status of reproductive isolating mechanisms between strains is not clear because matings in both directions occur (Table 1; Whitford et al. 1988). A prereproductive isolating mechanism between strains is not strongly fixed. This study and Pashley & Martin (1987) did not give females a choice between males of the two strains. However, preliminary studies reported by Pashley (1988b) indicated cross-attraction of strains occurs in the field even though males are preferentially attracted to females of their own strain. Pashley (unpublished) also reported that corn females did not mate with rice males but rice females accepted corn males. Studies must be conducted to further evaluate cross-attraction and mating in the field. In addition, extensive mate choice experiments should be performed to determine if mate preference serves as an isolating mechanism between strains.

Pashley (unpublished) suggests that temporal isolation by way of differences in mating times may be the primary isolating mechanism between strains. Corn strain mating occurs during the first part of the night while rice strain mate the last third. Thus, mating behavior and hybrid presence must be evaluated to establish if reproductive isolating mechanisms between fall armyworm strains exist.

In addition to fall armyworm strain differences influencing reproductive parameters, colonization of insects may cause changes in phenotypes (Mason et al. 1987). Phenotypic changes caused by random genetic drift, founder effects, nonrandom mating, or selection during colonization may influence reproductive behavior, fertility, and rates of reproduction (Dame et al. 1964, Fye & LaBrecque 1966, Raulston 1975, Economopoulos et al. 1976). Thus, inherent fall armyworm differences and colonization of insects potentially influenced the differences in reproduction observed in this study.

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References Cited

BURTON, R. L. 1967. Mass rearing the fall armyworm in the laboratory. USDA-ARS 33-117.

DAME, D. A., D. B. WOODARD, H. R. FORD, AND D. E. WEIDHAAS. 1964. Field behavior of sexually sterile *Anopeheles quadrimaculatus* males. Mosquito News 24: 6-14.

ECONOMOPOULOS, A. P., A. V. VOYADJOGLOU, AND A. GIANNAKAKIS. 1976. Reproductive behavior and physiology of *Dacus oleae*: Fecundity as affected by mating, adult diet, and artificial rearing. Ann. Entomol. Soc. America 69: 725-729.

FYE, R. L., AND G. C. LABRECQUE. 1966. Sexual acceptability of laboratory strains of male house flies in competition with wild strains. J. Econ. Entomol. 59: 538-540.

LYNCH, R. E., W. G. MONSON, B. R. WISEMAN, AND G. W. BURTON. 1983. Bermudagrass resistance to fall armyworm (Lepidoptera: Noctuidae). Environ. Entomol. 70: 1837-1840.

MASON, L. J., D. P. PASHLEY, AND S. J. JOHNSON. 1987. The laboratory as an altered habitat: phenotypic and genetic consequences of colonization. Florida Entomol. 70: 49-58.

PASHLEY, D. P. 1986. Host associated genetic differentiation in fall armyworm: a sibling species complex? Ann. Entomol. Soc. America 79: 898-904.

PASHLEY, D. P. 1988a. Quantitative genetics, development and physiological adaptation in sympatric host strains of fall armyworm. Evolution 42: 93-102.

PASHLEY, D. P. 1988b. Current status of fall armyworm host strains. Florida Entomol. 71: 227-234.

PASHLEY, D. P. 1989. Host-associated differentiation in armyworms (Lepidoptera: Noctuidae): an allozymic and mitochondrial DNA perspective, pp. 103-114 *in* H. D. Loxdale and J. den Hollander (eds.). Systematics Association Special Volume No. 39. Clarendon Press, Oxford.

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. 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., S. S. QUISENBERRY, AND T. JAMJANYA. 1987a. Impact of fall armyworm (Lepidoptera: Noctuidae) host strain on the evaluation of Bermudagrass resistance. J. Econ. Entomol. 80: 1127-1130.

PASHLEY, D. P., T. C. SPARKS, S. S. QUISENBERRY, J. JAMJANYA, AND P. DOWD. 1987b. Two fall armyworm strains feed on corn, rice, and Bermudagrass. Louisiana Agriculture 30: 8-9.

PERKINS, W. D. 1979. Laboratory rearing of the fall armyworm. Florida Entomol. 62: 87-91.

QUISENBERRY, S. S., AND F. WHITFORD. 1988. Evaluation of bermudagrass resistance to fall armyworm (Lepidoptera: Noctuidae): influence of host strain and dietary conditioning. J. Econ. Entomol. 81: 1463-1468.

RAULSTON, J. R. 1975. Tobacco budworm: Observation on the laboratory adaptations of a wild strain. Ann. Entomol. Soc. America 68: 139-142.

SAS INSTITUTE. 1985. SAS user's guide: statistics, version 5. SAS Institute, Cary, N.C.

WHITFORD, F., S. S. QUISENBERRY, T. J. RILEY, AND J. W. LEE. 1988. Oviposition preference, mating compatibility, and development of two fall armyworm strains. Florida Entomol. 71: 235-243.