Fitness and Mating Compatibility of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) Populations from Different Host Plant Species and Regions in Argentina

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ABSTRACT Two strains (corn and rice) of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), have been identified that differ in their host plant preferences and performance. Although these strains have been shown to be partially reproductively incompatible, the geographic and host-related variability within them has received less attention. In the current study, fall armyworm larvae were collected from a variety of different hosts and from six provinces in Argentina. The following populations were established in the laboratory: Salta province (corn), Tucumán province (corn, alfalfa, soybean, wheat, and weeds), Santiago del Estero province (corn and alfalfa), Chaco province (weeds), Santa Fé province (corn), and Buenos Aires province (corn). The populations were characterized with respect to egg, larval, and pupal duration; pupal mass; adult longevity; sex ratio; number of spermatophores per female; preoviposition; oviposition and postoviposition period; number of eggs and egg masses per female; and egg viability. Small but significant differences were observed among the populations collected from different hosts within Tucumán province with respect to the duration of different life stages, pupal mass, and reproductive characteristics. Similarly, small but significant differences were observed among the populations collected from corn in different provinces. Reproductive compatibility studies also were conducted among the different fall armyworm corn populations, looking at the same reproductive parameters, as well as adult longevity. Fall armyworm populations from the north of the country showed no incompatibility among populations. However, indications of incompatibility were observed between the northern populations and a geographically distinct population from Buenos Aires.

RESUMEN Dos biotipos (maíz y arroz) del "cogollero del maíz", *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), fueron identificados por sus diferencias en las preferencias de las plantas hospederas y sus parámetros de vida. Si bien estos biotipos mostraron ser incompatibles reproductivamente en forma parcial, la variabilidad relacionada a aislamiento geográfico y a las plantas hospederas dentro de estos biotipos no SE estudiaron en profundidad. En este estudio SE colectaron larvas del cogollero del maíz de diferentes plantas hospederas y en seis provincias de Argentina. Se establecieron las siguientes poblaciones en el laboratorio: Salta (maíz), Tucumán (maíz, alfalfa, soja, trigo y malezas), Santiago del Estero (maíz y alfalfa), Chaco (malezas), Santa Fé (maíz) y Buenos Aires (maíz). Se caracterizaron las poblaciones con respecto a duración del estado de huevo, larva y pupa, peso de las pupas, longevidad de los adultos, proporción de sexos, número de espermatóforos, período de preoviposición, oviposición y postoviposición, número de huevos y posturas por hembra, número de huevos por postura y viabilidad de los huevos. Se encontraron diferencias significativas pero de poca magnitud entre las poblaciones colectadas de las diferentes plantas hospederas en la provincia de Tucumán con respecto a la duración de los diferentes estados del ciclo de vida, peso de las pupas y características reproductivas. Del mismo modo, al analizar las poblaciones colectadas en maíz pero de distintas provincias SE encontraron diferencias significativas para las variables analizadas. También SE estudió la compatibilidad

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reproductiva entre las poblaciones colectadas en maíz, analizándose los mismos parámetros reproductivos y la longevidad de los adultos. Las poblaciones del cogollero del norte del país no mostraron incompatibilidad entre ellas. Sin embargo, SE evidenciaron signos de incompatibilidad entre dichas poblaciones y una población geográficamente distante proveniente de la provincia de Buenos Aires.

KEY WORDS fall armyworm, reproductive compatibility, strain, isolation

Within-species variation associated with different host plant preferences is common in polyphagous insect species. For example, two strains (corn and rice) of the highly polyphagous fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), have been identified previously (Pashley et al. 1985, Pashley 1986) that differ genetically (Pashley 1986, Lu et al. 1992, Lu and Adang 1996, Pashley et al. 2004, Clark et al. 2007) and in their patterns of host plant use. Larvae of the "corn strain" have been reported to feed on corn (*Zea mays* L.), sorghum (*Sorghum vulgare* Pers.), and cotton (*Gossypium hirsutum* L.), whereas the "rice strain" has been reported to feed on rice (*Oriza sativa* L.), Johnson grass (*Sorghum halepense* L.), and Bermuda grass [*Cynodon dactylon* (L.)] (Pashley 1988). Physiological (i.e., developmental) differences have been observed between these strains when reared on each other's host plants, on artificial diets, or on selected Bermuda grass genotypes (Quisenberry 1991, Pashley et al. 1995), and the strains differ in their ovipositional preferences (Quisenberry 1991).

Studies of interstrain hybridization and compatibility have been conducted to determine the taxonomic status of the strains. Pashley and Martin (1987) reported unidirectional reproductive isolation in interstrain matings; in no-choice matings, rice females mated with corn males but corn females did not mate with rice males (but see Whitford et al. 1988). Pashley et al. (1992) suggested that the strongest barrier to interstrain mating was temporal separation of mating activities throughout the night.

If the corn and rice strains of fall armyworm are reproductively isolated, this has important consequences for management strategies. However, the degree of isolation that exists under natural conditions is unclear. For example, molecular studies by Clark et al. (2007) with fall armyworm populations from the United States, México, Puerto Rico, Brazil (only collected from corn), and Argentina showed that the majority of the genetic variability was within populations and not among populations, suggesting that substantial gene flow occurs among fall armyworm strains and populations in the Western Hemisphere. In contrast, Murúa and Baigorí (2004) suggested that Argentina fall armyworm populations are genetically structured and López-Edwards et al. (1999) found that three corn fall armyworm populations from the eastern side of the Sierra Madre Mountains were reproductive incompatible with two corn populations from the western side. López-Edwards et al. (1999) also observed significant differences in fitness parameters such as pupal duration and pupal mass among these different populations.

Most of the work on fall armyworm strains and population structure has been conducted in the United States, even though fall armyworm is a significant pest of corn and other crops such as cotton and sorghum throughout Central and South America (Sparks 1979). Busato et al. (2005) affirmed that both the corn and rice strains of fall armyworm are present in Brazil, but in general little is known about the status of these strains in the remainder of the region, and the degree of genetic structuring among populations but within strains remains an open question.

The introduction and adoption of genetically modified (*Bacillus thuringiensis;* Bt) corn hybrids targeted against fall armyworm and other lepidopteran corn pests in the region, including Argentina, Colombia, and Honduras, has increased the need to understand these aspects of fall armyworm population structure. Widespread use of Bt corn hybrids could lead to the evolution of insect resistance to the insecticidal Bt proteins in these products. As a consequence, Bt corn hybrids are sold with a requirement that growers who purchase the seed also plant a non-Bt corn refuge on their farms as a source of susceptible pest insects (Roca 2002). For polyphagous target pests such as fall armyworm, common alternative hosts can act as an additional source of refuge so long as there as the pest populations on these alternative hosts are synchronous with those on Bt corn, and there are no barriers to insects coming from corn mating with those coming from alternative hosts. Therefore, it is important to understand the relative fitness of fall armyworm coming from different hosts and whether fall armyworm from different hosts (particularly those used by the corn strain) are capable of interbreeding.

The aim of this study is to determine whether there are fitness differences among fall armyworm populations collected from different host plants and different provinces in Argentina, and whether fall armyworm populations collected from corn in different locations are reproductively compatible. In particular, we focused on compatibility among populations collected from corn in five different provinces of Argentina.

Materials and Methods

Insect Collections. Fall armyworm were collected as larvae from different crops in commercial fields from six Argentinean provinces: Salta (SAL), Tucumán (TUC), Santiago del Estero (SDE), Chaco (CHA), Santa Fé (SFE), and Buenos Aires (BUE)

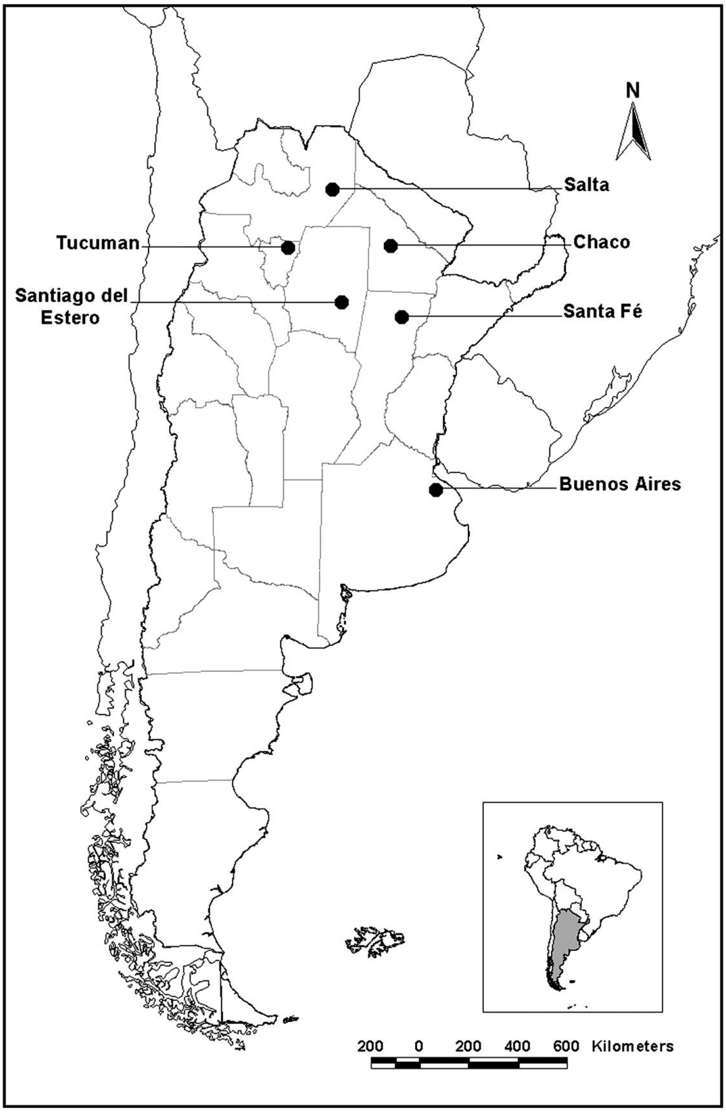

Fig. 1. Argentinian provinces where fall armyworm larvae were collected (SAL, Salta; TUC, Tucumán; SDE, Santiago del Estero; CHA, Chaco; SFE, Santa Fé; BUE, Buenos Aires).

(Fig. 1). For each province, the crops sampled were Salta: corn; Tucumán: corn, alfalfa (*Medicago sativa* L.), soybean [*Glycine max* (L.) Merr.], wheat (*Triticum aestivum* L.), and different weeds; Santiago del Estero: corn and alfalfa; Chaco: weeds; Santa Fé: corn; and Buenos Aires: corn. Sampling sites within a province were in adjacent fields. The weeds surveyed were Guinea grass (*Panicum maximum* Jacq.) and Bermuda grass [*Cynodon dactylon* (L.) Pers.]. Collections took place between January 2005 and March 2006, when corn was in later vegetative and reproductive stages and therefore supporting fall armyworm populations. In any given field, larvae of all instars were collected from at least 30 randomly selected plants. The collected larvae were taken back to the laboratory where they were placed in chambers under controlled conditions (27 ± 2°C and 70–75% RH) until adult emergence. Late instars and adults were examined to confirm that all individuals were fall armyworm. Each sampled crop in each province was maintained as a separate population.

Sample insects from each fall armyworm populations were deposited as voucher specimens in the collection of Sección Zoología Agrícola, Estación Experimental Agroindustrial Obispo Colombres, Tucumán, Argentina.

Insect Rearing. Rearing of each population were carried out between April 2005 and September 2006 in chambers under controlled conditions at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D). Adults were maintained in cylindrical polyethylene-terephthalate oviposition cages (30 cm in height and 10 cm

Table 1. Number of homotypic and heterotypic crosses performed between different populations of *S. frugiperda*

			♂										
	Province[a]	Host	SAL	TUC					SDE		CHA	SFE	BUE
			Corn	Corn	Alfalfa	Soybean	Wheat	Weed	Corn	Alfalfa	Weed	Corn	Corn
♀	SAL	Corn	23	24					25	5		6	7
	TUC	Corn	28	20					37	4		2	8
		Alfalfa			19								
		Soybean				18							
		Wheat					41						
		Weed						18					
	SDE	Corn	24	50					36	23		4	12
		Alfalfa	5	15					11			2	
	CHA	Weed									23		
	SFE	Corn	3	2					2	2		14	11
	BUE	corn	10	12					14			11	22

[a] SAL, Salta province; TUC, Tucumán province; SDE, Santiago del Estero province; CHA, Chaco province; SFE, Santa Fe province; and BUE, Buenos Aires province.

in diameter). For aeration, the top was covered with a nylon mesh cloth, and a hole was made on one side. These cages contained pieces of paper that allowed the females to rest and to lay the eggs. Food was provided via a cotton plug saturated with a mixture of honey and water [1:1 (vol:vol)], which was changed every day. Cages were checked daily for oviposition and adult mortality. Egg masses were collected and deposited in glass tubes (12 cm in height and 1.5 cm in diameter). Once emerged, the neonate larvae were placed individually in glass tubes with artificial larval diet (Osores et al. 1982) which was supplemented every 2 or 3 d. As larvae pupated, pupae were placed in cylindrical cages until adult emergence. Adults were used to initiate a new generation. After establishing a colony for each population and crop, individuals from the second to the seventh generation were used for studies of fitness and interpopulation reproductive compatibility.

Fitness of Fall Armyworm Populations. Populations were characterized using single-pair cages and cohort cages. For the single-pair cages, one virgin female and one virgin male (<24 h old) from the same fall armyworm population were paired in the cylindrical oviposition cages described above. Moths were maintained in their cages, and daily mortality and oviposition were recorded until both moths died. Dead females were dissected to determine the number of spermatophores present in their reproductive tract. Egg masses were collected and placed in glass tubes, and the percentage of eggs hatching was recorded. The single-pair cages were used to determine the number of spermatophores per female, the duration of the preoviposition, oviposition and postoviposition (days that the female survives after carrying out last oviposition) period, number of eggs, number of egg masses per female, percentage of egg hatch, and adult longevity. In addition, cages with several females and males from the same population (large cohort cages) were set up to obtain eggs and the duration of embryonic development was recorded. In addition, eggs from different egg masses were collected to obtain neonate larvae. These neonates were placed in glass tubes with artificial larval diet and larval development was followed until pupation and eventual adult emergence. The cohort cages were used to determine the following parameters: egg, larval and pupal duration, pupal mass (obtained 24 h after pupation), and adult sex ratio.

In total, 10 populations of fall armyworm, according to the province and crop from which they were sampled (Table 1), comprising 234 single-pair cages were analyzed. The population from alfalfa collected in Santiago del Estero could not be characterized because it was lost during rearing.

Reproductive Compatibility among Fall Armyworm Populations. Single-pair cages with males and females from different populations were set up as described above. Pairs of virgin, recently emerged (<24 h) fall armyworm adults were placed in cylindrical oviposition cages. Moths were maintained in their cages and daily oviposition and mortality were recorded until both moths died. Dead females were dissected to determine the number of spermatophores in their bursa copulatrix. The parameters measured were as follows: number of spermatophores, preoviposition, oviposition and postoviposition period, number of eggs and egg masses per female, adult longevity, and percentage egg hatch. Mating combinations were performed according to insect availability and a total of 28 heterotypic combinations were studied, consisting of 359 separate pairs of moths.

Data Analysis. For the fitness studies, data were analyzed using analysis of variance (ANOVA) to detect differences among fall armyworm populations. Multiple comparisons among the means for the different populations were performed with Tukey's test. The analysis was carried out in three parts: 1) comparisons were made among fall armyworm populations collected from different host plants in Tucumán province; 2) comparisons were made among fall armyworm populations collected from corn in different provinces of Argentina (Salta, Tucuman, Santiago del Estero, Santa Fé, and Buenos Aires); and 3) comparisons were made between two populations collected from weeds in different provinces (Tucumán and Chaco). For the reproductive compatibility studies, because of the large number of combinations set up

Table 2. Duration (mean ± SE) of egg, larval, and pupal stages; adult longevity; sex ratio; and pupal mass of *S. frugiperda* populations collected on different host plants in Tucumán province in Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Origin	Egg stage (d)	Larval stage (d)	Pupal stage (d)	Female life (d)	Male life (d)	Sex ratio (M:F)	Pupal mass (mg)
Corn	2.63 ± 0.03b	18.18 ± 0.31d	9.28 ± 0.16b	12.70 ± 1.03a	16.60 ± 1.29c	1:1.2	220 ± 3d
Alfalfa	3.05 ± 0.13c	16.51 ± 0.35c	8.75 ± 0.15a	12.16 ± 0.66a	13.84 ± 0.97bc	1.8:1	190 ± 3b
Soybean	3.59 ± 0.12d	19.19 ± 0.11e	8.97 ± 0.09ab	16.44 ± 1.96a	9.11 ± 1.27a	1:1.2	200 ± 2c
Wheat	2.39 ± 0.03a	12.22 ± 0.12a	9.33 ± 0.07b	14.07 ± 1.16a	14.05 ± 0.65bc	1.2:1	220 ± 2d
Weeds	2.85 ± 0.08bc	14.78 ± 0.11b	9.35 ± 0.11b	14.61 ± 1.29a	12.00 ± 1.12ab	1.2:1	180 ± 4a

Values followed by the same letters within a column are not significantly different according to Tukey's test ($P > 0.05$).

(28) and differences in sample size among the different mating combinations (Table 1), a descriptive analysis of those combinations were more than five single pairs was carried out first, followed by ANOVA of certain combinations. Subsequently, the data were pooled according to whether the cross involved moths from the same population (homotypic) or from different populations (heterotypic), and a *t*-test was performed comparing the homotypic and heterotypic crosses for each dependent variable. For all of these studies, the duration of preoviposition, oviposition and postoviposition periods were compared among the heterotypic combinations for those females that laid eggs. Total fecundity and number of egg masses laid per female were compared for all females including those that laid no eggs. For percentage egg hatch, females that laid eggs but had no spermatophores were not included. All data were analyzed with InfoStat (2006)).

Results and Discussion

Fitness Differences among Fall Armyworm Populations

Populations Collected from Different Host Plants in Tucumán Province. In total, five different hosts were sampled in Tucumán province, and the life history and reproductive characteristics of the five resulting fall armyworm populations were compared. Small but significant differences were found among these populations in most of the characteristics that were measured.

Life History Characteristics. The duration of each life stage is presented in Table 2. Egg, larval, and pupal stage duration varied significantly among the populations from the different host plants (egg: $F = 40.92$; df = 4, 991; $P < 0.001$; larva: $F = 229.5$; df = 4, 631; $P < 0.001$; and pupae: $F = 4.08$; df = 4, 608; $P = 0.003$). The longest duration in the egg and larval stages were observed in the soybean population and the longest duration for the pupal stage was found in the populations derived from weeds. Pupal mass also differed among populations ($F = 35.58$; df = 4, 736; $P < 0.001$). The corn and wheat populations had heavier pupae than the other three populations, with lighter pupae occurring in the population collected from weeds. In addition, male longevity varied significantly among populations ($F = 6.51$; df = 4, 111; $P < 0.001$), with the population derived from soybean having the shortest life span. Female longevity did not differ significantly among populations ($F = 1.32$; df = 4, 111; $P > 0.05$). However, in the corn population, males lived longer than females (paired *t*-test: $t = 2.78$, df = 19, $P = 0.012$), whereas in the soybean population, females lived longer than males ($t = 2.90$, df = 17, $P < 0.01$).

The duration of egg, larval, and pupae stages were similar to those observed by Valverde et al. (1995) for fall armyworm populations collected in Tucumán province from corn and reared on artificial diet (but see Murúa et al. 2003, Murúa and Virla 2004). Previous studies also have observed physiological differences between sympatric corn and rice fall armyworm strains, including differences in growth and development on artificial diets and on their respective host plants (Pashley 1988, Busato et al. 2005). These studies indicated that developmental characteristics were more strongly influenced by larval host than by strain. Therefore, larvae were reared on artificial diet in the current study to remove any larval host effect and thereby reveal any genetic differences among populations associated with different host plants. In the current study, the observed differences are among

Table 3. Number (mean ± SE) of spermatophores per female, duration of preoviposition, oviposition and postoviposition periods, number of eggs per female, egg masses per female, and percentage of egg hatch of *S. frugiperda* populations collected on different host plants in Tucumán province in Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Origin	Spermatophores per female	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Eggs/female	Egg masses/ females	% egg hatch
Corn	1.30 ± 0.15ab	3.50 ± 0.40ab	7.44 ± 0.96a	2.17 ± 0.48a	955.05 ± 149.06a	8.80 ± 1.13b	76.81 ± 7.80bc
Alfalfa	2.32 ± 0.47b	4.38 ± 0.76ab	5.38 ± 0.78a	2.44 ± 0.52a	885.89 ± 170.86a	6.32 ± 1.05ab	46.53 ± 12.70a
Soybean	0.83 ± 0.12a	4.23 ± 1.59ab	6.62 ± 1.95a	5.62 ± 2.10a	519.83 ± 148.42a	4.44 ± 1.05a	49.04 ± 12.19ab
Wheat	1.41 ± 0.19ab	2.25 ± 0.26a	5.31 ± 0.53a	3.72 ± 0.43a	978.10 ± 102.69a	5.66 ± 0.63ab	93.84 ± 1.36c
Weeds	0.78 ± 0.22a	6.20 ± 1.04b	6.13 ± 0.56a	2.27 ± 0.42a	758.89 ± 147.74a	7.22 ± 1.04ab	77.12 ± 12.79bc

Values followed by same letters within a column are not significantly different according to Tukey's test ($P > 0.05$).

Table 4. Duration (mean ± SE) of egg, larval and pupal stages, adult longevity, sex ratio, and pupal mass of *S. frugiperda* populations collected on corn in different provinces of Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Origin	Egg stage (d)	Larval stage (d)	Pupal stage (d)	Female life (d)	Male life (d)	Sex ratio (M:F)	Pupal mass (mg)
SAL[a]	2.99 ± 0.05b	16.82 ± 0.13a	9.85 ± 0.12c	13.83 ± 1.38a	16.52 ± 1.35b	1:1.2	220 ± 3b
TUC	2.63 ± 0.03a	18.18 ± 0.31b	9.28 ± 0.16ab	12.70 ± 1.03a	16.60 ± 1.29b	1:1.2	220 ± 3b
SDE	2.67 ± 0.04a	17.83 ± 0.16b	9.56 ± 0.12bc	13.47 ± 1.06a	13.08 ± 0.57ab	1:1.2	210 ± 3b
SFE	2.82 ± 0.05ab	18.41 ± 0.22b	9.31 ± 0.11ab	12.50 ± 1.56a	13.79 ± 0.78b	1.2:1	220 ± 3b
BUE	3.29 ± 0.07c	18.58 ± 0.25b	9.03 ± 0.11a	9.41 ± 0.79a	9.68 ± 1.01a	1:1	200 ± 3a

Values followed by same letters within a column are not significantly different according to Tukey's test ($P > 0.05$).

[a] SAL, Salta province; TUC, Tucumán province; SDE, Santiago del Estero province; SFE, Santa Fe province; and BUE, Buenos Aires province.

populations that came from collection sites in a single province. Although the differences observed were not large in biological terms, they still suggest that substantial genetic variability exists for these characteristics among fall armyworm populations at a relatively fine spatial scale.

Reproductive Parameters. Parameters related to reproduction are presented in Table 3. The mean number of spermatophores found in the female reproductive tract differed among the populations and ranged from one to nine ($F = 4.79$; df = 4, 111; $P = 0.001$). The alfalfa population had the greatest number, whereas the population derived from weeds had the lowest (Table 3). In general, the number of spermatophores obtained in all populations was similar to that found by García and Clavijo (1989) and Pashley et al. (1995). García and Clavijo (1989) also found that a fall armyworm strain bred on young corn leaves transferred a significantly higher number of spermatophores than those bred on >40-d-old plants, suggesting an important role of larval nutrition in the reproductive output of the adult. However, Pashley et al. (1995) found that the number of spermatophores transferred was not associated with either the strain or the larval host.

The longest preoviposition period was observed in the populations from weeds, which differed significantly from the soybean and wheat populations ($F = 4.39$; df = 4, 89; $P = 0.03$). No significant differences were found in the length of the oviposition period ($F = 1.04$; df = 4, 89; $P > 0.05$). After carrying out the last oviposition, the females lived from 0 to 27 d. Populations varied significantly in the length of this postoviposition period ($F = 2.68$; df = 4, 89; $P = 0.037$), but the Tukey test did not reveal differences between any specific pairs of populations ($P > 0.05$). These values are comparable with previous studies (Pashley et al.1995, Murúa and Virla 2004, Busato et al. 2005). Pashley et al. (1995) and Busato et al. (2005) also found significant differences among populations in the preoviposition period.

Total egg production varied from 0 to 2,900 eggs per female, but no significant differences were found among populations ($F = 1.71$; df = 4, 111; $P > 0.05$), although there was a tendency in the females derived from soybean to lay fewer eggs (Table 3). The values obtained in this study were similar to those reported by Murúa and Virla (2004) and Busato et al. (2005).

The number of egg masses laid per female varied significantly among populations ($F = 2.79$; df = 4, 111; $P = 0.03$). The highest number of egg masses came from the corn population, and the lowest came from the soybean population. The values obtained in this study were similar to those reported by Murúa and Virla (2004).

The mean percentage of eggs hatching ranged from 46 to 93% (Table 3), and there were significant differences among the populations ($F = 1.51$; df = 4, 77; $P < 0.001$). Soybean and alfalfa populations had the lowest values and the wheat population was highest. Some females showed very low fertility values (<10%), even when they laid a significant number of eggs (>100). The values obtained in this study were similar to those reported by Pashley et al. (1995) (but see Murúa and Virla (2004).

Populations Collected in Corn from Different Provinces. Populations collected from corn in five provinces were compared.

Life History Characteristics. The duration of each life stage is presented in Table 4. Significant differences were found among populations for the egg ($F =$

Table 5. Number (mean ± SE) of spermatophores per female, duration of preoviposition, oviposition and postoviposition periods, number of eggs per female, egg masses per female, and percentage of egg hatch of *S. frugiperda* populations collected on corn in different provinces of Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Origin	Spermatophores/ female	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Eggs/female	Egg masses/ female	% egg hatch
SAL[a]	1.22 ± 0.19a	5.17 ± 1.12a	6.91 ± 0.70b	1.74 ± 0.35a	1,165.04 ± 138.36b	9.61 ± 0.99a	90.12 ± 2.53b
TUC	1.30 ± 0.15a	3.50 ± 0.40a	7.44 ± 0.96b	2.17 ± 0.48a	955.05 ± 149.06ab	8.80 ± 1.13a	76.81 ± 7.80b
SDE	1.53 ± 0.30a	5.32 ± 0.81a	5.68 ± 0.65ab	2.16 ± 0.45a	608.86 ± 97.59a	8.36 ± 1.14a	32.35 ± 7.35a
SFE	1.50 ± 0.29a	2.50 ± 0.38a	6.83 ± 0.76b	2.25 ± 0.77a	1,233.93 ± 200.62b	9.64 ± 1.77a	85.63 ± 7.97b
BUE	1.59 ± 0.30a	3.80 ± 0.72a	3.35 ± 0.43a	2.65 ± 0.42a	717.82 ± 125.87ab	4.95 ± 0.92a	66.78 ± 8.69b

Values followed by same letters within a column are not significantly different according to Tukey's test ($P > 0.05$).

[a] SAL, Salta province; TUC, Tucumán province; SDE, Santiago del Estero province; SFE, Santa Fe province; and BUE, Buenos Aires province.

Table 6. Duration (mean ± SE) of egg, larval and pupal stages, adult longevity, sex ratio, and pupal mass of *S. frugiperda* populations collected on weeds in Tucumán and Chaco provinces in Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Origin	Egg stage (d)	Larval stage (d)	Pupal stage (d)	Female life (d)	Male life (d)	Sex ratio (M:F)	Pupal mass (mg)
TUC^2	2.85 ± 0.08b	14.78 ± 0.10a	9.35 ± 0.11a	14.61 ± 1.29a	12.00 ± 1.12a	1.2:1	180 ± 3.70a
CHA	2.36 ± 0.07a	14.8 ± 0.13a	9.71 ± 0.10b	15.43 ± 1.36a	14.43 ± 1.17a	1:1	220 ± 3.20b

Values followed by same letters within a column are not significantly different according to Student's *t*-test ($P > 0.05$).

[a] TUC, Tucumán province; CHA, Chaco province.

27.19; df = 4, 1,074; $P < 0.001$), larval ($F = 11.75$; df = 4, 721; $P < 0.001$), and pupal ($F = 6.28$; df = 4, 480; $P < 0.001$) stage durations. The longest egg duration and the shortest pupal duration were observed in the Buenos Aires population. The shortest larval duration was observed in the Salta population (Table 4). Female longevity did not vary significantly among the populations ($F = 2.23$; df = 4, 110; $P > 0.05$), but male longevity did vary among populations ($F = 7.79$; df = 4, 110; $P < 0.001$). Male longevity was shortest for the Buenos Aires population and longest for the Salta and Tucumán populations. In general, male and female longevity did not differ within populations, except for the Tucumán population where males lived longer than females (paired *t*-test: $t = 2.78$, df = 19, $P = 0.012$). Pupal mass ranged from 100 to 300 mg. Pupae from the Buenos Aires population were significantly lighter than the other populations (Table 4) ($F = 7.06$; df = 4, 820; $P < 0.001$).

These patterns were similar to those observed when comparing populations from different host plants in the same province; significant differences were seen among populations in most characteristics. This suggests that differences among fall armyworm populations may be a function of host plant, geographic location, and strain.

Reproductive Parameters. The number of spermatophores per female ranged from zero to nine but did not vary significantly among populations. Mean values were smaller than those mentioned by a previous study (Pashley et al. 1995).

The preoviposition period did not vary significantly among populations ($F = 1.73$; df = 4, 99; $P > 0.05$). In contrast, the oviposition period varied significantly among populations ($F = 4.8$; df = 4, 99; $P = 0.014$), with Tucumán and Salta having the longest oviposition periods (Table 5). In general similar values were reported by Busato et al. (2005).

Mean total egg production varied significantly among populations ($F = 4.27$, df = 4, 110; $P < 0.001$), with Santiago del Estero having the lowest production (608.86 ± 97.59) and Santa Fé the highest (1,233.93 ± 200.62). The number of egg masses laid per female did not vary significantly among populations ($F = 2.42$; df = 4, 110; $P = 0.053$).

The differences in egg viability were significant among fall armyworm populations ($F = 12.05$; df = 4, 83; $P < 0.001$). The lowest egg hatch was observed for the Santiago del Estero population.

Populations Collected from Weeds in Tucumán and Chaco Provinces. *Life History Characteristics.* The duration of each life stage is presented in Table 6. The egg (*t*-test: $t = 4.55$; df = 169; $P = 0.0001$) and pupal (*t*-test: $t = 2.31$; df = 171; $P = 0.022$) stages showed significant differences, whereas larval duration did not differ between the populations (*t*-test: $t = 0.1$, df = 162, $P = 0.922$). Pupal masses also differed significantly between the populations (*t*-test: $t = 8.13$, df = 216, $P < 0.0001$). Both female and male longevity were not significantly different between the populations ($t = 0.43$, df = 39, $P > 0.05$ and $t = 1.47$: df = 39, $P > 0.05$). The values obtained in this study were similar to the values reported by Busato et al. (2005) and López-Edwards et al. (1999).

Reproductive Parameters. None of the parameters measured differed significantly between the populations (*t*-tests: $P > 0.05$ in all cases; Table 7).

Reproductive Compatibility among Fall Armyworm Populations

In total, 28 heterotypic crosses were carried out between populations collected from corn and alfalfa in five provinces (Table 1). Of these, data were obtained from more than five pairs with 18 of these crosses (Table 8). Due to the high number of combinations and the heterogeneity in the number of pairs analyzed for each combination, the performance of all of the

Table 7. Number (mean ± SE) of spermatophores per female, duration of preoviposition, oviposition and postoviposition periods, number of eggs per female, egg masses per female, and percentage of egg hatch of *S. frugiperda* populations collected on weeds in Tucumán and Chaco provinces of Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Origin	Spermatophores/ female	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Eggs/female	Egg masses/ females	% egg hatch
TUC^a	0.78 ± 0.22a	6.20 ± 1.04a	6.13 ± 0.56a	2.27 ± 0.42a	758.89 ± 147.74a	7.22 ± 1.04a	77.12 ± 12.79a
CHA	1.22 ± 0.20a	5.85 ± 1.45a	5.40 ± 0.76a	3.45 ± 0.61a	702.09 ± 114.98a	5.91 ± 0.99a	61.69 ± 9.28a

Values followed by same letters within a column are not significantly different according to Student's *t*-test ($P > 0.05$).

[a] TUC, Tucumán province; CHA, Chaco province.

Table 8. Number (mean ± SE) of spermatophores per female, duration of preoviposition, oviposition and postoviposition periods, number of eggs per female, egg masses per female, and percentage of egg hatch from different heterotypic crosses of *S. frugiperda* using populations collected on corn and alfalfa in five provinces of Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

♀	♂	Spermatophores/ female	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Eggs/female	Egg masses/ females	% egg hatch
SDE corn[a]	SAL corn	1.79 ± 0.36	5.55 ± 1.26	5.86 ± 0.69	1.09 ± 0.28	1,226.46 ± 177.80	8.63 ± 1.28	81.91 ± 5.88
SAL corn	SDE corn	1.20 ± 0.15	4.78 ± 1.45	7.39 ± 0.76	1.35 ± 0.17	1,041.36 ± 141.54	8.72 ± 1.13	73.42 ± 8.49
SAL corn	TUC corn	1.96 ± 0.32	3.57 ± 0.56	8.26 ± 0.76	1.91 ± 0.27	1,214.13 ± 156.49	8.83 ± 1.02	74.22 ± 7.88
TUC corn	SAL corn	1.36 ± 0.33	3.26 ± 0.66	7.13 ± 1.05	1.74 ± 0.46	726.79 ± 93.75	7.54 ± 1.25	63.57 ± 9.22
SDE corn	SDE alfalfa	1.00 ± 0.22	5.95 ± 1.38	6.74 ± 1.02	3.21 ± 1.05	651.17 ± 123.58	8.13 ± 1.68	59.91 ± 12.58
SDE alfalfa	SDE corn	1.36 ± 0.24	3.10 ± 0.57	5.70 ± 0.21	2.10 ± 0.50	874.82 ± 162.90	6.55 ± 0.88	72.71 ± 8.31
SDE corn	TUC corn	1.22 ± 0.13	5.17 ± 0.70	6.46 ± 0.66	2.09 ± 0.38	1,000.38 ± 109.30	6.78 ± 0.67	82.19 ± 4.58
TUC corn	SDE corn	1.19 ± 0.18	4.32 ± 0.71	5.76 ± 0.80	1.68 ± 0.34	920.89 ± 119.26	6.78 ± 0.82	80.24 ± 5.93
SDE alfalfa	TUC corn	1.07 ± 0.18	3.50 ± 0.88	5.00 ± 0.75	2.50 ± 0.42	803.20 ± 129.88	4.67 ± 0.83	89.95 ± 2.92
SAL corn	SFE corn	1.67 ± 0.49	1.40 ± 0.24	6.80 ± 1.62	1.40 ± 0.68	1,365.33 ± 429.74	9.50 ± 2.59	99.12 ± 0.40
TUC corn	BUE corn	0.38 ± 0.18	8.00 ± 5.05	3.50 ± 1.44	7.25 ± 1.70	309.25 ± 197.10	3.50 ± 2.04	41.41 ± 41.22
BUE corn	TUC corn	1.08 ± 0.31	2.38 ± 0.38	3.75 ± 1.18	4.38 ± 1.07	478.92 ± 154.42	3.08 ± 1.06	83.87 ± 8.95
BUE corn	SFE corn	1.00 ± 0.23	4.11 ± 0.93	4.33 ± 0.58	4.56 ± 0.60	627.64 ± 168.79	3.45 ± 0.73	76.73 ± 14.01
SFE corn	BUE corn	0.64 ± 0.20	5.67 ± 1.73	4.78 ± 0.83	3.11 ± 0.99	702.18 ± 149.42	6.91 ± 1.34	55.15 ± 11.59
BUE corn	SDE corn	2.07 ± 0.34	2.83 ± 0.76	4.58 ± 0.66	3.83 ± 0.96	790.57 ± 125.54	5.79 ± 1.02	77.82 ± 9.50
SDE corn	BUE corn	0.42 ± 0.15	7.57 ± 1.81	6.14 ± 1.06	2.00 ± 0.49	375.08 ± 139.01	4.08 ± 1.55	43.65 ± 20.53
BUE corn	SAL corn	1.80 ± 0.59	6.00 ± 1.85	5.13 ± 0.99	5.00 ± 1.73	490.90 ± 126.44	4.60 ± 1.10	42.17 ± 15.72
SAL corn	BUE corn	0.43 ± 0.20	4.57 ± 1.17	5.14 ± 0.83	1.86 ± 0.26	774.14 ± 240.50	6.43 ± 0.92	63.62 ± 21.42

[a] SAL, Salta province; TUC, Tucumán province; SDE, Santiago del Estero province; SFE, Santa Fe province; and BUE, Buenos Aires province.

heterotypic crosses was first compared with that of all the homotypic crosses using *t*-tests. Significant differences were found in the number of spermatophores transferred ($t = 2.18$, df = 460, $P = 0.013$), egg hatch ($t = 2.33$, df = 339, $P = 0.020$), and number of egg masses laid ($t = 2.03$, df = 460, $P = 0.043$) (Table 9). Total fecundity was comparable for the two groups. The other variables showed no significant differences between the two types of crosses.

When the heterotypic crosses involving the Buenos Aires population, representing the Pampas region (PAM), are separated from the other heterotypic crosses involving only the populations from the north of Argentina (NOA), the Buenos Aires-related crosses were found to be significantly less productive than other crosses (Table 10; Fig. 2). To avoid any effect of larval host, the comparison in Table 10 is restricted to crosses involving NOA populations collected on corn because the Buenos Aires population was collected on corn. Significant differences were found between the regions (NOA versus PAM) and the type of cross (homotypic or heterotypic) for the number of spermatophores ($F = 6.80$; df = 3, 392; $P < 0.001$), the length of the oviposition period ($F = 8.84$; df = 3, 342; $P < 0.001$), the time elapsed between the last oviposition and the death of the female ($F = 15.65$; df = 3, 342; $P < 0.001$), the number of eggs per female ($F = 8.38$; df = 3, 392; $P < 0.001$), and the number of egg masses per female ($F = 10.87$; df = 3,392; $P < 0.001$). The average number of spermatophores was less than one in crosses that involved Buenos Aires males and NOA females, and it was only greater than one in a single, suggesting some degree of incompatibility. The number of spermatophores ranged from zero to two and from zero to six in the heterotypic crosses NOA × PAM and PAM × NOA, respectively, whereas spermatophore numbers ranged from zero to nine and from zero to four in the homotypic crosses NOA × NOA and PAM × PAM, respectively (Fig. 2). Percentage of egg hatch in PAM × NOA crosses were among the lowest, even when the females that received no spermatophores were not included in the analysis. In addition, the lowest total number of eggs laid (total fecundity) occurred in the heterotypic crosses (Table 10). PAM females that were mated to NOA males stopped laying eggs sooner than NOA females mated to NOA males. These results indicate that the population from Buenos Aires was partially incompatible with the other more northern populations, whereas the northern populations were compatible with each other (Table 10).

Reproductive isolation among fall armyworm populations previously has been attributed both to host adaptation (i.e., strain) (Pashley et al. 1992) and geo-

Table 9. Number (mean ± SE) of spermatophores per female, duration of preoviposition, oviposition and postoviposition periods, number of eggs per female, egg masses per female, and percentage of egg hatch of *S. frugiperda* heterotypic and homotypic crosses using populations collected on corn and alfalfa in various province of Argentina and reared at 27 ± 2°C, 70–75% RH, and a photoperiod of 14:10 (L:D) h

Type of cross	Spermatophore/ female	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Eggs/female	Egg masses/ female	% egg hatch
Heterotypic	1.27 ± 0.07a	4.52 ± 0.28a	6.13 ± 0.23a	2.34 ± 0.16a	861.70 ± 38.43a	6.78 ± 0.30a	74.51 ± 2.22a
Homotypic	1.56 ± 0.13b	4.36 ± 0.35a	5.87 ± 0.32a	2.21 ± 0.19a	878.47 ± 58.85a	7.93 ± 0.49b	64.65 ± 3.84a

Values followed by same letters within a column are not significantly different according to Student's *t*-test ($P > 0.05$).

Table 10. Number (mean ± SE) of spermatophores per female, duration of preoviposition, oviposition and postoviposition periods, number of eggs per female, egg masses per female, and percentage of egg hatch from different heterotypic crosses of *S. frugiperda* using populations collected on corn in five provinces and reared at 27 ± 2°C, 70–75% RH, and 14:10 (L:D) h

Type of cross (female × male)	Spermatophores/ female	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Eggs/female	Egg masses/ female	% egg hatch
NOA × NOA[a]	1.40 ± 0.08b	4.44 ± 0.28a	6.67 ± 0.25b	1.83 ± 0.13a	982.83 ± 42.95b	8.14 ± 0.33b	74.40 ± 2.31a
PAM × PAM	1.59 ± 0.30b	3.80 ± 0.72a	3.35 ± 0.43a	2.65 ± 0.42ab	717.82 ± 125.87ab	4.95 ± 0.92ab	66.78 ± 8.69a
NOA × PAM	0.47 ± 0.09a	6.22 ± 1.04a	5.04 ± 0.49ab	3.11 ± 0.54ab	529.42 ± 88.58a	5.21 ± 0.78a	51.94 ± 8.78a
PAM × NOA	1.51 ± 0.19b	3.73 ± 0.55a	4.46 ± 0.41ab	4.38 ± 0.54b	609.11 ± 72.60a	4.30 ± 0.51a	71.68 ± 6.19a

Values followed by same letters within a column are not significantly different according to Tukey's test ($P > 0.05$).

[a] NOA, populations from northern Argentina; PAM, populations from Pampas region.

graphic distance (López-Edwards et al. 1999). The results obtained here suggest that populations from the north of Argentina are compatible with each other. The same observation was reported by Quisenberry (1991), working with corn and rice fall armyworm strains in the United States. However, that study was performed with strains maintained in the laboratory for up to 4 yr, which raised concerns (Quisenberry 1991). In the current study, none of the populations analyzed were reared in the laboratory for more than seven generations, so laboratory adaptation is unlikely to have been a factor. Amplified fragment-length polymorphism analysis of fall armyworm populations collected in the United States, Mexico, Puerto Rico, Brazil, and Argentina found that the majority of the genetic variability occurred within populations and not among populations, indicating the presence of gene flow throughout the Western Hemisphere (Clark et al. 2007). However, López-Edwards et al. (1999) detected incompatibility among fall armyworm populations collected on corn in different regions of Mexico. In the current study, the most geographically separated population analyzed was the one from Buenos Aires, which showed some incompatibility with the populations from northern Argentina.

The immediate basis of the incompatibility was a lower number of spermatophores transferred to NOA females mated from PAM males, suggesting a failure of mating. In that combination, 50% of the crosses resulted in no transfer of spermatophores compared with the other three types of crosses in which only ≈20% of crosses resulted in no spermatophore transfer [$\chi^2_{(9)} = 34.19$, $P < 0.0001$]. Where spermatophores were found, egg hatch also tended to be lower, suggesting some additional postzygotic incompatibility. There is evidence that the mechanism responsible for unidirectional incompatibility in interstrain crosses

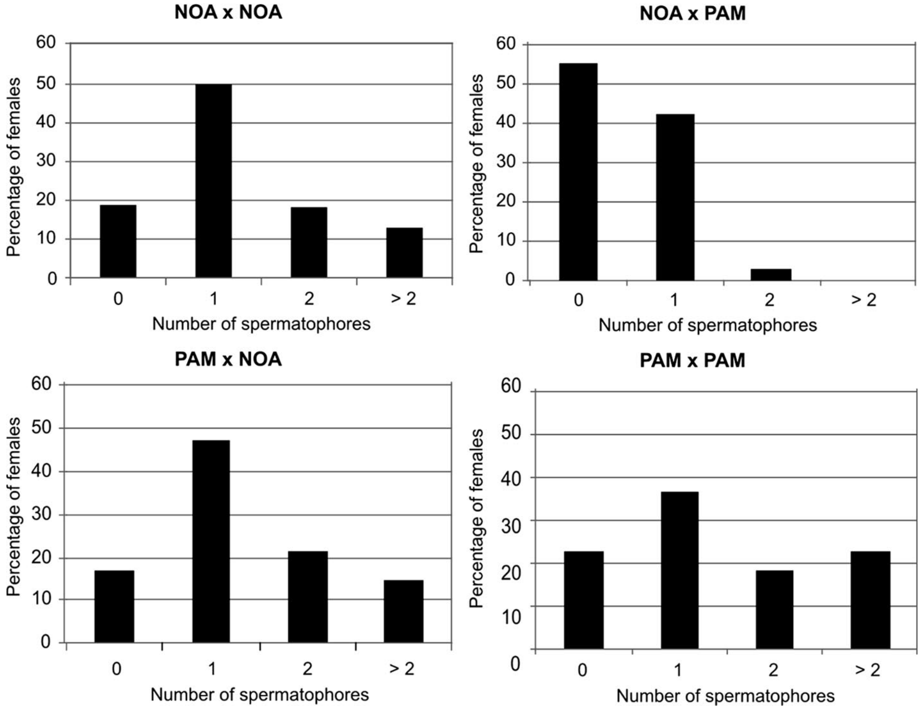

Fig. 2. Percentage of females with none, one, two, or more than two spermatophores from individual female × male crosses between NOA (northern Argentina) and PAM (Pampas) populations.

can be broken down during prolonged maintenance of laboratory colonies (Pashley and Martin 1987). Therefore, in our case, higher levels of isolation may occur under more natural conditions when moths have greater freedom in mating behavior.

Considerable evidence exists for reproductive incompatibility among the corn and rice strains. Unsuccessful crosses between the strains and in backcrosses result either from one or both of the sexes rejecting heterotypic individuals as mates, or from difficulties during pairing that inhibit the transfer of spermatophores (Pashley and Martin 1987, Whitford et al. 1988). Pashley et al. (1992) found the strongest barrier to interstrain mating was temporal partitioning of mating activities throughout the night; the corn strain mated exclusively in the first two thirds of the night, whereas the rice strain mated in the last one third. In addition, they found differences in the relative abundance of the two strains over the course of the season. Similar observations were made by Fuxa (1989); larval densities in Louisiana (United States) indicated an early presence of the corn strain (spring and midsummer) and a late presence of the rice strain (midsummer into fall).

The existence of these prereproductive isolating barriers suggests that the strains actually may be sibling species that do not readily interbreed in nature (Pashley and Martin 1987). Furthermore, López-Edwards et al. (1999) concluded that the different Mexican corn fall armyworm populations can be separated into two, or possibly three, different populations or strains; the Aguascalinetes, Nuevo León, and Yucatán populations were able to produce progeny when mated with each other but the Colima and Sinaloa populations were unable to produce progeny when mated with the other three populations or each other. They suggested that the strains developed through geographic isolation.

Conclusions

In the current study, fall armyworm populations derived from different hosts in the same area and populations collected from the same host but from different areas were characterized and tested for intercompatibility. This study represents the first comprehensive study of Argentinean fall armyworm populations aimed at detecting the presence of different strains either generated in sympatry, by host preferences, or in allopatry, by the presence of geographic barriers. The fall armyworm populations collected from different host plants in Tucumán province and bred on artificial diet differed in their developmental (life cycle, fertility, and viability) and reproductive (mating, number of spermatophores transferred) characteristics. Therefore, the larval host plant may affect subsequent generations of fall armyworm, although the host-related differences among populations tended to be relatively small.

Physiological and behavioral differences also were observed among fall armyworm populations collected from corn in different provinces of Argentina, but they were small in magnitude. In general, the fall armyworm populations from the Northern region were similar in their characteristics with the exception of Santiago del Estero population, which exhibited lower fitness. In addition, the population from Buenos Aires tended to differ in its developmental characteristics from the northern populations. Minimal differences were found between two populations collected from weeds in Tucumán and Chaco provinces.

No incompatibility was observed among the fall armyworm populations from the north of the country, which successfully mated in both directions, suggesting that substantial gene flow should occur among fall armyworm populations within a region, at least within the populations collected from corn. However, evidence of premating isolation was found between NOA corn populations and the population from Buenos Aires collected from corn, apparently related to geographical separation. The fall armyworm population from Buenos Aires may not be permanent; this area is recolonized every year during summer and fall. Therefore, it may be that this population reflects its original host source in another region (e.g., rice from northeastern Argentina, or even Uruguay or Brazil). Additional studies are needed with populations from Buenos Aires, the NOA region and other regions which may be the source of populations found in the Pampas to investigate if the incompatibility found resulted from host-associated divergence or geographical isolation.

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