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Growth and fecundity of *Spodoptera frugiperda* on native *Zea mays* and the teosinte *Z. luxurians*, from Oaxaca, Mexico

Crecimiento y fecundidad de *Spodoptera frugiperda* en *Zea mays* nativo y el teocintle *Z. luxurians*, de Oaxaca, México

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Abstract: Resistance to *Spodoptera frugiperda* (Lepidoptera: Noctuidae) damage has been documented in some Mexican maize races and teosintes. There are approximately 31 races of native maize and three races of teosinte in Oaxaca state, but little is known about their resistance to insect damage. This study compared the development and fecundity of *S. frugiperda* fed on native maize and the teosinte *Zea luxurians*, from Oaxaca, Mexico. No significant differences were determined in the development parameters of males and females according to the host plant types, except the pupal weight of males, which was higher on teosinte (0.189 g) than on native maize (0.174 g). Duration from hatching to adult emergence was 28.96 to 30.17 d on native maize and 28.51 to 30.34 d on teosinte. Females emerged before males in both host plant types. The sex ratio was approximately 0.5 for both sexes. Larval weight was higher on teosinte (0.451 to 0.459 g) than on native maize (0.442 to 0.454 g). According to the fecundity parameters, no significant differences in the duration of oviposition, the number of eggs per egg mass, eggs per female, and eggs per host plant types were determined. Fitness Index was positively correlated with the pupal weight of both sexes and the fecundity parameters of *S. frugiperda* females. Our results demonstrated that larval feeding on native maize and teosinte did not affect the development parameters and fecundity of *S. frugiperda*. Constitutive defenses in native maize leaves were similar to those of teosinte.

Keywords: Fall armyworm, fitness, maize phenotype, plant resistance, Zapalote Chico.

Resumen: La resistencia al daño por *Spodoptera frugiperda* (Lepidoptera: Noctuidae) se ha documentado para algunas razas mexicanas de maíz y teocintles. En el Estado de Oaxaca hay aproximadamente 31 razas de maíz y tres razas de teocintle, pero se conoce poco sobre su resistencia al daño por insectos. Este estudio comparó el desarrollo y fecundidad de *S. frugiperda* al alimentarse con maíz nativo y teocintle *Z. luxurians* de Oaxaca, México. No se determinaron diferencias significativas en los parámetros de desarrollo de machos y hembras de acuerdo con el tipo de planta hospedera, excepto en el peso de la pupa de machos, el cual fue mayor en teocintle (0,189 g) que en maíz nativo (0,174 g). El tiempo transcurrido desde eclosión a emergencia del adulto fue de 28,96 a 30,17 d en maíz nativo y de 28,51 a 30,34 d en teocintle. Las hembras emergieron antes que los machos en ambos tipos de planta hospedera. La proporción sexual fue de aproximadamente 0,5 para ambos sexos. El peso larval fue mayor en teocintle (0,451 a 0,459 g) que en maíz nativo (0,442 a 0,454 g). Respecto a los parámetros de fecundidad, no se determinaron diferencias significativas en el período de oviposición, número de huevos por masa de huevo, huevos por hembra, y huevos por tipo de planta hospedera. El Índice de Adecuación se correlacionó positivamente con el peso de la pupa en ambos sexos y con los parámetros de fecundidad de las hembras de *S. frugiperda*. Nuestros resultados demostraron que la alimentación larval en maíz nativo y en teocintle no afectaron los parámetros de desarrollo y fecundidad de *S. frugiperda*. Las defensas constitutivas de las hojas del maíz fueron similares a las de teocintle.

Palabras clave: Adecuación, fenotipo de maíz, gusano cogollero, resistencia vegetal, Zapalote Chico.

Introduction

Maize, *Zea mays* L. (Poales: Poaceae), is the main crop in Mexico with 7,481,137 ha planted per year and an average yield of 6.79 ton.ha^{-1} (SIAP 2021). *Spodoptera frugiperda* (J.E. Smith, 1797) (Lepidoptera: Noctuidae) is one of the main pests on the Americas' maize crop, causing mean yield losses of 17.31 to 35.57%, depending on data confidence (Overton *et al*. 2021).

Comparative studies between maize and teosintes have shown that the resistance mechanisms for herbivorous insects are stronger on teosinte than on maize, because of changes in life history, domestication process, and agronomic selection (Rosenthal and Welter 1995; Rosenthal and Dirzo 1997; Takahashi *et al*. 2012; Szczepaniec *et al*. 2013; Bernal *et al*. 2015; Moya-Raygoza 2016). Regarding this, perennial teosintes (*Z. perennis* (Hitchcock) and *Z. diploperennis* Iltis, Doebley and Guzmán) are more resistant than annual teosintes (*Z. mays* ssp. *parviglumis* Iltis and Doebley, *Z. mays* ssp. *mexicana* (Schrader)), followed by maize races, and finally by high-yielding hybrids (Rosenthal and Dirzo 1997; Dávila-Flores *et al*. 2013). However, the morphological, biochemical, and genetic mechanisms do not always explain why teosintes are more resistant than maize to herbivorous insects (Maag *et al*. 2015; Gaillard *et al*. 2018). Ontogeny of the plant (Maag *et al*. 2015), herbivore feeding specialization (Dávila-Flores *et al*. 2013; Köhler *et al*. 2015) and nutritional quality (Gaillard *et al*. 2018) may also play a role.

Nutritional quality of the host plant is one of the main factors involved in the development and fecundity of insects: the content of carbon, nitrogen, and defensive compounds (alkaloids, non-protein amino acids, glycosides, cyanogenic glucosinolates, terpenoids, and phenols) are important (Awmack & Leather 2002). In the assessment conducted by Takahashi *et al*. (2012), *S. frugiperda* larval growth was 1.2-fold higher on Tuxpeño maize than on *Z. mays* ssp. *parviglumis* teosinte. Szczepaniec *et al*. (2013) recorded a higher larval survival, a shorter duration of the larval stage, and a higher pupal weight on Tuxpeño maize than on teosinte (*Z. mays* ssp. *parviglumis* and *Z. diploperennis*). Gaillard *et al*. (2018) found that larvae of *S. frugiperda*, *S. exigua*, and *S. littoralis* were heavier on hybrid maize than on teosinte (*Z. mays* ssp. *parviglumis* and *Z. mays* ssp. *mexicana*). Finally, Turcotte *et al*. (2014) found that the feeding of *S. exigua* on *Z. mays* ssp. *parviglumis* teosinte affected more their survival and dry weight than on hybrid maize.

In Mexico, there are approximately 65 maize races (Serratos-Hernández 2012; Santillán-Fernández *et al*. 2021) and six species and subspecies of teosintes (Sánchez-González *et al*. 2018). Tuxpeño (De La Rosa-Cancino *et al*. 2016), Elotillo, Nal Tel (dos Santos *et al*. 2018), Uruapeño (Farias-Rivera *et al*. 2003), and Zapalote Chico (Widstrom *et al*. 2003; Nuessly *et al*. 2007; de Oliveira *et al*. 2018; Michereff *et al*. 2018; Crubelati-Mulati *et al*. 2019) have been documented as maize races with resistance or tolerance to *Spodoptera* spp. damage. In Oaxaca, Mexico, there are approximately 31 maize races (Serratos-Hernández 2012). One of them, called "Zapalote Chico", is a native maize of the Istmo de Tehuantepec region, and its resistance to *S. frugiperda* damage has already been documented (Widstrom *et al*. 2003). In a previous field study (unpublished data), Zapalote Chico was more tolerant than Cónico-Chalqueño and Bolita races to *S. frugiperda* damage. Regarding teosintes, *Z. mays* ssp. *mexicana*, *Z. mays* ssp. *parviglumis*, and *Z. luxurians* (Dorieu *et* Ascherson) are present in Oaxaca (Sánchez-González *et al*. 2018) as weeds and may have resistance genes to *S. frugiperda*. *Zea luxurians* is an annual teosinte found in San Felipe Usila in the Papaloapan region (Sánchez-González *et al*. 2018). There is no information on its resistance to insect damage. The aim of this study was to compare the development and fecundity of *S. frugiperda* fed on native *Z. mays*, Zapalote Chico, and the teosinte *Z. luxurians*, from Oaxaca, Mexico.

Materials and methods

Insect collection and rearing. To maintain *S. frugiperda* adults in laboratory conditions, continuous captures of larvae were carried out in maize plantations at the localities of Cuilapam de Guerrero, Santa Cruz Xoxocotlán, San Lorenzo Cacaotepec, and Santiago Apóstol, Oaxaca, Mexico. At the laboratory, larvae were fed with fresh leaves daily, *ad libitum*, until the larvae began pupating. Moths were confined in Kraft paper bags to favor their reproduction and were fed with a water and honey solution placed on a piece of cotton. For the feeding experiment with native maize or teosinte, *S. frugiperda* egg masses obtained during the first five days of oviposition were used. The study was conducted at the Biological Control laboratory of the Instituto Politécnico Nacional, CIIDIR (Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional) Unidad Oaxaca, under ambient environmental conditions.

Host plants. Seeds of Zapalote Chico maize and *Z. luxurians* teosinte collected in Santo Domingo Tehuantepec and San Felipe Usila, Oaxaca, respectively, were used. Plants were cultivated in 2 L pots with a mix of soil and compost. The teosinte seeds were sown in germination trays and transplanted into pots two weeks after emergence. On the same day that the teosinte was transplanted, native maize seeds were sown directly into pots. Three plants per pot and up to 20 pots per host plant type were used for experimental repetition. From sowing until the plants had two fully developed leaves (V2 stage), the pots were kept in a rustic greenhouse without humidity or temperature control. Later, the pots were placed outside the greenhouse and inside wooden cages covered with organza fabric to favor leaf development, increase plant height, and avoid insect damage. When the plants reached the V3 to V4 stage, an experiment with *S. frugiperda* egg masses was established.

Development parameters. Feeding groups were integrated with three *S. frugiperda* egg masses. Ten newly emerged larvae were randomly selected from each egg mass and placed individually in Petri dishes: five larvae on native maize leaves and five larvae on teosinte. In this manner, treatment pairs were established and feeding groups were integrated to form 12 repetitions (15 larvae per repetition). *Spodoptera frugiperda* larvae were fed with approximately 4 cm^2 of fresh leaves daily, *ad libitum*. The duration in days (d) of the developmental stages (larva, pupa, hatching to adult emergence, and adult), larval survival, pupal formation, adult emergence, mean and maximum weight per larva, and pupal weight were recorded. Every two days, the larval weight was recorded from the fifth day after hatching until the larva began pupating. The pupal weight was recorded on the third day of its formation. Larvae and pupae were weighed on an analytical balance Sartorius LP620P (SARTORIUS AG, Göttingen, Germany). For each feeding group, the adult lifespan was obtained by difference between the mean date of death and the mean date of the moths' emergence. To determine the performance of the offspring of males and females of *S. frugiperda*, the Fitness Index (*rL*) was calculated using the formula proposed by Nogueira *et al*. (2019): $rL = lx\ (mx\ /\ tl)$, where lx is the larval survival, mx is the mean pupal weight (mg), and tl is the duration of larval stage (d).

Fecundity parameters. When the adults emerged, the sex of each individual was determined to obtain the proportion of females and males (total females or males/total individuals) for each feeding group, and they were immediately confined in Kraft paper bags to promote mating. Once the oviposition process began, the moths were changed from the bags daily to remove the egg masses and to count the number of eggs produced. The eggs produced per day were counted with a stereoscope microscope Carl Zeis™ Stemi™ DV4 (ZEISS Group, Göttingen, Germany). The duration of oviposition, the number of eggs per egg mass, the number of eggs per female, and the total eggs per host plant type were determined.

Data analysis. All data were analyzed using the independent samples *t*-test and the Mann-Whitney U test as statistical analysis, with a confidence level of 95%. Differences were analyzed by host plant type and were considered significant when $P \leq 0.05$. Student's *t*-test was used for variables with normal distribution and the Mann-Whitney U-test for variables with non-normal distribution, as indicated by McKnight and Najab (2010). The normality of data was determined by Kolmogorov-Smirnov and Shapiro-Wilk tests, and the homogeneity of variances by Levene's test. For data presented as a percentage, before the statistical analysis, an arcsine transformation $[\sqrt{(x/100)}]$ was used. In addition, to determine the relationship between development parameters of the different stages of *S. frugiperda* males and females a Pearson correlation analysis was used. We employed in the analysis all the data from both types of plants. For females, fecundity parameters were added. All statistical analyses were performed using the SPSS-Windows 25.0 program (SPSS Inc., Chicago, USA) (IBM Corporation 2017). Data are presented as mean ± standard error of the mean (SEM).

Results

Development parameters. The larval survival of *S. frugiperda* fed on native maize leaves and teosinte was 92.22 ± 2.90% and 96.11 ± 1.92%, respectively, with no statistically significant differences between host plant types (Mann-Whitney U test, $U = 578.50$, $n = 35$, $p = 0.23$). No significant differences were found in pupal formation with 97.41 ± 1.28% on native maize and 94.07 ± 1.83% on teosinte (Mann-Whitney U test, $U = 558.00$, $n = 35$, $p = 0.13$), or in adult emergence with 90.00 ± 3.14% and 90.56 ± 2.58%, respectively (Mann-Whitney U test, $U = 634.50$, $n = 35$, $p = 0.85$).

Feeding of *S. frugiperda* larvae with native maize and teosinte did not cause differential changes in any of the development parameters evaluated for individuals that became males and females, except the pupal weight of males, which was higher on teosinte (0.19 mg) than on native maize (0.17 mg) (Table 1). Fitness Index values were slightly higher on teosinte but there were no statistically significant differences between host plant types (Table 1).

Table 1. Development parameters (mean ± sd) of males and females of S. frugiperda fed on native maize and teosinte from Oaxaca, Mexico.

	Parameter	Native maize (*Z. mays*)	Teosinte (*Z. luxurians*)
Males	Larval stage (d)	18.94 ± 0.33 a[‡1]	19.27 ± 0.53 a
	Pupal stage (d)	11.23 ± 0.19 a[‡2]	11.07 ± 0.20 a
	Hatching to adult emergence (d)	30.17 ± 0.49 a[‡3]	30.34 ± 0.67 a
	Adult stage (d)	13.71 ± 0.70 a[‡4]	12.82 ± 0.77 a
	Larval weight (g)	0.17 ± 0.00 a[‡5]	0.17 ± 0.00 a
	Maximum larval weight (g)	0.45 ± 0.01 a[‡6]	0.46 ± 0.01 a
	Pupal weight (g)	0.17 ± 0.00 b[‡7]	0.19 ± 0.00 a
	Sex ratio	0.51 ± 0.03 a[‡8]	0.54 ± 0.05 a
	Fitness Index	8.67 ± 0.53 a[‡9]	9.85 ± 0.83 a
	n	81	88
Females	Larval stage (d)	19.01 ± 0.32 a[†1]	18.44 ± 0.52 a
	Pupal stage (d)	9.95 ± 0.17 a[†2]	10.07 ± 0.17 a
	Hatching to adult emergence (d)	28.96 ± 0.45 a[†3]	28.51 ± 0.66 a
	Adult stage (d)	13.71 ± 0.70 a[†4]	12.82 ± 0.77 a
	Larval weight (g)	0.17 ± 0.00 a[†5]	0.17 ± 0.00 a
	Maximum larval weight (g)	0.44 ± 0.01 a[†6]	0.45 ± 0.01 a
	Pupal weight (g)	0.17 ± 0.00 a[†7]	0.17 ± 0.00 a
	Sex ratio	0.49 ± 0.03 a[†8]	0.46 ± 0.05 a
	Fitness Index	8.16 ± 0.59 a[†9]	9.68 ± 0.83 a
	n	81	75

Values with the same letter in a row do not differ significantly ($P > 0.05$): [‡1]Mann-Whitney U test ($U = 3{,}390.0$, $p = 0.58$); [‡2]Mann-Whitney U test ($U = 3{,}451.0$, n = 35, $p = 0.72$); [‡3]Mann-Whitney U test ($U = 3{,}314.00$, n = 35, $p = 0.43$); [‡4]*t*-test ($t = -0.84$, df = 22, $p = 0.41$); [‡5]*t*-test ($t = -0.97$, df = 17, $p = 0.33$); [‡6]*t*-test($t = 0.38$, df = 167, $p = 0.70$); [‡7]*t*-test ($t = 3.17$, df = 167, $p = 0.00$); [‡8]*t*-test ($t = 0.57$, df = 22, $p = 0.57$); [‡9]Mann-Whitney U test ($U = 56.00$, n = 35, $p = 0.36$); [†1]Mann-Whitney U test ($U = 2{,}507.00$, n = 35, $p = 0.06$); [†2]Mann-Whitney U test ($U = 2{,}928.50$, n = 35, $p = 0.69$); [†3]Mann-Whitney U test ($U = 2{,}629.00$, n = 35, $p = 0.15$); [†4]*t*-test ($t = -0.84$, df = 22, $p = 0.41$); [†5]*t*-test ($t = -0.07$, df = 154, $p = 0.94$); [†6]*t*-test ($t = 0.59$, df = 154, $p = 0.55$); [†7]*t*-test ($t = 1.92$, df = 154, $p = 0.06$); [†8]*t*-test ($t = -0.57$, df = 22, $p = 0.57$); [†9]Mann-Whitney U test ($U = 56.00$, n = 35, $p = 0.36$); n: number of larvae that constitute the sample size.

Fecundity parameters. There were no statistically significant differences (P > 0.05) between the fecundity parameters of *S. frugiperda* females and the host plant types (Table 2). The mean duration of oviposition was 14.30 and 13.20 d, the number of eggs per egg mass was 201.44 and 196.29, the number of eggs per female was 1,782.22 and 1,914.68, and the total number of eggs produced per host plant type was 11,462.20 and 12,150.40, for native maize and teosinte respectively.

Correlations among parameters of development and fecundity. Regarding males, positive and significant correlations were determined between the durations of all developmental stages. The prolonged duration of the larval stage led to an extended pupal stage, so the duration from hatching to adult emergence was also prolonged (Table 3). Adult emergence was positively correlated with larval survival and pupal formation. Adult lifespan was negatively correlated with larval survival and adult emergence, and positively correlated with larval weight. Larval weight was negatively correlated with larval survival, and maximum larval weight was negatively correlated with larval survival and adult emergence, but positively correlated with larval weight. Possibly, the heavier larvae had problems completing pupal formation. The Fitness Index was positively correlated with larval survival and pupal weight, but negatively correlated with the duration of developmental stages. Negative correlations between the Fitness Index and the duration of larval, pupal, and from hatching to adult emergence stages, are congruent with the formula, because the longer duration of developmental stages, the lower the value of the Fitness Index. An increase in pupal weight led to an increase in the performance of male offspring.

Concerning females, a similar pattern for the duration of developmental stages, adult emergence, and adult lifespan was determined (Table 4). In addition, the prolonged duration of developmental stages was negatively correlated with larval weight, maximum larval weight, and pupal weight. Maximum larval weight was positively correlated with larval and pupal weight. The Fitness Index was positively correlated with larval survival, adult emergence, and pupal weight, but negatively correlated with the duration of developmental stages. Regarding the fecundity parameters of *S. frugiperda* females, no significant correlations (P > 0.05) were found between the evaluated parameters and the duration of oviposition, but an increase in pupal weight favored the Fitness Index, so egg production was greater.

Table 2. Fecundity parameters (mean ± SEM) of *S. frugiperda* females fed on native maize and teosinte from Oaxaca, Mexico.

Parameter	Native maize (*Z. mays*)	Teosinte (*Z. luxurians*)	*p*-value
Duration of oviposition (d)	14.30 ± 1.25 a	13.20 ± 1.03 a	0.505[†1]
Eggs per egg mass	201.44 ± 7.56 a	196.29 ±8 .08 a	0.087[†2]
Eggs per female	1,782.22 ± 134.51 a	1,914.68 ± 145.49 a	0.512[†3]
Eggs per host plant type	11,462.20 ± 1,265.15 a	12,150.40 ± 2,085.91 a	0.781[†4]

Values with the same letter in a row do not differ significantly (P > 0.05): [†1]*t*-test (t = -0.68, df = 18), [†2]Mann-Whitney U test (U = 165,990.50, n = 35, p > 0.05), [†3]*t*-test (t = 0.67, df = 18), [†4]*t*-test (t = 0.287, df = 18).

Table 3. Pearson correlation coefficient among development parameters of *S. frugiperda* males.

	LS	PF	AE	DLS	DPS	HAE	DAS	LW	MLW	PW	*rL*
LS	1.00										
PF	0.33	1.00									
AE	**0.89****	**0.70****	1.00								
DLS	0.13	-0.19	0.01	1.00							
DPS	0.01	-0.17	-0.06	**0.80****	1.00						
HAE	0.09	-0.19	-0.01	**0.98****	**0.90****	1.00					
DAS	**-0.59****	-0.26	**-0.57****	0.0775	0.3979	0.1871	1.00				
LW	**-0.4272***	0.1072	-0.2773	-0.2173	0.0375	-0.1474	**0.4273***	1.00			
MLW	**-0.48***	-0.24	**-0.47***	0.15	0.12	0.15	0.20	**0.59****	1.00		
PW	0.25	-0.07	0.15	-0.23	-0.29	-0.26	-0.32	-0.32	0.04	1.00	
rL	**0.41***	0.18	0.38	**-0.74****	**-0.68****	**-0.76****	-0.39	-0.14	-0.28	**0.69****	1.00

*The correlation is significant at the 0.05 level; **The correlation is significant at the 0.01 level. LS: larval survival, PF: pupal formation; AE: adult emergence; DLS: duration of the larval stage; DPS: duration of the pupal stage; HAE: hatching to adult emergence; DAS: duration of the adult stage; LW: larval weight; MLW: maximum larval weight; PW: pupal weight; *rL*: Fitness Index.

Table 4. Pearson correlation coefficient among development parameters and fecundity of *S. frugiperda* females.

	LS	PF	AE	DLS	**DPS**	**HAE**	**DAS**	**LW**	**MLW**	**PW**	***rL***	**DO**	**E/EM**	**E/F**	**E/H**
LS	1.00														
PF	0.33	1.00													
AE	**0.89****	**0.71****	1.00												
DLS	-0.10	-0.11	-0.12	1.00											
DPS	-0.26	-0.42	-0.38	**0.51***	1.00										
HAE	-0.15	-0.19	-0.20	**0.98****	**0.68****	1.00									
DAS	**-0.69****	-0.30	**-0.66****	-0.18	0.38	-0.06	1.00								
LW	-0.08	0.25	0.06	**-0.68****	**-0.59****	**-0.73****	0.14	1.00							
MLW	0.05	0.28	0.17	-0.34	**-0.52***	-0.41	0.09	**0.73****	1.00						
PW	0.19	0.06	0.17	-0.44	**-0.63****	**-0.53***	0.18	0.29	**0.57****	1.00					
rL	**0.53***	0.17	**0.47***	**-0.78****	**-0.66****	**-0.83****	-0.24	0.44	0.43	**0.78****	1.00				
DO	-0.07	0.04	-0.04	0.02	0.17	0.06	0.42	0.17	-0.17	-0.37	-0.19	1.00			
E/EM	0.23	0.40	0.35	-0.34	**-0.66****	**-0.45***	-0.16	0.33	0.41	**0.62****	**0.58****	-0.01	1.00		
E/F	0.09	0.02	0.06	-0.37	-0.31	-0.394	0.13	0.24	0.21	0.36	**0.44***	0.39	**0.47***	1.00	
E/H	**0.48***	0.23	**0.46***	-0.37	-0.16	-0.36	-0.04	0.15	0.19	0.33	**0.54***	0.28	**0.46***	**0.59****	1.00

*The correlation is significant at the 0.05 level; **The correlation is significant at the 0.01 level. LS: larval survival, PF: pupal formation; AE: adult emergence; DLS: duration of the larval stage; DPS: duration of the pupal stage; HAE: hatching to adult emergence; DAL: duration of the adult stage; LW: larval weight; MLW: maximum larval weight; PW: pupal weight; *rL*: Fitness Index; DO: duration of oviposition; E/EM: eggs per egg mass; E/F: eggs per female; E/H: eggs per host plant type.

Discussion

In this study, it was hypothesized that there would be an increase or decrease in the development parameters and fecundity of *S. frugiperda* depending on the host plant type, according to the research conducted by Takahashi *et al*. (2012), Szczepaniec *et al*. (2013) and Gaillard *et al*. (2018), who compared feeding on maize and teosinte. However, our results did not differ significantly, except for the pupal weight of males.

The developmental pattern of *S. frugiperda* fed in the larval stage with native maize and teosinte was similar to that reported by Farias-Rivera *et al*. (2003) in their evaluation with leaf extracts of Uruapeño maize and *Z. diploperennis* teosinte. Larval development was affected by both extracts compared to a meridic diet, and these authors argued that this was due to the possible presence of allelochemical compounds on the leaves. The values of development for males and females fed on native maize and teosinte differ from those reported by Silveira *et al*. (1997), De La Rosa-Cancino *et al*. (2016), and Crubelati-Mulati *et al*. (2019), because of the differences in the *S. frugiperda* population evaluated, the age and portion of the leaves used for feeding and the environmental conditions.

No statistically significant differences were determined between the Fitness Index for both sexes and the host plant types but it was higher on teosinte than on native maize, and the highest value was determined for males. These results were consistent with the pattern observed in the pupal weight because the highest value was determined for males, and the difference was greater on teosinte. Similar data were reported by Nogueira *et al*. (2019) in their evaluation with Brazilian maize races that were tolerant to *S. frugiperda* damage, these authors pointed out that the highest Fitness Index values suggest that adults will be able to disperse, reproduce, and ensure population growth and survival. Boregas *et al*. (2013), Jallow and Zalucki (2003), and Costa *et al*. (2019, 2020) reported different values than those of this study because of the insect, host plant, and formula used.

Regarding the fecundity of *S. frugiperda* females, the host plant types did not significantly affect the evaluated parameters. Botton *et al*. (1998) determined significant differences between the number of eggs per female and larvae feed with rice leaves, *Oryza sativa* L. (Poales: Poaceae), and *Echinochloa* sp. (Poales: Poaceae). Murúa and Virla (2004) also determined significant differences in native maize leaves, *Panicum maximum* Jacquin, and *Cynodon dactylon* (L.) Persoon (Poales: Poaceae). Costa *et al*. (2019) reported 39.7±32.8 to 362.0±180.2 eggs per egg mass on cultivars of *Vigna unguiculata* (L.) Walpers (Fabales: Fabaceae), while with respect to races fecundity was not determined because of the low rate of adult emergence.

In Pearson correlation analyses, for both males and females, the Fitness Index was negatively correlated with the duration of developmental stages but positively correlated with the pupal weight. Similar results were reported by Boregas *et al*. (2013) on *S. frugiperda*, and Jallow and Zalucki (2003) on *Helicoverpa armigera* (Hübner, 1805) (Lepidoptera: Noctuidae). In addition, the last authors determined a positive correlation between the duration of the larval stage and pupal weight, while in the present study, this correlation was negative but not significant for both sexes. Regarding the evaluated parameters of *S. frugiperda* females, the prolonged duration of developmental stages was negatively correlated with larval weight, maximum larval weight, and pupal weight, possibly because the constitutive compounds of host plant types affected the feeding and growth of larvae as has been reported by some authors (Wiseman *et al*. 1992; Bushman *et al*. 2002; Rector *et al*. 2003; Maag *et al*. 2015; Gaillard *et al*. 2018). In addition, the duration of oviposition was not significantly correlated ($P > 0.05$) with any of the variables evaluated, but positive correlations were determined between pupal weight, Fitness Index, and fecundity. Similar results were reported by Leuck and Perkins (1972) on *S. frugiperda*, Tammaru *et al*. (2002) on *Orgya* spp. (Lepidoptera: Lymantriidae), Jallow and Zalucki (2003) on *H. armigera*, Moreau *et al*. (2006) on *Lobesia botrana* (Denis et Schiffermuller, 1808) (Lepidoptera: Tortricidae) and Zhang *et al*. (2012) on *Plutella xylostella* L. 1758 (Lepidoptera: Plutellidae). According to the correlation analyses, in our study the greater weight of the male pupae that had been fed on teosinte than larvae fed on Zapalote Chico will affect positively the performance of males.

Conclusions

Our results demonstrated that larval feeding on native maize and teosinte did not affect the development parameters and fecundity of *S. frugiperda*, except the pupal weight of males, which was higher on teosinte. The feeding response of *S. frugiperda* larvae observed on Zapalote Chico maize leaves may be a product of the antibiosis and/or antixenosis that characterizes this maize race. Finally, little is known about the chemical composition of leaves used in this study and they need to be evaluated to design an experiment that provides precise information to explain the results obtained.

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Literature cited

AWMACK, C. S.; LEATHER, S. R. 2002. Host plant quality and fecundity in herbivores insects. Annual Review of Entomology 47 (1): 817-844. https://doi.org/10.1146/annurev.ento.47.091201.145300

BERNAL, J. S.; MELANCON, J. E.; ZHU-SALZMAN, K. 2015. Clear advantages for fall armyworm larvae from feeding on maize relative to its ancestor Balsas teosinte may not be reflected in their mother's host choice. Entomologia Experimentalis et Applicata 155 (3): 206-217. https://doi.org/10.1111/eea.12299

BOREGAS, K. G. B.; MENDES, S. M.; WAQUIL, J. M.; FERNANDES, G. W. 2013. Fitness stage of *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) on alternative hosts. Bragantia 72 (1): 61-70. https://doi.org/10.1590/S0006-87052013000100009

BOTTON, M.; CARBONARI, J. J.; GARCIA, M. S.; MARTINS, J. F. S. 1998. Preferência alimentar e biologia de *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) em arroz e capim-arroz. Anais da Sociedade Entomológica do Brasil 27 (2): 207-212. https://doi.org/10.1590/S0301-80591998000200006

BUSHMAN, B. S.; SNOOK, M. E.; GERKE, J. P.; SZALMA, S. J.; BERHOW, M. A.; HOUCHINS, K. E.; McMULLEN, M. D. 2002. Two loci exert major effects on chlorogenic acid synthesis in maize silks. Crop Science 42 (5): 1669-1678. https://doi.org/10.2135/cropsci2002.1669

COSTA, E. N.; EVANGELISTA, B. M. D.; FERNANDES, M. G. 2019. Antibiosis levels to *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in cowpea commercial cultivars and landrace varieties. Journal of Economic Entomology 112 (4): 1941-1945. https://doi.org/10.1093/jee/toz096

COSTA, E. N.; MARTINS, L. O.; REIS, L. C.; FERNANDES, M. G.; SCALON, S. P. Q. 2020. Resistance of cowpea genotypes to *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and its relationship to resistance-related enzymes. Journal of Economic Entomology 113 (5): 2521-2529. https://doi.org/10.1093/jee/toaa179

CRUBELATI-MULATI, N. C. S.; BALERONI, A. G.; CONTRERAS-SOTO, R. I.; FERREIRA, C. J.B.; CASTRO, C. R.; DE ALBUQUERQUE, F. A.; SCAPIM, C. A. 2019. Evaluation of resistance to *Spodoptera frugiperda* in sweet and field corn genotypes. Maydica 64 (3): 1-7. https://journals-crea.4science.it/index.php/maydica/article/view/1951

DÁVILA-FLORES, A.; DEWITT, T. J.; BERNAL, J. S. 2013. Facilitated by nature and agriculture: performance of a specialist herbivore improves with host-plant life history evolution, domestication, and breeding. Oecologia 173 (4): 1425-1437. https://doi.org/10.1007/s00442-013-2728-2

DE LA ROSA-CANCINO, W.; ROJAS, J. C.; CRUZ-LOPEZ, L.; CASTILLO, A.; MALO, E. A. 2016. Attraction, feeding preference, and performance of *Spodoptera frugiperda* larvae (Lepidoptera: Noctuidae) reared on two varieties of maize. Environmental Entomology 45 (2): 384-389. https://doi.org/10.1093/ee/nvv229

DE OLIVEIRA, N. C.; SUZUKAWA, A. K.; PEREIRA, C. B.; SANTOS, H. V.; HANEL, A.; DE ALBUQUERQUE, F. A.; SCAPIM, C. A. 2018. Popcorn genotypes resistance to fall armyworm. Ciência Rural 48 (2): e20170378. https://doi.org/10.1590/0103-8478cr20170378

DOS SANTOS, L. F. C.; RUIZ-SÁNCHEZ, E.; GAMBOA-ANGULO, M.; GONZÁLEZ-COLOMA, A. 2018. Insect deterrent activity of ethanolic leaf extracts of landrace maize and determination of active compounds against *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae). Journal of Plant Diseases and Protection 126 (2): 107-114. https://doi.org/10.1007/s41348-018-0199-8

FARIAS-RIVERA, L. A.; HERNANDEZ-MENDOZA, J. L.; MOLINA-OCHOA, J.; PESCADOR-RUBIO, A. 2003. Effect of leaf extracts of teosinte, *Zea diploperennis* L., and a Mexican maize variety, criollo 'Uruapeño', on the growth and survival of the fall armyworm (Lepidoptera: Noctuidae). Florida Entomologist 86 (3), 239-243. https://doi.org/10.1653/0015-4040(2003)086[0239:EOLEOT]2.0.CO;2

GAILLARD, M. D. P.; GLAUSER, G.; ROBERT, C. A. M.; TURLINGS, T. C. J. 2018. Fine-tuning the 'plant domestication-reduced defense' hypothesis: specialist vs generalist herbivores. New Phytologist 217 (1): 355-366. https://doi.org/10.1111/nph.14757

IBM Corporation. 2017. IBM® SPSS® Statistics for Windows. IBM SPSS Statistics 25 Documentation. Armonk, NY: IBM Corporation. Available in: https://www.ibm.com/support/pages/node/618179 [Review date: 25 January 2021].

JALLOW, M. F. A.; ZALUCKI, M. P. 2003. Relationship between oviposition preference and offspring performance in Australian *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Australian Journal of Entomology 42 (4): 343-348. https://doi.org/10.1046/j.1440-6055.2003.00365.x

KÖHLER, A.; MAAG, D.; VEYRAT, N.; GLAUSER, G.; WOLFENDER, J. L.; TURLINGS, T. C. J.; ERB, M. 2015. Within-plant distribution of 1,4-benzoxazin-3-ones contributes to herbivore niche differentiation in maize. Plant, cell & environment 38 (6): 1081-1093. https://doi.org/10.1111/pce.12464

LEUCK, D. B.; PERKINS, W. D. 1972. A method of estimating fall amyworm progeny reduction when evaluating control achieved by host-plant resistance. Journal of Economic Entomology 65 (2): 482-483. https://doi.org/10.1093/jee/65.2.482

MAAG, D.; ERB, M.; BERNAL, J. S.; WOLFENDER, J.; TURLINGS, T. C. J.; GLAUSER, G. 2015. Maize domestication and anti-herbivore defenses: leaf-specific dynamics during early ontogeny of maize and its wild ancestors. PLoS ONE 10 (8): e0135722. https://doi.org/10.1371/journal.pone.0135722

MCKNIGHT, P. E.; NAJAB, J. 2010. Mann-Whitney U Test. The Corsini encyclopedia of psychology. Wiley Online Library. https://doi.org/10.1002/9780470479216.corpsy0524

MICHEREFF, M. F. F.; MAGALHÃES, D. M.; HASSEMER, M. J.; LAUMANN, R. A.; ZHOU, J. J.; RIBEIRO, P. E. A.; VIANA, P. A.; GUIMARÃES, P. E. O.; SCHIMMELPFENG, P. H. C.; BORGES, M.; PICKETT, J. A.; BIRKETT, M. A.; BLASSIOLI-MORAES, M. C. 2018. Variability in herbivore-induced defense signalling across different maize genotypes impacts significantly on natural enemy foraging behaviour. Journal of Pest Science 92 (2): 723-736. https://doi.org/10.1007/s10340-018-1033-6

MOREAU, J.; BENREY, B.; THIERY, D. 2006. Assessing larval food quality for phytophagous insects: are the facts as simple as they appear? Functional Ecology 20 (4): 592-600. https://doi.org/10.1111/j.1365-2435.2006.01145.x

MOYA-RAYGOZA, G. 2016. Early development of leaf trichomes is associated with decreased damage in teosinte, compared with maize, by *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 109 (5): 737-743. https://doi.org/10.1093/aesa/saw049

MURÚA, G.; VIRLA, E. 2004. Population parameters of *Spodoptera frugiperda* (Smith) (Lep.: Noctuidae) fed on corn and two predominant grasses in Tucuman (Argentina). Acta Zoológica Mexicana 20 (1): 199-210. http://www.scielo.org.mx/scielo.php?pid=S0065-17372004000100015&script=sci_abstract&tlng=en

NOGUEIRA, L.; COSTA, E. N.; DI BELLO, M. M.; DINIZ, J. F. S.; RIBEIRO, Z. A.; JÚNIOR, A. L. B. 2019. Oviposition preference and antibiosis to *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Brazilian maize landraces. Journal of Economic Entomology 112 (2): 939-947. https://doi.org/10.1093/jee/toy388

NUESSLY, G. S.; SCULLY, B.T.; HENTZ, M. G.; BEIRIGER, R.; SNOOK, M. E.; WIDSTROM, N. W. 2007. Resistance to *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and *Euxesta stigmatias* (Diptera: Ulidiidae) in sweet corn derived from exogenous and endogenous genetic systems. Journal of Economic Entomology 100 (6): 1887-1895.

OVERTON, K.; MAINO, J. L.; DAY, R.; UMINA, P. A.; BETT, B.; CARNOVALE, D.; EKESI, S.; MEAGHERF, R.; REYNOLDS, O. L. 2021. Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): A review. Crop Protection 145 (105641): 1-15. https://doi.org/10.1016/j.cropro.2021.105641

RECTOR, B. G.; LIANG, G.; GUO, Y. 2003. Effect of maysin on wild-type, deltamethrin-resistant, and Bt-resistant *Helicoverpa armigera* (Lepidoptera: Noctuidae). Journal of Economic Entomology 96 (3): 909-913. https://doi.org/10.1093/jee/96.3.909

ROSENTHAL, J. P.; DIRZO, R. 1997. Effects of life history, domestication and agronomic selection on plant defense against insects: evidence from maizes and wild relatives. Evolutionary Ecology 11 (3): 337-355. https://doi.org/10.1023/A:1018420504439

ROSENTHAL, J. P.; WELTER, S. C. 1995. Tolerance to herbivory by a stemboring caterpillar in architecturally distinct maizes and wild relatives. Oecologia 102 (2): 146-155. https://doi.org/10.1007/BF00333245

SÁNCHEZ-GONZÁLEZ, J. J.; RUIZ-CORRAL, J. A.; MEDINA-GARCÍA, G.; RAMÍREZ-OJEDA, G.; DE LA CRUZ-LARIOS, L.; HOLLAND, J. B.; MIRANDA-MEDRANO, R.; GARCÍA-ROMERO, G. E. 2018. Ecogeography of teosinte. PLoS ONE 13 (2): e0192676. https://doi.org/10.1371/journal.pone.0192676

SANTILLÁN-FERNÁNDEZ, A.; SALINAS-MORENO, Y.; VALDEZ-LAZALDE, J.R.; BAUTISTA-ORTEGA, J.; PEREIRA-LORENZO, S. 2021. Spatial delimitation of genetic diversity of native maize and its relationship with ethnic groups in Mexico. Agronomy 11 (4): 672. https://doi.org/10.3390/agronomy11040672

SERRATOS-HERNÁNDEZ, J. A. 2012. El origen y la diversidad del maíz en el continente americano. 2da Edición. Greenpeace México, México, D. F. 39 p.

SIAP. 2021. *Avance de siembras y cosechas. Resumen Nacional por cultivo*. Servicio de Información Agroalimentaria y Pesquera. Available in: http://infosiap.siap.gob.mx:080/agricola_siap_gobmx/AvanceNacionalSinPrograma.do/ [Review date: 25 January 2021].

SILVEIRA, L. C. P.; VENDRAMIM, J. D.; ROSSETTO, C. J. 1997. Effect of corn genotypes on the development of *Spodoptera frugiperda* (J.E. Smith). Anais da Sociedade Entomológica do Brasil 26 (2): 291-298. http://old.scielo.br/scielo.php?pid=S0301-80591997000200010&script=sci_abstract&tlng=en

SZCZEPANIEC, A.; WIDNEY, S. E.; BERNAL, J. S.; EUBANKS, M. D. 2013. Higher expression of induced defenses in teosintes (*Zea* spp.) is correlated with greater resistance to fall armyworm, *Spodoptera frugiperda*. Entomologia Experimentalis et Applicata 146 (2): 242-251. https://doi.org/10.1111/eea.12014

TAKAHASHI, C. G.; KALNS, L. L.; BERNAL, J. S. 2012. Plant defense against fall armyworm in micro-sympatric maize (*Zea mays* ssp. *mays*) and balsas teosinte (*Zea mays* ssp. *parviglumis*). Entomologia Experimentalis et Applicata 145 (3): 191-200. https://doi.org/10.1111/eea.12004

TAMMARU, T.; ESPERK, T.; CASTELLANOS, I. 2002. No evidence for costs of being large in females of *Orgyia* spp. (Lepidoptera, Lymantriidae): larger is always better. Oecologia 133 (3): 430-438. https://doi.org/10.1007/s00442-002-1057-7

TURCOTTE, M. M.; TURLEY, N. E.; JOHNSON, M. T. J. 2014. The impact of domestication on resistance to two generalist herbivores across 29 independent domestication events. New Phytologist 204 (3): 671-681. https://doi.org/10.1111/nph.12935

WIDSTROM, N. W.; WISEMAN, B. R.; SNOOK, M. E.; NUESSLY, G. S.; SCULLY, B. T. 2003. Registration of the Maize Population Zapalote Chico 2451F. Crop Science 43: 443-445. https://doi.org/10.2135/cropsci2003.4440

WISEMAN, B. R.; SNOOK, M. E.; ISENHOUR, D. J.; MIHM, J. A.; WIDSTROM, N. W. 1992. Relationship between growth of corn earworm and fall armyworm larvae (Lepidoptera: Noctuidae) and maysin concentration in corn silks. Journal of Economic Entomology 85 (6): 2473-2477. https://doi.org/10.1093/jee/85.6.2473

ZHANG, P. J.; LU, Y.; ZALUCKI, M. P.; LIU, S. S. 2012. Relationship between adult oviposition preference and larval performance of the diamondback moth, *Plutella xylostella*. Journal of Pest Science 85 (2): 247-252. https://doi.org/10.1007/s10340-012-0425-2

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Author contribution

Erika Padilla-Cortes: performed the collection, rearing and handling of insects, carried out the experiment and collected the data, realized the analysis and interpretation of results, and wrote the draft and the final manuscript.

Laura Martínez-Martínez: helped in the collection, rearing and handling of insects, supervised the experiment, and provided suggestions to improve the manuscript.

José Luis Chávez-Servia: provided the maize and teosinte seeds, contributed to the analysis and interpretation of results, and provided suggestions to improve the manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.