Damage and Entomophagy in Natural Infestations of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Maize Landraces in Oaxaca, Mexico[1]

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Abstract The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), seriously damages maize (*Zea mays* L.) crops in tropical, subtropical, and temperate zones of Mexico and around the world. This study was conducted to evaluate the damage caused by *S. frugiperda* to six native maize populations and the natural parasites of *S. frugiperda* in three localities from Oaxaca, Mexico. Two native maize populations each of the Zapalote Chico, Bolita, and Conico-Chalqueño races were used. Plantings were done at Coatecas Altas, Santa Lucia Miahuatlan, and Villa de Zaachila under a randomized complete block design with four replications. The agroecological conditions of cultivation influenced the damage caused by *S. frugiperda* and influenced its natural parasitism. The ordered weighted mean damage in the localities was Villa de Zaachila (1.40–4.92) $>$ Coatecas Altas (1.33–4.06) $>$ Santa Lucia Miahuatlan (0.53–1.00). The order of parasitism rates in the localities was Villa de Zaachila (56.16%) $\approx$ Santa Lucia Miahuatlan (37.59%) $>$ Coatecas Altas (14.27%). Zapalote Chico populations were less damaged by *S. frugiperda* larvae and flowered earlier than did the Conico-Chalqueño and Bolita populations. Thirteen parasitoid species and nematodes were recorded attacking *S. frugiperda. Chelonus insularis* Cresson was the most abundant parasitoid species across the locations. Members of 17 families of predators and 12 families of parasitoids also were identified as potential natural enemies of *S. frugiperda.* The population dynamics of this armyworm were determined by the environmental conditions of the location, maize population, transition from the vegetative to the reproductive stage, and presence of natural enemies, whereas natural parasitism was influenced only by location.

Key Words fall armyworm, flowering, host plant resistance, parasitoid richness, trophic interactions

Modern maize is the result of a long process of domestication (Matsuoka et al. 2002), and the classification of races is a strategy for managing the diversity conserved *in situ* by farmers. This process is constantly evolving (Kato-Yamakake et al. 2009), as are maize pests. The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a maize pest native to the American continent, and most terrestrial ecosystems are suitable for its development, except for the arid zones of tropical and subtropical regions and areas with temperate and boreal ecosystems (Tepa-Yotto et al. 2021). The most severe damage by this pest to

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maize occurs in its early stages of development and in areas in which crops are planted outside the recommended planting date for the region, particularly in tropical and subtropical regions where expected yield losses exceed 50% (Bahena-Juárez and Cortez-Mondaca 2015, Rodríguez-del Bosque et al. 2012). The increase in *S. frugiperda* populations and their damage to the maize crop are determined by four groups of factors: (a) the ecological–environmental factors that favor pest adaptation and reproduction, such as temperature and rainfall, the presence of alternative hosts when maize is not present, and the presence of natural enemies and surrounding vegetation; (b) cropping practices, such as sowing dates, the use of agrochemicals, or agroecological practices implemented in the field; (c) the domestication and evolution of maize populations (genotypes) in the hands of small farmers; and (d) interactions among the environment, pests, natural enemies, and maize genotypes (Du Plessis et al. 2020, Murúa et al. 2009, Nexticapan-Garcéz et al. 2009, Ni et al. 2014, Reséndiz-Ramírez et al. 2018).

Differences in *S. frugiperda* damage among maize genotypes are due to the tolerance mechanisms conferred by genes inherited from their wild ancestors, morphological characteristics, the biochemical composition of leaves and stigmas (de Oliveira et al. 2018, Gaillard et al. 2018, Ni et al. 2011, Nuessly et al. 2007, Takahashi et al. 2012), the duration of the life cycle or vegetative phase (Reséndiz-Ramírez et al., 2016), and the population characteristics of the infestation of *S. frugiperda,* all of which occur in a pest–host adaptive context. Maize plants release volatile compounds as part of the response to *S. frugiperda* damage, which attract parasitoids and predators (Bosak et al. 2013, Danner et al. 2018, Degen et al. 2012, de Lange et al. 2018). The Oaxacan maize race Zapalote Chico has genes for tolerance and/or resistance to *S. frugiperda* damage (Nuessly et al. 2007), but the variability in resistance or tolerance in other races is unknown.

There are several strategies for controlling and managing *S. frugiperda* larvae in maize crops, such as the application of insecticides (Barbosa et al. 2020, Wan et al. 2021), plant extracts (Figueroa-Gualteros et al. 2019, Phambala et al. 2020, Sombra et al. 2020), nucleopolyhedrosis virus (García-Banderas et al. 2020, Ordóñez-García et al. 2020), other entomopathogens (Cruz-Avalos et al. 2019, Silva et al. 2012), entomophages (Hoballah et al. 2004, Molina-Ochoa et al. 2003a, Ni et al. 2014), pheromone traps (Cruz-Esteban et al. 2020), changes in sowing dates, and the use of improved damage-tolerant varieties and varieties genetically modified with the *Bacillus thuringiensis* transgene (Botha et al. 2019, Wan et al. 2021). Among these techniques, chemical control is the most widely used; however, *S. frugiperda* has acquired resistance to the primary insecticides used (Gutiérrez-Moreno et al. 2018). In recent decades, there have been efforts to identify sustainable management practices that have no negative impact on the environment or agroecosystem and are easy to implement by small-scale farmers (Kumela et al. 2019).

In tropical, subtropical, and transitional or subtemperate lowland regions, the incidence of and damage caused by *S. frugiperda* in maize crops are high, with annual or seasonal fluctuations, as are the populations of *S. frugiperda* parasitoids and predators. The damage varies according to the maize genotype cultivated. In this context, the aim of this study was to evaluate the damage caused by *S. frugiperda* to six native maize populations and to determine the natural parasitism of *S. frugiperda* in three localities in Oaxaca, Mexico.

Materials and Methods

Maize landraces, locations, and experimental management. From November 2017 to February 2018, native maize populations were collected in communities from the Valles Centrales, Istmo, and Mixteca regions of Oaxaca, Mexico. Two population samples phenotypically close to the Bolita race were collected in the municipalities of Cuilapam de Guerrero and Coatecas Altas in communities at 1,546 $\pm$ 50 m of elevation under a semiwarm climate, two samples of the Zapalote Chico race were collected at Santo Domingo Tehuantepec (elevation of 70 $\pm$ 20 m, hot subhumid climate), and two samples of the Conico-Chalqueño race were collected in Santo Domingo Yanhuitlan (elevation of 2,140 m $\pm$ 100 m, temperate subhumid climate). Each sample was labeled with the race name and a number according to the phenotypic similarities of the races as described by Wellhausen et al. (1951) and Aragón-Cuevas et al. (2006): Bolita 1, Bolita 2, Zapalote Chico 1, Zapalote Chico 2, Conico-Chalqueño 1, and Conico-Chalqueño 2.

The experimental sowing of native maize populations occurred at three localities in Oaxaca with contrasting environments (Instituto Nacional de Estadística y Geografía 2018): (a) Coatecas Altas, 16°31′40.2″ N, 96°40′20.7″ W, elevation of 1,524 m, mean annual rainfall of 579 mm, semihot climate; (b) La Cofradia, Santa Lucia Miahuatlan, 16°07′25.7″ N, 96°37′6.5″ W, elevation of 853 m, mean annual rainfall of 1,324 mm, subtropical climate; and (c) Villa de Zaachila, 16°57′04″ N, 96°44′58″ W, elevation of 1,560 m, mean rainfall of 675 mm, semihot climate. A randomized block design was used with six treatments (populations) and four replications. The experimental plots consisted of five rows of 10 m each with 0.80 m between rows and 0.80 m between planting points within a row. In Coatecas Altas, Santa Lucia Miahuatlan, and Villa de Zaachila, seeds were sown on 25 June 2018, 12 July 2018, and 5 February 2019, respectively. Water was supplied by rain at the first two locations and by irrigation at Villa de Zaachila. No insecticides were used for *S. frugiperda* control, and traditional practices were implemented with fertilization with 120-90-60 N-P-K.

Evaluation of damage caused by *S. frugiperda* larvae and flowering in maize plants. The damage to maize plants caused by *S. frugiperda* larvae was evaluated using the scale proposed by Davis et al. (1992) based on 10 categories of damage to the leaves and plants. The plants in the five central rows of each experimental plot were evaluated for damage at two vegetative stages of plant growth: 30 and 62 d after sowing (das). Based on the evaluation of the number of damaged plants and the intensity of damage caused by *S. frugiperda* larvae according to the scale, the weighted mean damage for each experimental plot was estimated: weighted mean damage = $[(X1 \times Y1) + (X2 \times Y2) + (X3 \times Y3)]/T$, where X is the number of plants in each damage category, Y is the damage level according to the scale (Davis et al. 1992), and T is the total number of sampled plants.

The number of days from sowing to male and female maize flowering in each experimental plot was recorded when >50% of the plants had shed pollen and when silks had emerged on 50% of the plants, respectively. This information was used to estimate the duration of the vegetative stage of each maize population and to determine the relationship between stage duration and *S. frugiperda* damage. The mean rainfall and temperature for each location were obtained from the

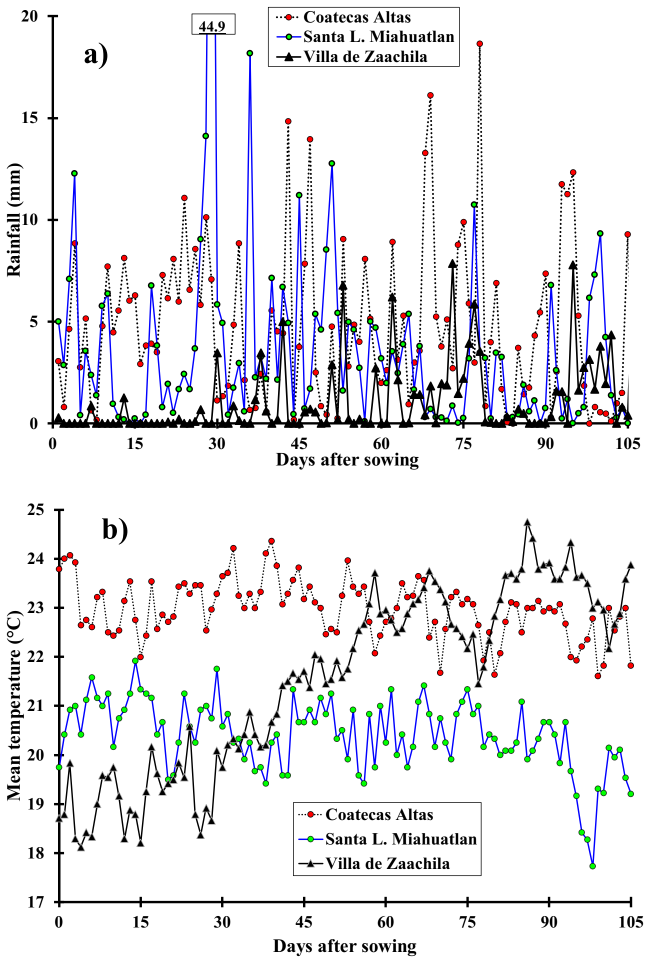

Fig. 1. Mean values of rainfall (mm) (a) and temperature (°C) (b) across crop localities From Servicio Meteorológico Nacional (2020) database for 2010–2018.

daily climatological records of the Servicio Meteorológico Nacional (2020) database from 2010 to 2018 (Fig. 1).

Parasitoids and predators of *S. frugiperda*. Ten *S. frugiperda* larvae, from the first to fourth instars, were captured on maize plants at the V8 to V10 vegetative stage in the three central rows of each experimental plot. In the laboratory, larvae were fed fresh maize leaves daily *ad libitum* until the emergence of parasitoid larvae or the beginning of pupation. The number of individuals that emerged per parasitized larva was used as an indirect measure of the natural parasitism of *S. frugiperda,* and for each value, the equivalent percentage was calculated using the formula: percent parasitism = [number of parasitized larvae reaching adult stage/total number of emerged adults from parasitized and unparasitized larvae] × 100. Adult parasitoids were identified with the taxonomic keys of Cave (1995) and by comparison with specimens kept in the collection of beneficial arthropods of the CIIDIR-Oaxaca, Instituto Politécnico Nacional.

Before the damage level was evaluated in each experimental plot, samples of all were collected with a standard entomological sweep net. Figure-8 sweeps of the foliage were made along the length and width of each experimental plot, and seven samples were collected per plot. Arthropod specimens were placed in plastic containers with 70% ethyl alcohol and transported to the laboratory, where arthropods with predatory and parasitoid habits were separated and identified with the taxonomic keys of Goulet and Huber (1993), Triplehorn et al. (2005), and Ubick et al. (2017).

Statistical analysis. After compiling the weighted means of damage, days to male and female flowering, and natural parasitism data, various combined analyses of variance were performed in which the repetitions were considered nested within evaluation locations. When significant differences were found between principal factors and their interactions (sowing localities, native maize populations, and location × population interactions), multiple comparisons of means were performed with Tukey's test ($P \leq 0.05$). Before analysis, the parasitism percentage was transformed using the arcsine $\sqrt{(x/100)}$ function as part of the normalization function. Pearson's correlation was determined to evaluate the relationships between the *S. frugiperda* damage level and natural parasitism and days to flowering. To evaluate the relationship between sowing location and the abundance of parasitoid species, a chi-square test of independence was used. All statistical analyses were performed with SPSS-Windows 25.0 (SPSS, IBM Corp., Armonk, NY).

Results

Evaluations of flowering times and damage caused by *S. frugiperda* larvae in maize plants. According to the analysis of variance, significant differences ($P \leq 0.05$, $P \leq 0.01$) were detected among crop locations, maize populations, and location × population interactions for the weighted mean of damage caused by *S. frugiperda* larvae and the days to male and female flowering. However, under natural parasitism, the only significant differences ($P \leq 0.01$) were between evaluation locations for individuals emerged per parasitized larva (IE/PL) and percentage of parasitized larvae (PL), but differences were not significant for maize populations or location × population interactions (Table 1). These findings indicated that there were no differences among populations or in location × population interactions; therefore, location × population interactions did not affect the percentage of parasitism of the *S. frugiperda* larvae.

The weighted means of damage to maize plants caused by *S. frugiperda* differed significantly according to the number of days to male and female flowering among the locations and maize populations evaluated. The response patterns to damage were very different; for example, in the first evaluation, 30–41 das, the damage level pattern was Coatecas Altas > Villa de Zaachila > Santa Lucia Miahuatlan, whereas in the second evaluation, 51–62 das, the damage level pattern was Villa de Zaachila > Coatecas Altas > Santa Lucia Miahuatlan. The incidence

Table 1. Comparisons and significance of the weighted mean *S. frugiperda* larval damage, days to flowering, and parasitism of *S. frugiperda* larvae in native maize populations growing in three locations.[1]

Source of variation	Weighted mean damage		Days to flowering		Parasitism[3]	
	30–41 das[2]	51–62 das	Male	Female	IE/PL	PL
Location of evaluation (L)	18.32**	22.60**	812.68**	996.50**	0.19**	4.15**
Population (P)	0.68**	2.04**	1972.68**	3724.46**	0.01	0.21
L × P	0.38**	0.18**	19.56**	51.53**	0.01	0.06
Replicates/L	0.15	0.10*	6.5*	5.2	0.03*	0.34
Error	0.08	0.05	2.91	3.77	0.01	0.17
Coefficient of variation (%)	16.69	12.23	2.45	2.43	5.13	26.19

[1] Significance: *$P \leq 0.05$; ** $P \leq 0.01$.
[2] das, days after sowing.
[3] IE, number of individual parasites emerged per parasitized larva; PL, percentage of parasitized larvae.

Table 2. Comparisons of the weighted mean *S. frugiperda* larval damage and days to flowering among crop locations and native maize populations evaluated in Oaxaca, Mexico.[1]

Location and maize population factor	Weighted mean damage[2]		Days to flowering	
	30–41 das	51–62 das	Male	Female
Crop location				
Coatecas Altas	4.06 a	1.33 b	71.9 b	85.0 a
Santa Lucia Miahuatlan	0.53 c	1.00 c	63.1 c	73.0 c
Villa de Zaachila	1.40 b	4.92 a	74.1 a	81.0 b
Native maize population				
Zapalote Chico 1	1.54 ba	1.29 b	63.1 bc	68.8 cd
Zapalote Chico 2	1.60 b	1.29 b	59.5 d	66.8 d
Conico-Chalqueño 1	1.58 b	3.15 a	86.0 ab	102.5 ab
Conico-Chalqueño 2	2.03 ab	3.08 a	86.3 a	102.8 a
Bolita 1	2.55 a	2.67 a	61.5 cd	68.9 cd
Bolita 2	2.66 a	2.75 a	61.7 cd	69.8 bc

[1] Within locations or populations, means followed by the same letter are not significantly different (Tukey's test, $P > 005$).
[2] das, days after sowing.

of damage caused by *S. frugiperda* larvae varied between Coatecas Altas and Villa de Zaachila but was constant in Santa Lucia Miahuatlan. The native maize populations also exhibited differential responses to *S. frugiperda* damage, and for both evaluations the pattern was Bolita populations > Conico-Chalqueño populations > Zapalote Chico populations; in the second evaluation, the damage was similar for the Bolita and Conico-Chalqueño populations (Table 2).

For days to male flowering, the patterns among crop locations from latest to earliest were Villa de Zaachila > Coatecas Altas > Santa Lucia Miahuatlan, and the patterns for days to female flowering were Coatecas Altas > Villa de Zaachila > Santa Lucia Miahuatlan. The means of floral asynchrony were 13.1, 9.9, and 6.9 days in Coatecas Altas, Santa Lucia Miahuatlan, and Villa de Zaachila, respectively. Thus, there was greater coincidence in days to male and female flowering in Villa de Zaachila and Santa Lucia Miahuatlan than in Coatecas Altas. The maize populations with different geographical origins were highly variable in days to flowering. For example, the Conico-Chalqueño populations collected in the Mixteca region were late flowering and differed significantly from the Bolita populations collected in the Valles Centrales region and from the Zapalote Chico populations collected in the Istmo region. Nevertheless, when the effects of location were evaluated, Villa de Zaachila populations had late male flowering and intermediate female flowering, Coatecas populations had the opposite pattern, and Santa Lucia Miahuatlan populations had early male and female flowering (Table 2).

The native maize populations interacted significantly with the crop location, which influenced the evaluated variables, such as the damage caused by *S. frugiperda* larvae and the days to flowering. In the Coatecas Altas location, all maize populations had the greatest damage caused by the fall armyworm, followed by Villa de Zaachila and Santa Lucia Miahuatlan. During the first evaluation (30–41 das) at Coatecas Altas, the Bolita populations had the greatest damage, followed by the Zapalote Chico and Conico-Chalqueño populations. In Santa Lucia Miahuatlan, there were no significant differences among the maize populations (30–41 das), and in the second evaluation (51–62 das), the Bolita population incurred more damage. In Villa de Zaachila, the Bolita and Conico-Chalqueño 2 populations had the greatest damage at both evaluation times (Table 3). For days to male and female flowering, the Zapalote Chico and Bolita populations interacted significantly with crop location, whereas the Conico-Chalqueño populations had late flowering in all three localities, 78.7–93.5 days and from 100.0–105.0 days to male and female flowering, respectively. The flowering of the Zapalote Chico and Bolita populations occurred first in Santa Lucia Miahuatlan, later in Villa de Zaachila, and latest in the Coatecas Altas (Table 3).

The highest values for weighted mean damage caused by *S. frugiperda* larvae coincided with the lowest mean rainfall recorded at the Coatecas Altas location at 30–41 das. According to field observations, before the first damage evaluation the mean rainfall was greater in Santa Lucia Miahuatlan than in Coatecas Altas. The lowest rainfall was recorded for Villa de Zaachila because the experiment was conducted after the rainy season, but this location was irrigated; therefore, the damage caused by fall armyworms to maize occurred both during rainfall and at 51–62 das. In general, the mean temperature in Santa Lucia Miahuatlan was 17.5–22°C, that in Coatecas Altas was 21.5–24°C, and that in Villa de Zaachila was 18–24.5°C. The highest rainfall and lowest temperature (Fig. 1) contributed to the early flowering of the evaluated native maize populations (Table 3).

Significant correlations were detected between the weighted mean damage caused by fall armyworm larvae and the days to flowering of the maize populations evaluated. For example, positive and significant relationships were found between the second damage evaluation and days to male ($r = 0.46$, $P \leq 0.01$) and female ($r = 0.28$, $P \leq 0.05$) flowering. However, in the first damage evaluation, the correlations were not significant between damage and days to male ($r = 0.08$, $P > 0.05$) or female ($r = 0.17$, $P > 0.05$) flowering. The significant correlation suggested that the damage caused by fall armyworm larvae was greater in late flowering than in early flowering populations, but this finding is not definitive because there was no significant correlation in the first evaluation, which also indicates that this effect is dependent on the vegetative stage. For example, the Coatecas Altas location incurred greatest damage in the first evaluation, but more major damage was recorded in the early Bolita populations than in the late populations of Conico-Chalqueño (Table 3).

Abundance and richness of *S. frugiperda* natural enemies. There were significant differences in the natural parasitism of fall armyworms among the evaluation locations, with the highest parasitism levels recorded in Santa Lucia

Table 3. Mean location × population interactions according to the weighted mean *S. frugiperda* larval damage and days to flowering for maize populations cultivated in Oaxaca, Mexico.[1]

Maize population per crop location	Weighted mean of damage[2]		Days to flowering	
	30–41 das	51–62 das	Male	Female
Coatecas Altas				
Zapalote Chico 1	3.56 cd	0.60 ghi	68.5 de	76.2 cd
Zapalote Chico 2	3.94 bc	0.41 i	61.2 gh	74.7 cd
Conico-Chalqueño 1	2.54 def	1.79 ef	86.7 bc	105.0 a
Conico-Chalqueño 2	3.42 cde	2.02 de	86.7 bc	103.7 a
Bolita 1	5.04 ab	1.44 efg	64.7 efg	77.0 cd
Bolita 2	5.85 a	1.72 ef	63.2 fg	78.0 bc
Santa Lucia Miahuatlan				
Zapalote Chico 1	0.34 i	0.31 i	57.0 hi	61.7 fg
Zapalote Chico 2	0.30 i	0.46 hi	53.5 i	56.7 g
Conico-Chalqueño 1	0.77 ghi	1.07 fghi	78.7 cd	100.0 ab
Conico-Chalqueño 2	0.55 hi	1.16 efghi	78.7 cd	100.5 a
Bolita 1	0.69 hi	1.63 ef	55.5 i	60.2 g
Bolita 2	0.51 i	1.36 efgh	55.0 i	59.0 g
Villa de Zaachila				
Zapalote Chico 1	0.71 hi	2.98 cd	63.7 fg	68.5 ef
Zapalote Chico 2	0.56 hi	3.01 c	63.7 fg	69.0 e
Conico-Chalqueño 1	1.43 fghi	6.59 a	92.5 ab	102.5 a
Conico-Chalqueño 2	2.13 efg	6.06 a	93.5 a	104.2 a
Bolita 1	1.92 fgh	4.94 b	64.2 efg	69.5 e
Bolita 2	1.63 fghi	5.93 a	66.7 ef	72.5 de

[1] Within each column, means followed by the same letter are not significantly different (Tukey's test, $P > 005$).
[2] das, days after sowing.

Miahuatlan and Villa de Zaachila followed by Coatecas Altas (Table 4). The low rainfall and high temperatures recorded at the Coatecas Altas (Fig. 1) probably affected the parasitism of *S. frugiperda,* and the results suggest that further in-depth study is needed. The differences among the maize populations were not significant in terms of the percentage of parasitism, which was 29.8–46.4%, and the average percentage of parasitoids that emerged per parasitized larva (Table 4).

Table 4. Mean parasitism of *S. frugiperda* larvae collected in maize populations cultivated in three locations in Oaxaca, Mexico.[1]

Location and maize population	Mean number of parasitoids emerged per parasitized larva	Percentage of parasitized larvae based on total number of collected larvae
Crop location		
Coatecas Altas	0.17 b	14.3 c
Santa Lucia Miahuatlan	0.36 a	37.6 b
Villa de Zaachila	0.44 a	56.1 a
Native maize population		
Zapalote Chico 1	0.31 a	36.5 a
Zapalote Chico 2	0.26 a	29.8 a
Conico-Chalqueño 1	0.38 a	43.5 a
Conico-Chalqueño 2	0.35 a	46.4 a
Bolita 1	0.35 a	33.2 a
Bolita 2	0.33 a	30.0 a

[1] Within each column, means followed by the same letter are not significantly different (Tukey's test, $P >$ 005).

Among the location × maize population interactions, no significant differences ($P > 0.05$) were found for parasitism, and the evaluation revealed that parasitism rates at the crop locations were 5.90–30.5%, 26.6–46.9%, and 45.7–71.6% at Coatecas Altas, Santa Lucia Miahuatlan, and Villa de Zaachila, respectively (Table 5). No significant correlations were detected between parasitism and days to male flowering ($r = 0.14$ for individuals emerged per parasitized larva and $r = 0.20$ for the percentage of parasitized larvae, $P > 0.05$) or days to female flowering ($r = 0.05$ for individuals emerged per parasitized larva and $r = 0.09$ for the percentage of parasitized larvae, $P > 0.05$).

The abundance of parasitoid and nematode species attacking *S. frugiperda* larvae captured in the field was significantly associated with crop location ($\chi^2 = 209.75$, df $= 26$, $P \leq 0.01$), indicating that some species were recorded only under certain environmental conditions related to the crop locations within the limitations of the study. For example, *Meteorus laphygmae* (Viereck) and *Goniozus* sp. were recorded only in Coatecas Altas; *Chelonus cautus* (Cresson), *Chelonus sonorensis* (Cameron), *Eiphosoma vitticolle* (Cresson), and *Microcharops anticarsiae* Gupta were recorded in Santa Lucia Miahuatlan, and *Lespesia* sp. was recorded in Villa de Zaachila. *Cotesia marginiventris* (Cresson), *Pristomerus spinator* (F.), *Campoletis sonorensis* (Cameron), and *Ophion flavidus* Brullé were recorded in Coatecas Altas and Villa de Zaachila. Nematodes were recorded only in Santa Lucia Miahuatlan. *Chelonus insularis* was the only parasitoid species present in all

Table 5. Means of the location × population interactions for native maize populations cultivated in Oaxaca, Mexico and parasitism of *S. frugiperda* larvae in these maize populations.[1]

Location and maize population	Mean number of parasitoids emerged per parasitized larva	Percentage of parasitized larvae based on total number of collected larvae
Coatecas Altas		
Zapalote Chico 1	0.13	8.7
Zapalote Chico 2	0.15	10.9
Conico-Chalqueño 1	0.16	14.5
Conico-Chalqueño 2	0.22	30.5
Bolita 1	0.06	5.9
Bolita 2	0.22	13.3
Santa Lucia Miahuatlan		
Zapalote Chico 1	0.27	40.5
Zapalote Chico 2	0.33	30.6
Conico-Chalqueño 1	0.24	40.5
Conico-Chalqueño 2	0.31	46.9
Bolita 1	0.50	40.9
Bolita 2	0.38	26.6
Villa de Zaachila		
Zapalote Chico 1	0.39	54.4
Zapalote Chico 2	0.30	45.7
Conico-Chalqueño 1	0.55	71.6
Conico-Chalqueño 2	0.53	62.0
Bolita 1	0.40	52.8
Bolita 2	0.41	50.2

[1] No significant differences were detected by Tukey's test ($P > 0.05$).

three crop locations. Among the total parasitoids, seven entomophagous species were recorded at each location, but the greatest number of individuals was recorded in Villa de Zaachila (Table 6).

Of the natural enemies collected from fall armyworm larvae in the three crop locations, 17 families had predatory habits and 12 families were parasitoids. Members of families Thomisidae, Forficulidae, Vespidae, and Braconidae were common among the three locations. Members of Theridiidae, Geocoridae, Coccinellidae,

Table 6. Number of parasitized larvae of *S. frugiperda* per parasitoid and nematode species based on the number of larvae collected in the maize populations cultivated at three locations in Oaxaca, Mexico.

Family	Species	Coatecas Altas	Santa Lucia Miahuatlan	Villa de Zaachila	Total
Braconidae	*Chelonus insularis*	18	16	142	176
	Cotesia marginiventris	1	0	1	2
	Chelonus cautus	0	3	0	3
	Chelonus sonorensis	0	1	0	1
	Meteorus laphygmae	1	0	0	1
Ichneumonidae	*Pristomerus spinator*	1	0	31	31
	Campoletis sonorensis	5	0	6	11
	Ophion flavidus	5	0	1	6
	Eiphosoma vitticolle	0	5	0	5
	Microcharops anticarsiae	0	2	0	2
Tachinidae	*Archytas marmoratus*	0	6	1	7
	Lespesia sp.	0	0	2	2
Bethylidae	*Goniozus* (=*Periseriola*) sp.[1]	1	0	0	1
Mermithidae	Nematodes[2]	0	11	0	11
Total parasitized larvae of *S. frugiperda*		32	44	184	260
Total parasitoid and nematodes species		7	7	7	14

[1] Gregarious parasitoid (four parasitoids emerged per larva).
[2] One to nine nematodes emerged per larva.

Cicindelidae, Trichogrammatidae, Elasmidae, and Torymidae were exclusive to Coatecas Altas, members of Tetragnatidae, Anyphaenidae, and Lycosidae were found in Santa Lucia Miahuatlan, and members of Pteromalidae, Eucolidae, Bethylidae, Scelionidae, Ichneumonidae, Eucharitidae, and Perilampidae were found in Villa de Zaachila. Predators were frequent in Coatecas Altas and Santa Lucia Miahuatlan, and parasitoids were more abundant in Villa de Zaachila. The greatest number of arthropods was captured at Coatecas Altas (Table 7).

Discussion

Evaluations of the damage caused by *S. frugiperda* revealed that the distribution of larvae was influenced by the evaluation locations, maize populations, and location × maize population interactions at the two evaluation dates or growing stages, considering that damage depends on the population dynamics of the fall armyworm and the plant developmental stage. According to our evaluations, the maize in the Coatecas Altas and Villa de Zaachila locations had more damage than did that in the Santa Lucia Miahuatlan location because the transition from the vegetative to reproductive stages was more accelerated in the Santa Lucia Miahuatlan maize population than in the Coatecas Altas and Villa de Zaachila

Table 7. Number of arthropods with predatory and parasitoid feeding habits based on captures on the maize populations cultivated in three locations in Oaxaca, Mexico.

			Number of individuals		
Class	Order	Family	Coatecas Altas	Santa Lucia Miahuatlan	Villa de Zaachila
Predatory arthropods					
Arachnida	Araneae	Thomisidae	1	2	1
		Salticidae	5	1	0
		Oxyopidae	3	3	0
		Araneidae	2	1	0
		Theridiidae	1	0	0
		Tetragnathidae	0	2	0
		Anyphaenidae	0	1	0
		Lycosidae	0	1	0
Insecta	Dermaptera	Forficulidae	5	1	4
	Hymenoptera	Vespidae	4	4	1
	Diptera	Syrphidae	1	2	0
	Hemiptera	Reduviidae	3	2	0
		Geocoridae	1	0	0
	Coleoptera	Carabidae	4	1	0
		Coccinellidae	1	0	0
		Cicindelidae	1	0	0
	Neuroptera	Chrysopidae	1	0	1
Parasitoid arthropods					
Insecta	Hymenoptera	Braconidae	4	2	2
		Trichogrammatidae	1	0	0
		Elasmidae	1	0	0
		Torymidae	1	0	0
		Pteromalidae	0	0	1
		Eucolidae	0	0	1
		Bethylidae	0	0	1
		Scelionidae	0	0	5
		Ichneumonidae	0	0	2
		Eucharitidae	0	0	1
		Perilampidae	0	0	1
	Diptera	Tachinidae	1	2	0
Total number of individuals			41	25	21
Total number of families			19	14	12

maize populations (Table 2). Similar results were obtained by Ahmad and Ibrahim (2021), where the percentage of the eight varieties of maize infested by *S. frugiperda* larvae varied among genotypes and was associated with variations in developmental stages. In this study, the infestation rate decreased from 0% in the first week of evaluation, at approximately 30 das, but increased gradually from the second to the fifth week. A decrease in the percent infestation was observed from the 6th to the 10th week, when the varieties reached maturity. In the present study, the weighted mean damage values recorded in the first evaluation were lower than those in the second evaluation across locations, except for the Coatecas Altas and Zapalote Chico populations (Table 2).

The subtropical climate, rainfall, and temperature (Fig. 1) of Santa Lucia Miahuatlan seem to have had a great influence on decreasing the incidence of and damage caused by *S. frugiperda* larvae to maize populations. According to the results of Ahmad and Ibrahim (2021), the periods with the highest percentage of infestation were associated with high temperature, whereas relative humidity had a weak negative influence. Piñango et al. (2001) and Mailafiya et al. (2010) further noted that high rainfall reduces damage because the maize whorl fills with water, sometimes drowning *S. frugiperda* larvae. High rainfall also negatively affects the parasitism, species richness, and abundance of parasitoids (Mailafiya et al. 2010). In this study, a lower abundance of parasitoids was recorded in Coatecas Altas and Santa Lucia Miahuatlan than in Villa de Zaachila, but neither the species richness nor parasitism status was affected (Table 6). The periods of time with greater infestation by *S. frugiperda* larvae were consistent with the results obtained by Piñango et al. (2001) and Wyckhuys and O'Neil (2006) in the subtropical cropping systems of Venezuela and Honduras. Murúa et al. (2009) reported that the greatest abundance of *S. frugiperda* larvae occurs during the summer season, followed by the rainy season. Different patterns of damage also may occur within the same experimental plot (Hay-Roe et al. 2016), as we observed in the present study. These patterns regularly occur under natural infestations.

In reference to the maize populations, the Zapalote Chico populations had a weighted mean damage $<$1.60, and the Bolita and Conico-Chalqueño populations had weighted mean damages $>$2.03 (Table 2). Llamas-Guzmán (2016) also reported greater damage from *S. frugiperda* larvae in a native population of Conico-Chalqueño from Tlaxcala and a native population of Bolita from Oaxaca, but a native population of the Olotillo race from Oaxaca was the most tolerant to damage. The reduced damage corresponded to that in Zapalote Chico, which was attributed to the short period of time from the vegetative to the reproductive stage (Table 2) and to the compounds synthesized and released during this transition. For example, Nuessly et al. (2007) reported that silks of the Zapalote Chico race had higher concentrations of chlorogenic acid, isoorientin, maysin, and apimaysin than did those of other maize genotypes. Michereff et al. (2019) reported that these maize plants release volatile compounds such as indole and mono-, sesqui-, and homoterpenes within 15 h after damage to attract *S. frugiperda* natural enemies and reduce the damage caused by these larvae.

With respect to comparison between male and female flowering, both were early in Santa Lucia Miahuatlan, occurring at 63.1 and 73.0 das, respectively; in Coatecas Altas, male flowering was intermediate (71.9 das) and female flowering was late (85.0 das); and in Villa de Zaachila, male flowering was late (74.1 das) and female flowering was intermediate (81.0 das) (Table 2). The number of days to flowering is an indirect indicator of the time from sowing to the differentiation of vegetative buds into reproductive buds, that is, floral initiation (Stevens et al. 1986). In this study, the evaluation location had a significant effect on floral initiation and initial development of the ear, which occurred first in Santa Lucia Miahuatlan and later in Villa de Zaachila and Coatecas Altas (Table 2). Floral initiation also influenced *S. frugiperda* population dynamics, as indicated by the positive correlations between the second damage evaluation and the number of days to male ($r = 0.46$, $P \leq 0.01$) and female ($r = 0.28$, $P \leq 0.05$) flowering. Floral asynchrony (noncoincidental male and female flowering) occurred in Villa de Zaachila with an average 13 d, 10 d in Santa Lucia Miahuatlan, and 14 d in the Coatecas Altas (Table 2). These similarities can be explained by the subtropical climate and rainfall recorded in Santa Lucia Miahuatlan (Fig. 1) and by the crop management conditions (irrigation) used in Villa de Zaachila. These conditions may have accelerated the reproductive development of maize plants compared with that in Coatecas Altas. Rainfall in Coatecas Altas was low (Fig. 1), and a period of intrasummer drought was recorded before the first damage evaluation. This period of drought is common in the rainy season in the Valles Centrales de Oaxaca (Ruíz-Vega 1998).

With respect to overall days to flowering, each maize population reflected the characteristics of the race group; for example, Conico-Chalqueño populations flowered late, at 86.0–102.8 das (Table 2), similar to the descriptions of Diego-Flores et al. (2012) and Torres-Escamilla et al. (2019). The Bolita populations flowered at 61.5–69.8 das (Table 2), similar to the results reported by Aragón-Cuevas et al. (2006). Zapalote Chico populations ultimately flowered early, at 59.5–68.8 das (Table 2), similar to the findings of López-Romero et al. (2005) and Cabrera-Toledo et al. (2015). The Conico-Chalqueño populations had longer vegetative stages and were more susceptible to damage by *S. frugiperda* larvae than were the Bolita and Zapalote Chico populations, as suggested by the results during the second evaluation at Villa of Zaachila (Table 3) and the positive and significant correlations between damage and days to flowering. Early flowering maize may escape damage or be less damaged by *S. frugiperda* larvae than late flowering maize. In this study, the number of days to flowering did not significantly differ between the Zapalote Chico and Bolita populations (Table 3). Consequently, evasion or escape from damage due to early flowering in Zapalote Chico was discounted because Bolita did not exhibit the same response to damage. The results suggest that the low damage level caused by *S. frugiperda* larvae in the Zapalote Chico populations (Table 3) reflects a biochemical–physiological response of the plants due to the presence of resistance genes and high levels of maysin and homologous compounds (Gueldner et al. 1992, Nuessly et al. 2007, Widstrom et al. 2003). Llamas-Guzmán (2016) evaluated resistance in the Olotillo race and tolerance in the Tablita race to damage by *S. frugiperda* larvae; both of these maize races are native to Oaxaca, Mexico. In that study, the stem diameter and leaf area of expanded leaves was involved in tolerance, whereas the number of trichomes was involved in resistance. Yadav et al. (2021) reported the negative influence of plant height, trichome number, and leaf angle and the positive influence of trichome length on the percentage of *Chilo partellus* (Swinhoe) (Lepidoptera:

Crambidae) infestations on maize. The influence of these morphological traits on the damage response of native maize should be considered in future studies.

The natural parasitism of *S. frugiperda* larvae was significantly different among Coatecas Altas, Santa Lucia Miahuatlan, and Villa de Zaachila, with rates of 14.3, 37.7, and 56.1%, respectively (Table 4). Ruíz-Nájera et al. (2007) reported that the parasitism rate varied among locations and maize populations, and the richness of parasitoid species was greater when larvae were collected at the V3 growth stage. Bosak et al. (2013) found that juvenile plants release more volatile compounds than do maize seedlings, which makes juvenile plants more attractive to herbivores, parasitoids, and predators. In the present study, the highest percentage of parasitism observed in Villa de Zaachila was consistent with the observed abundance of larvae collected in the field (observations during the first evaluation, 30–41 das), and the percentage of parasite-related damage increased at the second evaluation (51–62 das) compared with that in Santa Lucia Miahuatlan (Tables 4, 5). Intrasummer drought in Coatecas Altas had a negative influence on the parasitism rate. Mailafiya et al. (2010) reported that altitude and rainfall had negative effects on the parasitism, species richness, and abundance of parasitoids, whereas temperature increase had a positive effect.

No significant differences were found among the maize populations regarding the mean number of individual parasites that emerged from parasitized larvae, and the parasitism rate was 29.8–46.4% (Table 4). No significant differences were detected in the location $\times$ maize population interaction for the mean number of individuals emerged per parasitized larva, and parasitism was 5.9–71.6% (Table 5). The percentages of natural parasitism of *S. frugiperda* larvae obtained in this study are similar to those reported for other studies carried out in other regions of Mexico (Jourdie et al. 2008; Molina-Ochoa et al. 2004, 2003b; Ruíz-Nájera et al. 2007, 2013).

Twelve parasitoid species in the Braconidae, Ichneumonidae, and Tachinidae families were identified parasitizing *S. frugiperda* (Table 6). All of these species have been recorded in Mexico as parasitoids of insect pests (Bahena-Juárez and Cortez-Mondaca 2015, Hoballah et al. 2004, Jourdie et al. 2008, Molina-Ochoa et al. 2003a, Ruíz-Nájera et al. 2013), but *Goniozus* sp. has been recorded only in the United States (Bahena-Juárez and Cortez-Mondaca 2015). *Chelonus insularis* was the most abundant parasitoid species in the three evaluation locations (Table 6) and is widely distributed and abundant in Mexico (González-Maldonado et al. 2014; Molina-Ochoa et al. 2003a, 2004). Its worldwide distribution coincides with the presence of *S. frugiperda,* making it a key parasitoid for the biological control of this insect pest (Tepa-Yotto et al. 2021). In this sense, we propose the use of *C. insularis* for managing *S. frugiperda* populations during maize cultivation.

The environmental conditions of each crop location significantly influenced the abundance and species richness of *S. frugiperda* parasitoid species ($\chi^2 = 209.75$, df $= 26$, $P \leq 0.01$). Mailafiya et al. (2010) noted a greater richness of parasitoid species in natural habitats, but in cultivated areas the number of individuals was higher and the species richness was reduced. In the present study, the parasitoid species richness was similar across the evaluation locations; nevertheless, differences in the surrounding vegetation of each location were common in maize production by small-scale farmers. The highest parasitoid abundance was recorded in Villa de Zaachila (Table 6), which is consistent with the abundance of larvae collected in the field, compared with Coatecas Altas and Santa Lucia Miahuatlan.

Some species were found in only one location. For example, *M. laphygmae* and *Goniozus* sp. were recorded only in Coatecas Altas; *C. cautus, C. sonorensis, E. vitticolle,* and *M. anticarsiae* were exclusive to Santa Lucia Miahuatlan, and *Lespesia* sp. was found only in Villa de Zaachila (Table 6). These types of distributions have been reported in previous studies (Mailafiya et al. 2010, Meagher et al. 2016, Otim et al. 2021, Sisay et al. 2019, Wyckhuys and O'Neil 2006). Members of the Mermithidae were recorded only in Santa Lucia Miahuatlan. These nematodes are common in subtropical climates and have been previously reported as natural enemies of *S. frugiperda* larvae in the Mexican states of Colima (Lezama-Gutiérrez et al. 2001), Chiapas (Ruíz-Nájera et al. 2013), and Veracruz (Bahena-Juárez and Cortez-Mondaca 2015).

Twenty-nine families of predatory and parasitoid arthropods habits were recorded as potentially entomophagous natural enemies of *S. frugiperda* (Table 7). Among the parasitoids, members of the orders Hymenoptera and Diptera (insects) are the most common parasitoids (Molina-Ochoa et al. 2003a). Of the predators, the most common were members of the orders Araneae (members of eight families) and Coleoptera (members of three families) (Table 7). Members of the Thomisidae, Forficulidae, and Vespidae were common at the three crop locations, but the Coatecas Alta location had the greatest number of individuals recorded. In this study, the species richness of potential natural enemies of *S. frugiperda* was similar to that reported by Hoballah et al. (2004) in Veracruz, Mexico, by Wyckhuys and O'Neil (2006) in Honduras, and by Ni et al. (2014) in the United States. For the biological control of *S. frugiperda,* we recommend studying the species from the families Braconidae, Forficulidae, Vespidae, and Reduviidae in more detail (Table 7).

In conclusion, the damage to maize plants caused by *S. frugiperda* larvae was influenced by the location in which the maize was cultivated, the maize population, and location $\times$ population interactions, and the damage severity was determined by the transition from the vegetative to the reproductive stage, which was measured by time of male and female flowering. The environmental conditions and surrounding vegetation of the locations also influenced the level of damage. Compared with damage to the Bolita and Conico-Chalqueño maize populations, the damage to the Zapalote Chico populations, which had early flowering and probable biosynthesis, was lower, perhaps because of differences in the biochemical–physiological mechanisms in each race of maize. These findings make Zapalote Chico a probable pool of resistance genes against herbivore attack with potential use in breeding and development programs for maize that is resistant to *S. frugiperda*. The natural parasitism of *S. frugiperda* differed among crop locations (Villa de Zaachila $>$ Santa Lucia Miahuatlan $>$ Coatecas Altas), and the abundances of parasitoids and nematodes were homogeneous across the maize populations and environments under evaluation. At each evaluation location, various entomophagous species were recorded; therefore, more detailed monitoring of their presence should be conducted at each location. *Chelonus insularis* was the most abundant parasitoid species in the three crop locations, and it is widely distributed in Mexico and other countries; therefore, we propose evaluating the effectiveness of this parasitoid for the biological control of *S. frugiperda*.

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