Diversity and Density-Dependence Relationship between Hymenopteran Egg Parasitoids and the Corn Leafhopper (Hemiptera: Cicadellidae) in Maize Agroecosystem vs. Teosinte Wild Habitat

Author: Moya-Raygoza, Gustavo

Diversity and density-dependence relationship between hymenopteran egg parasitoids and the corn leafhopper (Hemiptera: Cicadellidae) in maize agroecosystem vs. teosinte wild habitat

Gustavo Moya-Raygoza[1],*

Abstract

Little is known about the differences between the habitats of domesticated plants and their wild ancestors with respect to the third trophic level. A field study was conducted in the region of origin of domesticated maize to investigate the differences between a maize landrace and the teosinte *Zea mays* ssp. *parviglumis* Iltis & Doebley (Poaceae) (the maize ancestor) plants in diversity and density-dependence relationship in the egg parasitoids of corn leafhopper, *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae), within the maize and teosinte habitats. Comparing exposure of both plants within the maize agroecosystem vs. the teosinte wild habitat, eggs of *D. maidis* were attacked by a community or complex of parasitoids. A higher diversity of adult parasitoids was found in teosinte plants (H' = 0.73) than in maize landrace plants (H' = 0.30) within the maize habitat. In addition, within the teosinte habitat a higher diversity of adult parasitoids was seen in the teosinte plants (H' = 0.88) than in maize landrace plants (H' = 0.40). Adult egg parasitoids were abundant within maize habitat and included *Anagrus virlai* Triapitsyn (Hymenoptera: Mymaridae), *Paracentrobia* sp., and *Pseudoligosita* sp. (both Hymenoptera: Trichogrammatidae). Within the teosinte habitat, the community of parasitoids included *A. virlai*, *Anagrus incarnatus* Haliday (Hymenoptera: Mymaridae), *Paracentrobia* sp., and *Pseudoligosita* sp. In the maize habitat, a strong positive density-dependent association was seen between the number of *D. maidis* eggs and the community of adult parasitoids, and *A. virlai*, the most abundant and common parasitoid. However, a weak density-dependent association was seen in the teosinte wild habitat. Differences in density-dependent association in *D. maidis* and the community of egg parasitoids between teosinte wild habitat and maize crop contribute to the understanding of changes in the third trophic level through maize domestication.

Key Words: *Dalbulus maidis*; Mymaridae; Trichogrammatidae; insect pest; biological control

Resumen

Poco se conoce sobre las diferencias entre el hábitat de plantas domesticadas y el hábitat de sus ancestros, respecto al tercer nivel trófico. Un estudio de campo fue efectuado en la región de origen del maíz para investigar las diferencias entre una variedad nativa de maíz y el teosinte *Zea mays* ssp. *parviglumis* Iltis & Doebley (Poaceae) (ancestro del maíz) en diversidad y denso-dependencia de los parasitoides que atacan a los huevos de la chicharrita del maíz *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) dentro del hábitat de maíz y dentro del hábitat de teosinte. Comparando huevos expuestos de ambas plantas dentro del agroecosistema de maíz vs. el hábitat de teosinte, huevos de *D. maidis* fueron atacados por una comunidad o complejo de parasitoides. Una mayor diversidad de parasitoides adultos fue encontrada en plantas de teosinte (H' = 0.73) que en la variedad nativa de maíz (H' = 0.30) dentro del hábitat de maíz. Además, dentro del hábitat de teosinte una mayor diversidad de parasitoides adultos fue vista en plantas de teosinte (H' = 0.88) que en la variedad nativa de maíz (H' = 0.40). Los parasitoides de huevos fueron abundantes dentro del hábitat de maíz e incluyeron a *Anagrus virlai* Triapitsyn (Hymenoptera: Mymaridae), *Paracentrobia* sp., y *Pseudologosita* sp. (ambos Hymenoptera: Trichogrammatidae). Dentro del hábitat de teosinte la comunidad de parasitoides incluyo a *A. virlai*, *Anagrus incarnatus* Haliday (Hymenoptera: Mymaridae), *Paracentrobia* sp., y *Pseudoligosita* sp. En el hábitat de maíz, una fuerte denso-dependencia fue encontrada entre el número de huevos de *D. maidis* y la comunidad de parasitoides adultos y *A. virlai*, el parasitoide más abundante y común. Sin embargo, una débil denso-dependencia fue vista en el hábitat de teosinte. Diferencias en denso-dependencia en *D. maidis* y la comunidad de parasitoides adultos entre teosinte y maíz hábitats contribuyen a entender cambios en el tercer nivel trófico durante la domesticación del maíz.

Palabras Claves: *Dalbulus maidis*; Mymaridae; Trichogrammatidae; insecto plaga; control biológico

Maize (*Zea mays* ssp. *mays* L.; Poaceae) is one of the most important crops in the world (de Lange et al. 2014), and it was domesticated directly from the ancestor annual wild teosinte (*Zea mays* ssp. *parviglumis* Iltis & Doebley; Poaceae) in Mexico about 9,000 yr ago (Matsuoka et al. 2002). *Zea mays* ssp. *parviglumis* populations grow in Mexico along the Sierra Madre del Sur, in Nayarit, Jalisco, Michoacán, Guerrero, and Oaxaca states (Sánchez González et al. 2018), and most of these populations are located in dry tropical forests (Zizumbo-Villareal & Colunga-GarcíaMarín 2010). In Jalisco, populations of *Z. mays* ssp. *parviglumis* grow among herbs, shrubs, and trees in the

[1]Departamento de Botánica y Zoología, CUCBA, Universidad de Guadalajara, Camino Ramón Padilla Sánchez #2100, Nextipac, Zapopan, C.P. 45110, Jalisco, Mexico; E-mail: moyaraygoza@gmail.com (G. M. R.)
*Corresponding author; E-mail: moyaraygoza@gmail.com

seasonal dry tropical forest where plant species present green foliage during the wet season (Moya-Raygoza et al. 2019). On the other hand, maize crops generally are planted as monocultures and supported by humans, through fertilization, insecticides, and herbicides.

A high number of herbivore insect pests are expected in domesticated maize due to its richness as a food resource; conversely, a low number of insect pests are expected in teosinte (Rosenthal & Dirzo 1997). Comparing maize crops vs. *Z. mays* ssp. *parviglumis* habitats from the Jalisco region, we found a 50% reduction in herbivore leafhopper diversity in the maize crop (Moya-Raygoza et al. 2019). We reported that within the maize crop, the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) was the most abundant leafhopper species. The corn leafhopper is a specialist on maize and teosintes, and is the most important leafhopper pest in maize throughout Latin America (Nault 1990). Females of *D. maidis* insert the eggs singly into the plant tissue in the leaf blade or in the leaf midrib (Heady & Nault 1984). Also, *D. maidis* has a high degree of egg clustering, and most of its eggs are laid on the midrib of the upper leaf surface (Heady et al. 1985).

Egg parasitoids that attack *D. maidis* in maize crops are important in biological control, in part because they reach high levels of parasitism. In Mexico, Central America, and South America, *Anagrus virlai* Triapitsyn (Hymenoptera: Mymaridae) and *Paracentrobia* sp. (Hymenoptera: Trichogrammatidae) are abundant and common egg parasitoids of *D. maidis* in maize habitats (Gladstone et al. 1994; Virla et al. 2013; Moya-Raygoza et al. 2014; Luft Albarracin et al. 2017). In Latin America, finding 2 or more egg parasitoid species attacking *D. maidis* in the same maize field is common, and the percentage of egg parasitism reaches high levels. For example, in Mexico and Argentina, the percentage of egg parasitism by the 2 most abundant parasitoids, *A. virlai* and *Paracentrobia* sp., reaches 60.9% and 44.8 %, respectively (Moya-Raygoza et al. 2012).

Herbivore leafhopper diversity is known in maize and its direct ancestor *Z. mays* ssp. *parviglumis*; however, little is known about the differences in diversity and density-dependence relationship between parasitoids that attack insect pests in maize plants vs. teosinte plants within maize habitat, and those parasitoids that attack insect pests in the annual teosinte habitat. The objective of the present study was to investigate the diversity of egg parasitoids and relationships between the number of *D. maidis* eggs and the community of adult parasitoids in maize landrace and teosinte plants within the wild habitat of *Z. mays* ssp. *parviglumis*, and egg parasitoids in maize landrace and teosinte plants within the maize agroecosystem. This study contributes to the understanding of how parasitoid diversity and parasitoid-host relationships has changed from teosinte wild habitat to cultivated maize habitat.

Materials and Methods

STUDY SITES

The study was conducted at 2 habitats in Jalisco, Mexico. The first site, El Grullo, is located at 19.4927000°N, 104.1428000°W, and 888 masl. Here a 300 m² maize field was cultivated as a monoculture, and local farmers applied agrochemicals according to the common practices in the region. The El Grullo site is in the El Grullo agriculture valley or region in which maize has been cultivated for about 2,000 yr (Benz & Laitner 1998). A dry tropical forest may have existed in this valley before human occupation (B. F. Benz, personal communication). The second site, Ejutla, is located at 19.5359000°N, 104.1024000°W, and 1,336 masl. In Ejutla, the annual wild teosinte *Z. mays* ssp. *parviglu-*

mis grows naturally in the dry tropical forest among herbs, shrubs, and trees (Moya-Raygoza et al. 2019). The teosinte in Ejutla grew in a 300 m² patch during the wet season and has green foliage from Jue to Oct. There were no maize fields near wild teosinte from Ejutla. The distance between the Ejutla and El Grullo sites is approximately 11 km.

PARASITOIDS OF *DALBULUS MAIDIS* EGGS ON MAIZE AND TEOSINTE

Experiments with the egg parasitoids were conducted during the maize-growing wet season. Laboratory-reared *D. maidis* were used in the experiments. In all experiments, 2-wk-old *D. maidis* females were used for oviposition on live maize (*Z. mays* ssp. *mays*; native maize race Ancho-pozolero) or on wild teosinte (*Z. mays* ssp. *parviglumis*). Potted teosinte plants used in the lab and field experiments came from seeds collected at the Ejutla site. For oviposition on each plant, 5 females were confined in a cage enclosing a single leaf of a live host plant. Maize and teosinte plants at the 6–leaf stage with sentinel eggs were placed in both habitats The oviposition period was 72 h, and was conducted under laboratory conditions at the University of Guadalajara in a rearing room at 25 ± 2 °C, 50% RH, with a photoperiod of 12:12 h (L:D). After the oviposition period, adult females were removed, and pots containing the leaves with sentinel eggs were transported immediately to the El Grullo and Ejutla habitats. A first set of experiments was performed on 12 Aug 2016: at the El Grullo habitat 29 maize leaves and 28 teosinte leaves were placed. Also, at the Ejutla habitat, 29 maize leaves and 28 teosinte leaves were placed. A second set of experiments with sentinel maize and teosinte plants at the 6–leaf stage was performed on 16 Sep 2016; 19 maize leaves on Grullo maize, 20 teosinte leaves on Grullo teosinte, 21 maize leaves on Ejutla maize, and 20 teosinte leaves on Ejutla teosinte. In total, the treatment Grullo maize had 48 potted maize plants, the treatment Grullo teosinte had 48 potted teosinte plants, the treatment Ejutla maize had 50 potted maize plants, and the treatment Ejutla teosinte had 48 potted teosinte plants. This second set of pots was placed 100 m distant from the first set in each habitat. The sentinel plants were distributed into the teosinte and maize habitats. The pots remained in the teosinte and maize habitats for 5 days to allow exposure to egg parasitoids.

After 5 days, the sentinel plants were returned to the laboratory, where the number of *D. maidis* eggs on each exposed leaf was determined. Eggs were counted under a stereoscope (Stemi DV4, Carl Zeiss, Oberkochen, Germany). Once the number of eggs on each exposed leaf was counted, it was cut from the maize plant and transferred to a Petri dish. Each dish was covered with clear plastic food wrap to prevent escape of emerged adult parasitoids, and maintained in the rearing room under the previously described conditions. This technique of collecting egg parasitoids using sentinel eggs has been used by Virla et al. (2009), Moya-Raygoza et al. (2012, 2014), and Moya-Raygoza & Triapitsyn (2015) in previous studies with maize plants.

Eggs were checked every other d until adult parasitoids emerged to be collected; these were placed in 95% ethanol for future mounting and identification. Egg parasitoids of *D. maidis* should emerge as adults before the end of a 35-d period (Moya-Raygoza & Becerra-Chiron 2014). For each treatment, the adult parasitoids that emerged were counted and identified. The parasitoids were identified using available keys of Pinto (2006), Triapitsyn (2015), and Triapitsyn et al. (2019). Representatives of each species were slide-mounted in Faure liquid, and deposited in the entomological collection of the University of Guadalajara, Guadalajara, Jalisco, Mexico. In addition, species identifications were confirmed by S. Triapitsyn (Entomology Research Museum, University of California at Riverside, Riverside, California, USA).

DATA ANALYSIS

The average numbers of *D. maidis* eggs laid on maize and teosinte leaves within the same habitat were compared using a *t*-test with log transformed data. The same *t*-test with log transformed data was conducted to compare the number of emerged parasitoids in the maize habitat (Grullo maize vs. Grullo teosinte) and teosinte habitat (Ejutla maize vs. Ejutla teosinte). These tests were performed using SPSS software (SPSS, vers. 22 for Windows, Chicago, Illinois, USA). Diversity was calculated using the abundance and richness of adult parasitoids obtained in maize and teosinte plants within each habitat. The Shannon-Weaver (H') index was calculated using natural logarithm data. The Shannon-Weaver diversity index represents the diversity of a population and is calculated as $H' = -\Sigma\ pi \times \ln\ pi$, where pi is the proportion of each species in the total sample (Price 1997). The diversity of adult parasitoids collected in the maize vs. teosinte plants within each habitat were compared using the *t* Hutcheson test. The relationship between Ln (Eggs + 1) and Ln (Parasitoids + 1) was analyzed for the parasitoid complex in the maize habitat (El Grullo site) and in the wild teosinte habitat (Ejutla site) by linear regression. This was conducted using a redundancy canonical analysis with the program CANOCO 4.1 (Ter Braak & Smilauer 2002). The statistical model Trace was used as analogous to the coefficient of determination R². In addition, a liner regression between Ln (Eggs + 1) and Ln (*A. virlai* + 1) was performed in maize plants and in teosinte plants placed within the maize habitat by using R vers. 3.5.2 software (R Core Team 2018).

Results

No differences in oviposition rate by *D. maidis* females were found between the maize plants and teosinte plants. *Dalbulus maidis* females laid similar numbers of eggs on maize (Grullo maize) and teosinte (Grullo teosinte) plants (*t*-test: $t = 0.89$; df = 94; $P = 0.37$) under laboratory conditions, and also when placed within the maize habitat. In addition, females oviposited similar number of eggs on maize (Ejutla maize) and teosinte (Ejutla teosinte) plants (*t*-test: $t = 1.41$; df = 96; $P = 0.16$) under laboratory conditions, and also when placed within the teosinte habitat (Table 1).

In addition, no differences were found in the number of emerged egg parasitoids from the maize and teosinte plants within the same habitat. Similar numbers of emerged adult parasitoids from the maize and teosinte sentinel plants within the maize habitat (Grullo maize vs. Grullo teosinte: $t = 0.69$; df = 44; $P = 0.49$). The same occurred within the teosinte wild habitat, because similar number of emerged adult parasitoids from the maize and teosinte sentinel plants (Ejutla maize vs. Ejutla teosinte: $t = 0.49$; df = 13; $P = 0.62$) (Table 1). However, adult parasitoids were more abundant in the maize habitat from El Grullo than in the teosinte habitat from Ejutla (Table 2). The egg parasitoid

communities differed at the 2 habitats: that in the maize habitat (El Grullo) consisting of *A. virlai*, *Paracentrobia* sp., and *Pseudoligosita* sp., and the community in the teosinte habitat (Ejutla) consisting of *A. virlai*, *A. incarnatus*, of which *Anagrus columbi* Perkins (Hymenoptera: Mymaridae) is a synonym (Triapitsyn et al. 2018), and also *Paracentrobia* sp., and *Pseudoligosita* sp. Also, *A. virlai* was the most abundant and common species in the maize habitat, because it emerged from 17 maize leaves and 14 teosinte leaves, whereas *A. incarnatus* was the most abundant but not common species in the teosinte habitat, because it emerged only from 3 maize leaves and 3 teosinte leaves.

Moreover, different diversity of adult parasitoids occurred within the maize habitat (*t* Hutcheson test: $t = 5.34$; df = 346.82; $P = 0.0001$). More diversity ($H' = 0.73$) of parasitoids was seen over the teosinte sentinel plants than in the maize sentinel plants, which had a diversity of $H' = 0.30$. Similar results were found within the teosinte habitat due to different diversity of adult parasitoids being found (*t* Hutcheson test: $t = 2.70$; df = 82.00; $P = 0.008$). A higher diversity ($H' = 0.88$) of parasitoids was observed in the teosinte sentinel plants than in the maize sentinel plants, which had a diversity of $H' = 0.40$.

At the El Grullo site, the number of parasitoids in the complex as a whole was positively and significantly influenced by the number of *D. maidis* eggs oviposited on maize leaves (Trace = 0.541; $F = 36.508$; $P = 0.0001$) (Fig. 1A) and teosinte leaves (Trace = 0.641; $F = 50.041$; $P = 0.0001$) (Fig. 1B) placed within the maize agroecosystem. In contrast, in the teosinte wild ecosystem, a weak density-dependence association was seen between the number of *D. maidis* eggs and the number of emerged parasitoids. This was observed for the parasitoid complex as a whole, on both maize leaves (Trace = 0.281; $F = 12.928$; $P = 0.0004$) (Fig. 2A) and teosinte leaves (Trace = 0.233; $F = 7.908$; $P = 0.0071$) (Fig. 2B). In the maize habitat from El Grullo, a significant increase in the number of emerged *A. virlai* was seen when the number of *D. maidis* eggs increased in maize leaves (R² = 0.403; $y = 0.691 \times + 0.219$; $P = 0.0061$) (Fig. 3A) and in teosinte leaves (R² = 0.679; $y = 0.774 \times + 0.055$; $P = 0.0002$) (Fig. 3B).

Discussion

Little is known about the community of egg parasitoids of an insect pest in maize crops vs. wild teosinte habitat in the region of origin of domesticated maize. Eggs of the corn leafhopper were parasitized by micro-hymenopteran species (Mymaridae and Trichogrammatidae) within maize and teosinte habitats. The composition of egg parasitoid communities found in the teosinte wild and maize habitats differed. Whereas *A. incarnatus* was the most abundant in the teosinte habitat, *A. virlai* was the most abundant in the maize habitat. *Anagrus incarnatus*, previously described as *A. columbi*, parasitize eggs of the planthopper *Prokelisia crocea* (Van Duzee) (Hemiptera: Delphacidae) (Reeve

Table 1. *Dalbulus maidis* eggs laid on maize and teosinte leaves, parasitoid adults emerged, and percentage of emerged parasitoids from maize habitat (Grullo maize and Grullo teosinte treatments) and teosinte habitat (Ejutla maize and Ejutla teosinte treatments). SE = standard error.

	Dalbulus maidis eggs laid	Emerged parasitoids	Parasitoids	Leaves per treatment
	Mean per leaf (± SE)	Mean per leaf (± SE)	Percentage	Total
Maize habitat				
Grullo maize	9.41 (1.99)	6.78 (1.89)	49.55	48
Grullo teosinte	6.31 (1.62)	5.20 (1.30)	51.48	48
Teosinte habitat				
Ejutla maize	10.28 (2.51)	1.51 (1.15)	10.31	50
Ejutla teosinte	6.02 (1.65)	1.39 (0.71)	13.49	48

Table 2. Total abundance of adult parasitoids emerged that attack *Dalbulus maidis* eggs within maize habitat (Grullo maize and Grullo teosinte treatments) and teosinte habitat (Ejutla maize and Ejutla teosinte treatments).

Parasitoid species	Maize habitat		Teosinte habitat	
	Grullo maize	Grullo teosinte	Ejutla maize	Ejutla teosinte
Anagrus virlai	207	117	0	2
Anagrus incarnatus	0	0	47	27
Paracentrobia sp.	14	24	1	2
Pseudoligosita sp.	3	15	5	8
Total	224	156	53	39

& Cronin 2010) and eggs of the corn leafhopper (Moya-Raygoza & Becerra-Chiron 2014). In addition, *A. virlai* is a generalist parasitoid of leafhoppers and planthoppers (Triapitsyn 2015; Hill et al. 2019). Previous studies found a complex of multiple species of egg parasitoids that attack *D. maidis* on sentinel maize plants in maize crops cultivated in Mexico, Central America, and South America (Virla et al. 2009; Moya-Raygoza et al. 2012, 2014; Moya-Raygoza & Becerra-Chiron 2014; Triapitsyn 2015; Luft Albarracin et al. 2017). In accordance with the present study, these studies also found *A. virlai* (which first was identified as *Anagrus breviphragma* Soyka [Hymenoptera: Mymaridae] and then as *A. incarnatus*) and *Paracentrobia* sp. to be the most common and abundant species in maize agroecosystems. Both species in the maize agroecosystems in Mexico and Argentina showed a high percentage of egg parasitism, reaching 60.9% and 44.8 %, respectively (Moya-Raygoza et al. 2012).

Parasitoid-attracting volatiles emitted by plants damaged by sap feeder hoppers was reported in egg parasitoids. For instance, in rice the planthopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) induces volatile compounds that attract the egg parasitoid *A. incarnatus* (Lou et al. 2005), of which *Anagrus nilaparvatae* Pang & Wang (Hymenoptera:

Mymaridae) is a synonym (Triapitsyn et al. 2018). Also, *A. breviphragma*, another current synonym of *A. incarnatus* (Triapitsyn et al. 2018), responds to the volatiles emitted by the leaves of *Carex riparia* Curtis (Cyperaceae) in response to damage by the leafhopper *Cicadella viridis* (L.) (Hemiptera: Cicadellidae) (Chiappini et al. 2012). Chiappini et al. (2012) suggest that a synergetic effect of a local plant synomone and an egg kairomone serve to attract *A. breviphragma* females to plants with the leafhopper eggs, and provide the parasitoid with information to find the leaf with the leafhopper eggs, increasing host searching efficiency. Another potential source of attraction for adult egg parasitoids is honeydew. *Dalbulus maidis* adults produce honeydew as excrement (Larsen et al. 1992), and honeydew is used as a food resource by parasitoid adults (Tena et al. 2013). In the present study, different egg parasitoid diversity occurs within the maize and teosinte habitats with the highest diversity in the teosinte sentinel plants rather than in the maize sentinel plants. This difference could be due to *Z. mays* ssp. *parviglumis* plants producing more quality or quantity of specific volatiles than the maize landrace variety (Ancho-pozolero) (Gouinguené et al. 2001), thus increasing egg parasitoid evenness. Perhaps volatile, honeydew, or both are key factors in the attraction of egg parasitoid adults into the maize field.
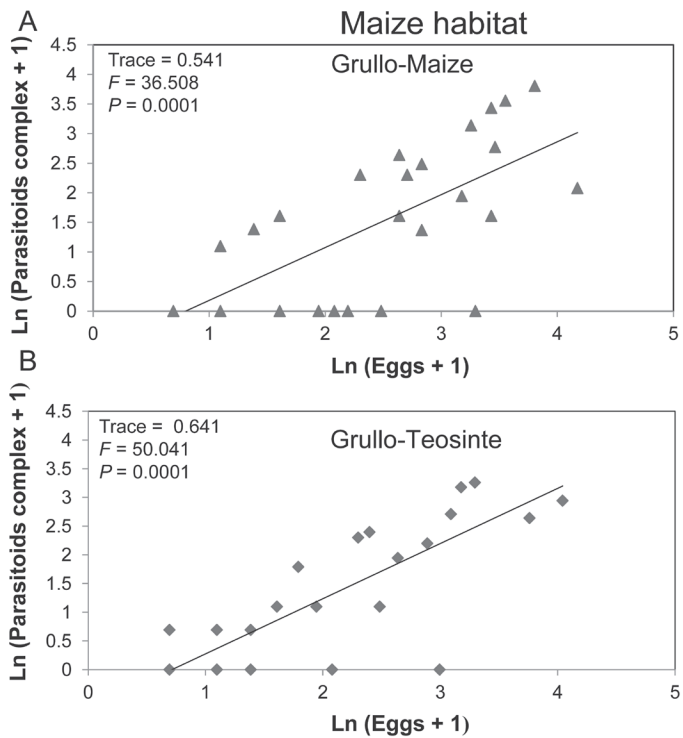

Fig. 1. Relationship between the number of exposed *Dalbulus maidis* eggs and number of adult parasitoids (of any species) found in the crop maize habitat on (A) maize sentinel plants, and (B) teosinte sentinel plants.
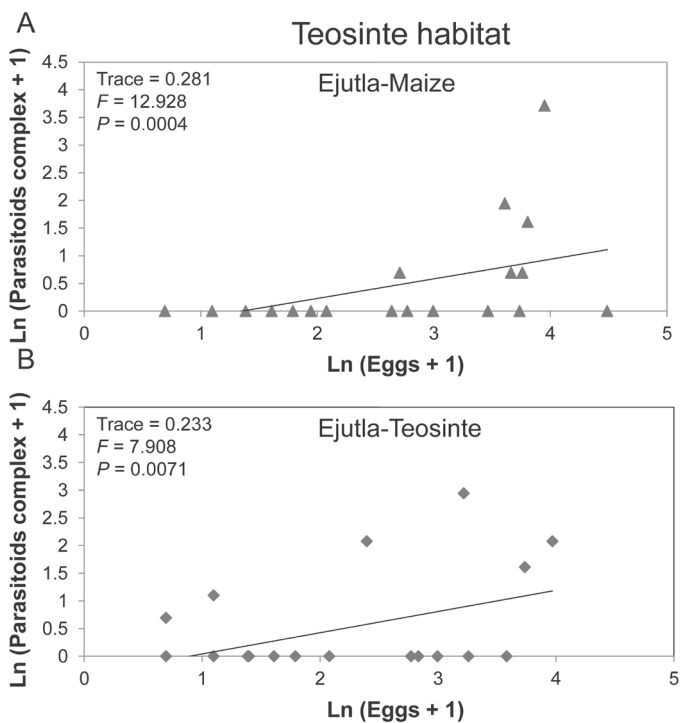
Fig. 2. Relationship between the number of exposed *Dalbulus maidis* eggs and number of adult parasitoids (of any species) in the wild teosinte habitat on (A) maize sentinel plants, and (B) teosinte sentinel plants.
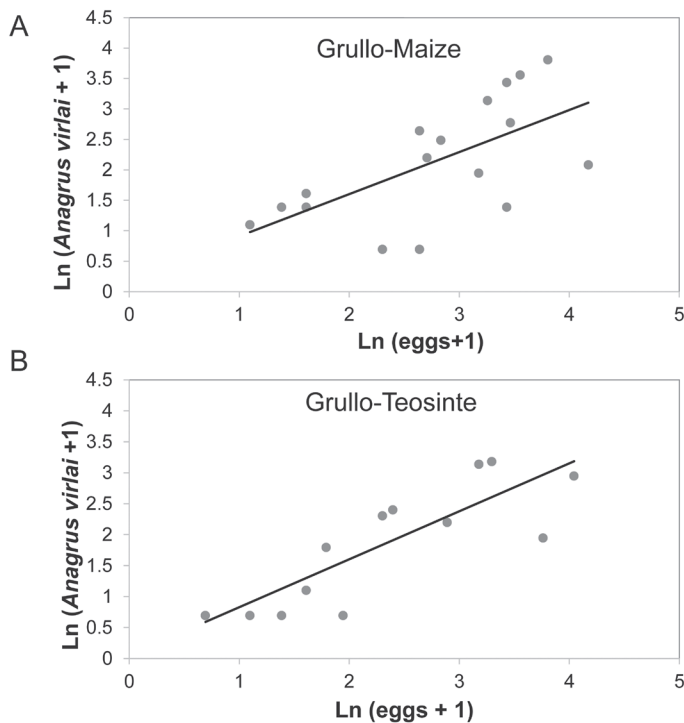
Fig. 3. Relationship between the number of exposed *Dalbulus maidis* eggs and number of *Anagrus virlai* within the crop maize habitat on (A) maize sentinel plants, and (B) teosinte sentinel plants.

The egg parasitoid complex as a whole and *A. virlai* were positively associated with the number of *D. maidis* eggs within the maize agroecosystem in both maize and teosinte sentinel plants. These data, based on regression analysis, suggest that the association in maize is density-dependent. This positive association in the maize field agrees with the prediction, based on optimal foraging or host-parasitoid interaction, that there should be a positive association between parasitoids and host density in agricultural habitats. A positive density-dependence association between leafhopper density and egg parasitoids was found in several agroecosystems. For example, in a vineyard habitat in California, USA, it was found that a density-dependent association exists between the parasitoid *Anagrus daanei* Triapitsyn (Hymenoptera: Mymaridae) and its host leafhoppers *Erythroneura* spp. (Hemiptera: Cicadellidae) (Segoli & Rosenheim 2013). Also, in apple habitat a density-dependent association was reported between the parasitoid *Anagrus epos* Girault (Hymenoptera: Mymaridae) and the leafhopper *Typhlocyba pomaria* McAtee (Hemiptera: Cicadellidae) (Seyedoleslami & Croft 1980), although the egg parasitoid was likely misidentified.

The maize agroecosystem exerted a positive effect on both the corn leafhopper abundance and egg parasitoid abundance. Maize plants cultivated in an agroecosystem are a rich food resource for herbivores such as *D. maidis*, a species that can rapidly reach a large number of adults because of its high fecundity (Nault & Madden 1985). Recently, Moya-Raygoza et al. (2019) reported a low number of *D. maidis* adults collected on 7 populations of *Z. mays* ssp. *parviglumis*, compared with the high number of *D. maidis* adults collected on 7 maize crops in Jalisco, Mexico. In the present study, more parasitoids attacked eggs of *D. maidis* in the maize agroecosystem. In the case of the maize habitat, environmental conditions such as monoculture may favor both the insect pest and the community of egg parasitoids. These results are in agreement with those of other studies reporting that maize plants are a high-quality resource for herbivorous chewing insects which, due to

their great abundance in agroecosystems, leads to higher levels of herbivory compared with wild teosinte relatives (Rosenthal & Dirzo 1997). This positive effect was reported for parasitoids that attack chewing insects. For example, Gols et al. (2008) found that the generalist parasitoid *Diadegma fenestrale* (Holmgren) (Hymenoptera: Ichneumonidae) developed better on the cultivated populations of cabbage *Brassica oleracea* L. (Brassicaceae) than on a wild population of a related plant. Similarly, Benrey et al. (1998) showed that the parasitoid *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) performed better on cultivated *Brassica* sp. and *Phaseolus* sp. than on their wild relatives. Plants damaged by the herbivores in agroecosystems may benefit parasitoids because more damage produces more volatiles, which serve as signals to attract natural enemies of the herbivores (Turlings & Benrey 1998; Tamiru et al. 2011).

On the other hand, a weak density-dependence association was found within the teosinte wild habitat in both maize landrace and teosinte sentinel plants. Moya-Raygoza & Triapitsyn (2017) found a low number of adult egg parasitoids during 4 consecutive yr using *Z. mays* ssp. *parviglumis* with *D. maidis* eggs to attract parasitoids within the teosinte habitat. Similar results were found in the present study using maize and teosinte sentinel plants, because few leaves with sentinel eggs were localized by the parasitoids within the teosinte habitat. Although a high number of *D. maidis* eggs was available in the teosinte habitat, few leaves with sentinel eggs were found by the parasitoids. Also, the low number of eggs found by the adult parasitoids may be due to the high habitat complexity in the annual teosinte habitat. Within the Ejutla teosinte habitat *Z. mays* spp. *parviglumis* grows in high density among plants of the families Rubiaceae, Poaceae, Malvaceae, Fabaceae, Euphorbiaceae, Asteraceae, Amaranthaceae, and Acanthaceae (Moya-Raygoza et al. 2019). In the parasitoid *Cotesia glomerata*, host location success is determined mostly by habitat characteristics, and it responds more weakly when habitat complexity increases (Martijn Bezemer et al. 2010).

In conclusion, diversity of adult parasitoids was different in maize and teosinte sentinel plants within the same habitat, and in the teosinte plants the highest diversity of adult parasitoids was recorded. Adult parasitoids were more abundant in the maize habitat. In addition, a density-dependent relationship between parasitoids and the corn leafhopper eggs occurred in both habitats, although this relationship was stronger in the maize habitat than in the teosinte habitat.

Acknowledgments

References Cited

Benrey B, Callejas A, Rios L, Oyama K, Denno RF. 1998. The effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. Biological Control 11: 130–140.

Benz BF, Laitner L. 1998. Relaciones culturales de la cerámica de Morett y Tuscacuesco visto desde El Colomo, Jalisco, pp. 265–275 *In* Avila R, Emphoux JP, Gastélum LG, Ramírez S, Schönduble O, Valdéz F [eds.], El Occidente de México: Arqueología, Historia y Medio Ambiente. Universidad de Guadalajara, Jalisco, Mexico.

Chiappini E, Salerno G, Berzolla A, Lacovone A, Reguzzi MC, Conti E. 2012. Role of volatile semiochemicals in host location by the egg parasitoid *Anagrus breviphragma*. Entomological Experimentalis et Applicata 144: 311–316.

de Lange ES, Balmer D, Mauch-Mani B, Turlings TCJ. 2014. Insect and pathogen attack and resistance in maize and its wild ancestors, teosintes. New Phytologist 204: 329–341.

Gladstone SM, de La Llana A, Rios R, Lopez L. 1994. Egg parasitoids of the corn leafhopper, *Dalbulus maidis* (DeLong and Wolcott) (Homoptera: Cicadellidae) in Nicaraguan maize. Proceedings of the Entomological Society of Washington 96: 143–146.

Gols R, Bukovinszky T, Van Dam NM, Dicke M, Bullock J, Harvey JA. 2008. Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild *Brassica* populations. Journal of Chemical Ecology 34: 132–143.

Gounguené S, Degen T, Turlings TCJ. 2001. Variability in herbivore-induced odour emissions among maize cultivars and their wild ancestors (teosinte). Chemoecology 11: 9–16.

Heady SE, Nault LR. 1984. Leafhopper egg microfilaments (Homoptera: Cicadellidae). Annals of the Entomological Society of America 77: 610–615.

Heady SE, Madden LV, Nault LR. 1985. Oviposition behavior of *Dalbulus* leafhoppers (Homoptera: Cicadellidae). Annals of the Entomological Society of America 78: 723–727.

Hill JG, Luft Albarracin E, Coll Araoz MV, Virla EG. 2019. Effects of host species and host age on biological parameters of *Anagrus virlai* (Hymenoptera: Mymaridae), an egg parasitoid of *Dalbulus maidis* (Hemiptera: Cicadellidae) and *Peregrinus maidis* (Hemiptera: Delphacidae). Biological Control 131: 74–80.

Larsen KJ, Heady SE, Nault LR. 1992. Influence of ants (Hymenoptera: Formicidae) on honeydew excretion and escape behaviors in a myrmecophile, *Dalbulus quinquenotatus* (Homoptera: Cicadellidae), and its congeners. Journal of Insect Behavior 5: 109–122.

Lou YG, Ma B, Cheng JA. 2005. Attraction of the parasitoid *Anagrus nilaparvatae* to rice volatiles induced by the rice brown planthopper *Nilaparvata lugens*. Journal of Chemical Ecology 31: 2357–2372.

Luft Albarracin E, Triapitsyn SV, Virla EG. 2017. Egg parasitoid complex of the corn leafhopper, *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae), in Argentina. Neotropical Entomology 46: 666–677.

Martijn Bezemer T, Harvery JA, Kamp AFD, Wagenaar R, Gols R, Kostenko O, Fortuna TA, Engelkes T, Vet LEM, Van Der Putten WH, Soler R. 2010. Behaviour of male and female parasitoids in the field: influence of patch size, host density, and habitat complexity. Ecological Entomology 35: 341–351.

Matsuoka Y, Vigouroux Y, Goodman MM, Sanchez GJ, Buckler E, Doebley J. 2002. A single domestication for maize shown by multilocus microsatellite genotyping. Proceeding of the National Academy of Science of the United States of America 99: 6080–6084.

Moya-Raygoza G, Becerra-Chiron IM. 2014. Overwintering biology of egg parasitoids of *Dalbulus maidis* (Hemiptera: Cicadellidae) on perennial grasses, volunteer maize, stubble, and drip-irrigated maize. Annals of the Entomological Society of America 107: 926–932.

Moya-Raygoza G, Triapitsyn SV. 2015. Egg parasitoids (Hymenoptera: Mymaridae and Trichogrammatidae) of *Dalbulus quinquenotatus* (Hemiptera: Cicadellidae), with description of a new species of *Anagrus* (Mymaridae) from Mexico. Annals of the Entomological Society of America 108: 289–298.

Moya-Raygoza G, Triapitsyn SV. 2017. Egg parasitoids of *Dalbulus maidis* on wild teosinte in Mexico. Southwestern Entomologist 42: 691–700.

Moya-Raygoza G, Luft Albarracin E, Virla EG. 2012. Diversity of egg parasitoids attacking *Dalbulus maidis* (Hemiptera: Cicadellidae) populations at low and high elevation sites in Mexico and Argentina. Florida Entomologist 95: 105–112.

Moya-Raygoza G, Cuevas-Guzmán R, Pinedo-Escatel JA, Morales-Arias JG. 2019. Comparison of leafhopper (Hemiptera: Cicadellidae) diversity in maize and its wild ancestor teosinte, and plant diversity in the teosinte habitat. Annals of the Entomological Society of America 112: 99–106.

Moya-Raygoza G, Renteria IC, Luft Albarracin E, Virla EG. 2014. Egg parasitoids of the leafhoppers *Dalbulus maidis* and *Dalbulus elimatus* (Hemiptera: Cicadellidae) in two maize habitats. Florida Entomologist 97: 309–312.

Nault LR. 1990. Evolution of an insect pest: maize and the corn leafhopper, a case study. Maydica 35: 165–175.

Nault LR, Madden LV. 1985. Ecological strategies of *Dalbulus* leafhoppers. Ecological Entomology 10: 57–63.

Pinto JD. 2006. A review of the New World genera of Trichogrammatidae (Hymenoptera). Journal of Hymenoptera Research 15: 38–163.

Price PW. 1997. Insect Ecology, 3rd edition. John Wiley & Sons, Inc., Hoboken, New Jersey, USA.

R Core Team. 2018. R: a language and environment for statistical computing. R. Foundation for Statistical Computing, Vienna, Austria. https//www.R-project.org/ (last accessed 25 Oct 2019).

Reeve JD, Cronin T. 2010. Edge behavior in a minute parasitic wasp. Journal of Animal Ecology 79: 483–490.

Rosenthal JP, Dirzo R. 1997. Effects of life history, domestication and agronomic selection on plant defence against insects: evidence from maize and wild relatives. Evolutionary Ecology 11: 337–355.

Sánchez González JJ, Ruiz Collar JA, Garcia GM, Ojeda GR, Larios LDIC. 2018. Ecogeography of teosinte. PLoS ONE 13: e0192676. doi.org/10.1371/journal.pone.0192676

Segoli M, Rosenheim JA. 2013. The link between host density and egg production in a parasitoid insect: comparison between agricultural and natural habitats. Functional Ecology 27: 1224–1232.

Seyedoleslami H, Croft BA. 1980. Spatial distribution of overwintering eggs of the white apple leafhopper, *Typhlocyba pomaria*, and parasitism by *Anagrus epos*. Environmental Entomology 9: 624–628.

Tamiru A, Bruce TJA, Woodcock CM, Caulfield JC, Midega CAO, Ogol CKPO, Mayon P, Birkett MA, Pickett JA, Khan ZR. 2011. Maize landraces recruit egg and larval parasitoids in response to egg deposition by a herbivore. Ecology Letters 14: 1075–1083.

Tena A, Pekas A, Wäckers F, Urbaneja A. 2013. Energy reserves of parasitoids dependent on honeydew from non-hosts. Ecological Entomology 38: 278–289.

Ter Braak CJF, Smilauer P. 2002. CANOCO reference manual and cano draw for windows user's guide: software for canonical community ordination (vers. 4.5). Microcomputer Power, Ithaca New York, USA.

Triapitsyn SV. 2015. Taxonomy of the genus *Anagrus* Haliday (Hymenoptera: Mymaridae) of the world: an annotated key to the described species, discussion of the remaining problems, and a ckecklist. Acta Zoológica Lilloana 59: 3–50.

Triapitsyn SV, Rugman-Jones PF, Tretiakov PS, Shih H-T, Huang S-H. 2018. New synonymies in the *Anagrus incarnatus* Haliday 'species complex' (Hymenoptera: Mymaridae) including a common parasitoid of economically important planthopper (Hemiptera: Delphacidae) pests of rice in Asia. Journal of Natural History 52: 2795–2822.

Triapitsyn SV, Rugman-Jones PF, Tretiakov PS, Luft Albaracin E, Moya-Raygoza G, Querino RB. 2019. Molecular, morphological, and biological differentiation between *Anagrus virlai* sp. n., an egg parasitoid of the corn leafhopper *Dalbulus maidis* (Hemiptera: Cicadellidae) in the New World, and *Anagrus incarnatus* from the Paleartic region (Hymenoptera: Mymaridae). Neotropical Entomology 48: 87–97.

Turlings TC, Benrey B. 1998. Effects of plant metabolites on the behavior and development of parasitic wasps. Ecoscience 5: 321–333.

Virla EG, Luft Albarracin E, Moya-Raygoza G. 2009. Egg parasitoids of *Dalbulus maidis* (Hemiptera: Cicadellidae) in Jalisco State, Mexico. Florida Entomologist 92: 508–510.

Virla EG, Moya-Raygoza G, Luft Albarracin E. 2013. Egg parasitoids of the corn leafhopper, *Dalbulus maidis*, in the southernmost area of its distribution range. Journal of Insect Science 13: 1–7.

Zizumbo-Villareal D, Colunga-GarcíaMarín P. 2010. Origin of agriculture and plant domestication in west Mesoamerica. Genetic Resources and Crop Evolution 57: 813–825.