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Authors: Moya-Raygoza, Gustavo, Albarracin, Erica Luft, and Virla, Eduardo G.

DIVERSITY OF EGG PARASITOIDS ATTACKING *DALBULUS MAIDIS* (HEMIPTERA: CICADELLIDAE) POPULATIONS AT LOW AND HIGH ELEVATION SITES IN MEXICO AND ARGENTINA

Gustavo Moya-Raygoza[1], Erica Luft Albarracin[2]* and Eduardo G. Virla[2]

[1]Departamento de Botánica y Zoología, CUCBA, Universidad de Guadalajara, Km 15.5 Carretera Guadalajara-Nogales, Las Agujas, Zapopan, C.P. 45110, Apdo. Postal 139, Jalisco, México

[2]PROIMI-Biotecnología, Av. Belgrano y Pje. Caseros (T4001 MBV), Tucumán, Argentina

Abstract

The corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott), is one of the most important pests of maize in Latin America because of its efficiency as a vector of 3 species of plant pathogens. In spite of its significance, however, little is known about its egg parasitoids. In this study, we present new data on *D. maidis* egg parasitoids in Mexico and Argentina. We surveyed the egg parasitoids in 2 locations: Mexico and Argentina, representing the farthest expansion of the *D. maidis* populations from Mexico. Using maize plants with sentinel eggs, parasitoids were surveyed in central Mexico and northwestern Argentina, at both low (<1,000) and high (>1,000) elevation sites, during 2 maize-growing wet seasons. Parasitoids of the families Mymaridae and Trichogrammatidae were found in both countries. Argentinean sites showed the highest richness, with 10 species, whereas in Mexico we found 6 species. Also, the Shannon diversity index was 1.6 times greater in Argentina than in Mexico. Higher percentages of parasitized eggs were recorded at the low elevation sites in both Mexico and Argentina. *Anagrus breviphragma* Soyka, a generalist parasitoid, was the only species found attacking eggs of *D. maidis* in both Mexico and Argentina at both high and low elevations.

Key Words: corn leafhopper, vector, maize diseases, natural enemies, Mymaridae, Trichogrammatidae

Resumen

La chicharrita del maíz *Dalbulus maidis* es una importante plaga del maíz en América Latina, debido a su eficiencia como vector de tres especies de patógenos de plantas. A pesar de su importancia, el conocimiento sobre sus parasitoides de huevos es escaso. En este estudio, presentamos nueva información sobre los parasitoides de huevos de *D. maidis* en México y Argentina. Estudiamos los parasitoides de huevos de *D. maidis* en dos localidades: México y Argentina, que representa la distribución más lejana desde México. Los parasitoides fueron colectados utilizando plantas de maíz con huevos trampa, en el centro de México y noroeste de Argentina, en ambos lugares se monitorearon sitios de elevación baja (<1.000) y alta (>1.000), durante dos campañas agrícolas. En ambos países se registraron parasitoides pertenecientes a las familias Mymaridae y Trichogrammatidae. Los sitios de Argentina mostraron la mayor riqueza, con diez especies, mientras que en México se encontraron seis especies. Además, el índice de diversidad de Shannon fue 1.6 veces mayor en Argentina que en México. Los porcentajes de huevos parasitoidizados más altos fueron registrados en los sitios de baja elevación tanto en México como en Argentina. *Anagrus breviphragma* Soyka, un parasitoide generalista, fue la única especie que afectó los huevos de *D. maidis* en ambos países, tanto en elevaciones bajas como altas.

The corn leafhopper, *Dalbulus maidis* (De-Long & Wolcott) (Hemiptera: Cicadellidae), is considered the most important leafhopper pest of maize, *Zea mays* spp. *mays* L., in Latin America because of its efficiency as a vector of three major plant pathogens: corn stunt spiroplasma (CSS) (*Spiroplasma kunkelii* Whitcom et al.), maize bushy stunt phytoplasma, and maize rayado fino virus (*Marafivirus*) (Nault 1990). Throughout Latin America, the highest infection rates have been found in Central America, Peru, and Argentina, where in many corn crops 100% of the maize plants had symptoms of CSS (Nault et al.

1981; Hruska & Gomez 1997; Gimenez Pecci et al. 2002).

Dalbulus maidis likely evolved in Mexico when maize was first domesticated from its teosinte relative (Nault 1990; Moya-Raygoza & Garcia-Medina 2010), the annual teosinte (*Zea mays* ssp. *parviglumis* Iltis & Doebley) around 9,000 yr ago (Matsuoka et al. 2002). Later, maize was also cultivated in Central America (7,800-7,000 yr ago) (Dickau et al. 2007). Finally, isotopic and macrobotanical data show that maize arrived about 2,000 yr ago to the lowlands and 1,000 yr ago to the highlands of central western

Argentina (Gil *et al.* 2006). Maize has been dispersed via seed exchange rather than movement of human populations practicing agriculture (Dickau et al. 2007). It is likely that maize could be colonized by *D. maidis* adults through the process of maize dispersal, because leafhopper adults are able to migrate and survive for several months without maize (Larsen et al. 1992). A possible consequence of this long association between maize and *D. maidis* is that the corn leafhopper is broadly distributed throughout the American continent (Moya-Raygoza & Garcia-Medina 2010). The corn leafhopper is found from Mexico to northern Argentina, and throughout much of southeastern and southwestern United States (Triplehorn & Nault 1985; Summers et al. 2003). The farthest southern latitude of the corn leafhopper range is 30 °S in Argentina (Paradell et al. 2001), and this is the most distant point of the population's distribution from its likely center of origin in Mexico. Although *D. maidis* prefers to live at low elevations, it is found in a wide range of elevations from sea level to 3,200 m in the Peruvian Andes (Nault et al. 1979). In Mexico, at low elevations (<1,000 m) 2 or more overlapping crops are grown under irrigation supplying water during the dry season and rainfall during the wet season. But at high elevations (>1,000 m), maize usually is grown only during the wet season. This is where most of the maize is grown in Mexico; in these regions, the corn leafhopper is deprived of its hosts during the dry winter months when maize has died off (Nov-Apr) (Moya Raygoza et al. 2007a). The situation in most of Argentina is similar to that at high elevations in Mexico, with one or at least 2 sowing dates during the wet and hotter season (Oct-Apr).

The corn leafhopper has a rich natural enemy complex, including fungal pathogens, predators, and parasitoids. The parasitoids are antagonists that can be divided into 2 guilds: those attacking eggs (including embryophagous and oophagous species), and those affecting nymphs and adults. The egg parasitoids are all members of the Chalcidoidea (Hymenoptera), and are known from Nicaragua (Gladstone et al. 1994), Peru (Marin 1987), Brazil (Oliveira & Lopes 2000), Mexico, and Argentina. In Mexico, the eggs of *D. maidis* are parasitized by 2 Mymaridae and 3 Trichogrammatidae species (Virla et al. 2009a), whereas in Argentina they are parasitized by 3 Mymaridae, 4 Trichogrammatidae, 1 Eulophidae and 1 Aphelinidae species (Triapitsyn 1997; Virla 2001; Luft Albarracin et al. 2006; Luft Albarracin & Triapitsyn 2007; Polaszek & Luft Albarracin 2011).

Little is known about the egg parasitoids of *D. maidis*. Of potential importance is information on parasitoid dominance and parasitism rates at low (<1,000 m) and high (>1,000 m) elevations. Therefore, the objectives of this study were to determine richness, abundance, and diversity indices of the egg parasitoids that attack *D. maidis* at low and high elevation sites in Mexico and Argentina.

MATERIALS AND METHODS

Field Sites and Sampling Period in Mexico and Argentina

Parasitoids were surveyed in the state of Jalisco in central Mexico and Tucumán Province of northwestern Argentina, during the maize-growing wet season, when maize crops were available. We chose 2 sites in each country that represented the environmental conditions in which maize is planted. The high (>1,000 m) elevation sites included the Zapopan site (1,650 m asl; 20°74'N 103°30'W) in Mexico and the El Mollar site (1,945 m asl; 26°55' S, 65°43' W) in Argentina. The low (<1,000 m) elevation sites included the El Grullo site (868 m asl; 19°47'N 104°12'W) in Mexico and the Los Nogales site (588 m asl; 26°42'S 65°13'W) in Argentina. In Jalisco, Mexico, the wet season, which is characterized by higher rainfall and higher temperatures than the dry season, starts in Jun and ends in Sep (Larsen et al. 1992). The El Grullo site is characterized by high temperatures and high precipitation, whereas the Zapopan site is characterized by cooler temperatures and high precipitation during the maize growing season. In Tucumán, Argentina, the wet season, which starts in Dec and ends in Mar, also is characterized by higher rainfall and higher temperatures compared with the dry season De Fina (1992).

Samples were taken during 2 growing seasons in each country: Jun to Sep 2006 and Jun to Sep 2009 in Mexico, and Dec 2006 to Feb 2007 and Jan to Mar 2009 in Argentina, in cornfields free of pesticide applications. In both countries the same methodology was used to find and collect egg parasitoids.

Survey of Egg Parasitoids and Identification

Lab-reared *D. maidis* females of the same age (2 weeks old) were allowed to oviposit on three leaves of old maize plants. The maize variety used in Mexico was a race of maize ancho ('pozolero'), while that used in Argentina was 'Leales 25 plus'. Five females were confined for oviposition in a single leaf cage containing a leaf of a live maize plant during a period of 48 h. For each field sampling date, this was repeated 20 times with new cohorts of naive females. A potted plant with eggs was considered a single replicate. The replicates were maintained in a rearing room at 25 °C ± 2 °C. After 48 h, the adult females were removed, and the eggs oviposited on each maize leaf by the five females were counted. This was conducted in the laboratories in Mexico and Argentina. The

maize plants with eggs (sentinel eggs) were transported immediately to the field sites; a total of 120 replicates were exposed at the sites described above. In Mexico, the transportation time to get to the Zapopan site was approximately 1 h, while the time to get to the El Grullo site was approximately 3 h. In Argentina, transportation time to get to the Los Nogales site was approximately 0.5 h, and that to the El Mollar site was approximately 1.5 h.

The areas of the corn fields employed for exposure were 1.5 to 2 hectares. Once transported, the sentinels were placed in the maize field 3 m from the border and 10 m from each other. The sentinel eggs were exposed to egg parasitoids for 6 d in the cornfields. The period from oviposition to hatching of eggs at the local temperature range is 14-15 d (Nault 1990). After 6 days, the sentinels were brought into the lab, where the exposed egg masses were cut from the plant and transferred to a Petri dish with a bottom containing wet tissue paper. The dishes were covered with clear plastic food wrap to avoid desiccation and prevent escape by the wasps. Parasitized egg masses were checked daily until the hatching of the nymphs and/or the emergence of the adult wasps. Adults egg parasitoids were collected, counted, and identified to species level.

The parasitoids were identified using available specific keys (Triapitsyn 1999, 2002; Viggiani 1981) and, when necessary, by comparing with the type specimens. *Dalbulus maidis* determination was based on the key to the genus species of *Dalbulus* DeLong (Triplehorn & Nault 1985).

Diversity of Egg Parasitoids

For each Mexican and Argentinean site, we determined the number of eggs exposed, number of eggs parasitized, number of emerged adults, percentage of emerged adults, and parasitoid richness. Parasitized eggs were defined as those that changed color to brownish or reddish after five to seven days of field exposure, while those developing nymph embryo eyespots were considered to be unparasitized.

Regarding species diversity, we used the Shannon Wiener index (H'), the dominance index of Simpson (D) and Berger-Parker (*d*), and the Pielou Evenness index (J′), as follows:

$H' = -\sum pi \times log2pi$; $D = 1 - \sum (pi)^2$; $d = Nmax/N$; and $J' = H'/H'max$ where $pi = ni/N$, ni = number of individuals of species i, N = number of individuals of all species, Nmax = number of individuals of the most abundant species, H'max = log2S, and S = number of species (Moreno 2001).

The Jaccard's similarity index was calculated as: $I_j = c/A+B-c$ where A is the number of species found at site a, B is the number of species found at site b, and C is the number of species found at both site a and site b (Moreno 2001).

For each locality sampled, the relative importance (RI) of the species was determined only for the second growing season sampled, using the formula: $RI = (ni/nt) \times (mi/mt) \times 100$ where ni = number of individuals of species "i", nt = number of individuals of all species, mi = number of samples containing species "i", and mt = total number of samples. The species with RI > 0.5 were considered "common", and those with RI ≤ 0.5, were designated "rare".

Rates of parasitism were analyzed for high and low elevation sites in both countries, performing Student's t-test for mean separation at 0.05 level of significance (using InfoStat version 2010).

Voucher specimens were deposited at the entomological collection of the Instituto y Fundación "Miguel Lillo", San Miguel de Tucumán, Argentina (IFLA) and the Entomological collection of the University of Guadalajara, Mexico. Additionally, voucher specimens of *Paracentrobia tapajosae* Viggiani were deposited in the Entomology Research Museum, University of California, Riverside, California, USA (UCRC).

RESULTS

Dalbulus maidis eggs were attacked by oophagous species in Mexico and Argentina at low and high elevations during the two wet growing seasons. Higher percentages of parasitized eggs were recorded at the low elevation sites in both Mexico and Argentina. The mean percentage of parasitized eggs was 60.9% in El Grullo and 44.8% in Los Nogales, vs. 22.6% in Zapopan and 3.4% in El Mollar. The rates of parasitism were significantly different (*t*-test) when high and low elevation sites were compared in Mexico (El Grullo vs Zapopan): $t = 13.96$, df. = 169, $P < 0.0001$; and Argentina (Los Nogales vs El Mollar): $t = -17.46$, df. = 96, $P < 0.0001$. The mean percentage of emergence of adult parasitoids at low elevations were 55.6% and 56.1% for the Mexican and Argentinean sites, respectively, while at high elevations the percent of emergence was 50.9 for the Mexican site and 21.3 for the Argentinean site (Table 1).

Although the percentage of adult emergence and percentage of parasitized eggs were higher in Mexico than in Argentina, we found higher levels of species richness in Argentina (10 species) than in Mexico (6 species) (Table 2).

Anagrus breviphragma Soyka, *P. tapajosae* Viggiani, and *P. longifrangiata* (Viggiani) were all found attacking eggs of the corn leafhopper in Mexico and Argentina, but only *A. breviphragma* occurred at both high and low elevations in both countries (Table 2). In Mexico, at the low elevation site (El Grullo), *P. tapajosae* was dominant and very common (considering its abundance and frequency), while the other 5 species were rare.

TABLE 1. NUMBER OF PARASITIZED EGGS, NUMBER OF EMERGED ADULTS, AND PERCENTAGE OF PARASITISM IN *DALBULUS MAIDIS* FROM LOW (<1,000) AND HIGH (>1,000) ELEVATION SITES IN MEXICO AND ARGENTINA, DURING 2 MAIZE GROWING SEASONS.

Country	Locality	No. of eggs tested	Rpl.*	No. of parasitized eggs (%)	No. of wasps emerged	% of emergence
Mexico	El Grullo <1000 m	3040	96	1851 (60.9)	1030	55.6
	Zapopan >1000 m	6170	98	1398 (22.6)	711	50.9
Argentina	Los Nogales <000 m	6337	89	2839 (44.8)	1592	56.1
	El Mollar >1000 m	9282	95	320 (3.4)	68	21.3

(*) Rpl., number of healthy replicates recovered from the field.

At the high elevation site (Zapopan), both *P. tapajosae* and *A. breviphragma* were common. The mymarid was the most abundant but occurred only in a few samples, while the trichogrammatid was the most frequently encountered over the course of the corn growing season. In Argentina, the attack rates of the different egg parasitoids were more even. At the low elevation site (Los Nogales), 3 of 7 species were common (in order of RI, *A. breviphragma*, *P. longifrangiata*, and *P. tapajosae*), whereas at the high elevation site (El Mollar), *Polynema* sp. near *P. orientale* Girault and *A. breviphragma* were common (Table 2).

The diversity of egg parasitoids found in the center of origin of *D. maidis* (Mexico) and that of those in its southernmost distribution range (Argentina) were compared between the 2 countries, the 4 sampled sites, and the 2 elevation lev-

TABLE 2. SPECIES RICHNESS AND ABUNDANCE OF EGG PARASITOIDS THAT ATTACKED *DALBULUS MAIDIS* EGGS DURING 2 MAIZE GROWING SEASONS IN MEXICO AND ARGENTINA FROM LOW (EL GRULLO AND LOS NOGALES) AND HIGH (ZAPOPAN AND EL MOLLAR) ELEVATION SITES. THE RELATIVE IMPORTANCE OF THE SPECIES FOR EACH SITE, MEASURED FOR THE SECOND SAMPLED YEAR, IS PRESENTED IN BRACKETS.

Species	Mexico		Argentina	
	El Grullo	Zapopan	Los Nogales	El Mollar
Anagrus breviphragma Soyka	42 (0.01)	581 (12.18)	797 (23.62)	34 (1.05)
Anagrus flaveolus Waterhouse	—	—	45 (0.22)	—
Anagrus miriamae Triapitsyn & Virla	—	—	—	9 (0.14)
Polynema sp. near *P. orientale* Girault	—	—	—	20 (*) (2.17)
Polynema sp. near *P. reticulatum* (Ogloblin)	—	—	10 (*) (0.03)	—
Polynema saga (Girault)	4 (*) (**) (0.006)	—	—	—
Aphelinoidea semifuscipennis Girault	14 (**) (0.02)	3 (0.05)	—	—
Oligosita clarimaculosa (Girault)	5 (*) (**) (0.03)	2 (0.02)	—	—
Oligosita desantisi Viggiani	—	—	—	2 (0.03)
Oligosita giraulti Crawford	—	—	3 (0.002)	—
Paracentrobia tapajosae Viggiani	957 (**) (85.28)	125 (13.53)	334 (9.9)	—
Pseudoligosita longifrangiata (Viggiani)	8 (**) (***)	—	401 (16.13)	3 (0.09)
Zagella nanula De Santis	—	—	2 (0.001)	—

(*) new record as *Dalbulus maidis* parasitoid.
(**) new record for this county.
(***) not found during 2009.

els. The Shannon diversity index was 1.6 times greater in Argentina than in Mexico, while Simpson's dominance index was 1.4 times greater for Mexico. Considering the sites individually, the highest Shannon diversity index was recorded for El Mollar and the lowest was found in El Grullo (Table 3). Also, the Shannon diversity index shows higher values in the high elevation Mexican and Argentinean sites. This is because, in the Zapopan and El Mollar sites, few species of egg parasitoids are dominant. On the other hand, the Simpson's dominance index shows higher values for the Mexican sites than for the Argentinean sites. Also, the equitability of the distribution of individuals among parasitoid species (Pielou's evenness index) was relatively low for the assemblage of species affecting the corn leafhopper in its native range in comparison with the colonized range (Table 3). The Mexican localities shared a higher number of species in comparison with the Argentinean localities; the Jaccard similarity index values calculated between the sampled sites are showed in Table 4.

Discussion

The present report represents the largest study of corn leafhopper egg parasitoids thus far conducted in the New World. The previously reported corn leafhopper egg parasitoids are: *Anagrus flaveolus* Waterhouse, from Peru (Marín 1987); *A. breviphragma* and *Oligosita* sp., from Brazil (Oliveira & Lopes 2000); *Anagrus* sp. and *Paracentrobia* sp. from Nicaragua (Gladstone et al. 1994); 5 species from Mexico (Virla et al. 2009a); and 8 species from Argentina (Triapitsyn 1997; Virla 2001; Luft Albarracin & Triapitsyn 2007; Luft Albarracin et al. 2006, Polaszek & Luft Albarracin 2011). Here, we found 10 species of egg parasitoids in Argentina and 6 in Mexico; in total, 13 species were found in both countries. The present study includes the first finding of *Polynema* sp. near *P. orientale* and *Polynema* sp. near *P. reticulatum* (Ogloblin) in Argentina, parasitoids at low and high elevations, respectively. Also we are reporting for the first time the presence of *Polynema saga* (Girault) and *Oligosita clarimaculosa* (Girault) in Mexico. We are recording for the first time *Aphelinoidea semifuscipennis* Girault

at high elevation Mexican sites. In the course of this study, we also elucidated the specific status of some species from Mexico cited in Virla et al. (2009a): the species described as *Polynema* sp. is *P. saga*; *Paracentrobia* near *P. subflava* (Girault) is *P. tapajosae* Viggiani; *Aphelinoidea* sp. is *A. semifuscipennis*; and *Pseudoligosita* sp. is *P. longifrangiata* (Viggiani).

The low percentage of parasitism found at high elevation sites (>1,000 m), both in Mexico and Argentina (22.6% and 3.4%, respectively), is consistent with the behavior reported for parasitoids attacking other species of herbivores in similar conditions (Hodkinson 2005). For instance, Hodkinson (2005) mentioned that populations living at the upper elevation extremes experience quite variable environmental conditions, especially with respect to the local climate. He found that levels of parasitism of a host species by various host-specific parasitoids representing several insect orders generally appear to decline with increasing elevation. This could be explained by the fact that the searching efficiency and thus the success of parasitoids are impaired under the cooler and often misty conditions at higher elevations. The fact that we found a high (60.9% in Mexico and 44.8% in Argentina) percentage of parasitism at low elevation sites (<1,000 m) is promising, because at low elevations the various environments and conditions preferred by the corn leafhopper tend to overlap or intertwine, and this also true for the corn stunt spiroplasma, which causes the highest levels of damage to maize throughout Latin America (Moya-Raygoza et al. 2007b).

We found the percentage of emergence of the adult parasitoids to range from 21.3% to 56.1% in both Mexican and Argentinean sites. The low percentage of emergence of adult parasitoids in the laboratory was likely due to damage (rotting or drying of the leaves and the host eggs) during the long preimaginal period of some species of parasitoids, mostly the trichogrammatids. A similar situation was reported by other researchers studying egg parasitoids (Logarzo et al. 2004; Virla et al. 2005, 2009b).

Empirical studies suggest that most exotic species have fewer parasitoid species in their introduced range than in their native range, but our results contradict this assumption. Having

TABLE 3. Diversity index of egg parasitoids of *Dalbulus maidis* in Mexico and Argentina from low (El grullo and Los nogales) and high (Zapopan and El mollar) elevation sites during 2 maize growing seasons.

Index	Mexico			Argentina		
	General	El Grullo	Zapopan	General	Los Nogales	El Mollar
Shannon index (H´)	0.78	0.36	0.51	1.25	1.17	1.22
Simpson's dominance index (D)	0.51	0.86	0.69	0.36	0.36	0.35
Berger-Parker index (d)	0.61	0.92	0.82	0.50	0.50	0.50
Pielou's evenness index (J´)	0.44	0.20	0.37	0.54	0.60	0.76

TABLE 4. JACCARD SIMILARITY INDEX OF EGG PARASITOIDS OF *DALBULUS MAIDIS* IN MEXICO AND ARGENTINA FROM LOW (EL GRULLO AND LOS NOGALES) AND HIGH (ZAPOPAN AND EL MOLLAR) ELEVATION SITES DURING 2 MAIZE GROWING SEASONS.

| | Mexico | | Argentina | |
	El Grullo	Zapopan	Los Nogales	El Mollar
El Grullo	1	—	—	—
Zapopan	0.67	1	—	—
Los Nogales	0.30	0.22	1	—
El Mollar	0.22	0.12	0.20	1

arrived in Argentina 1,000-2,000 yr ago when maize was moved by the natives (Gil et al. 2006), and being an oligophagous species that feeds only on maize and teosinte, perhaps the number of egg parasitoid taxa found in Argentina is high because the corn leafhopper has been residing in this foreign location for a long time and may have accumulated more native parasitoid species. The accumulation of native parasitoids in invader herbivores is gradual in many cases and may occur over long periods of time because native parasitoids need to adjust their behavior, phenology, or ecology before exploiting the introduced host (Cornell & Hawkins 1993).

Three species (*A. breviphragma*, *P. tapajosae*, and *P. longifrangiata*) were collected in both countries and show generalist habits. The mymarid wasp *A. breviphragma* attacks 15 species, including the leafhoppers *Agalliana ensigera* Oman, *D. maidis, Chlorotettix fraterculus* (Berg), *Cicadella viridis* L., *Ciminius platensis* (Berg), *Dechacona missionum* (Berg), *Exitianus obscurinervis* (Stål), *Hortensia similis* (Walker), and *Xerophloea viridis* (Fabricius) (all Cicadellidae); the planthoppers *Conomelus anceps* (Germar), *Delphacodes kuscheli* Fennah, *Dicranotropis hamata* (Boheman), *Muellerianella fairmairei* (Perris), and *Peregrinus maidis* (Ashmead) (all Delphacidae); and the mired plant bug *Orthotylus virescens* (Douglas & Scott) (Triapitsyn 1997; Virla 2001; Luft Albarracin *et al*. 2009). Of the species recovered from *D. maidis*, *A. breviphragma* was the most widespread and frequently recovered species. A similar case is that of the trichogrammatid, *Paracentrobia tapajosae*, which has been previously reported to parasitize eggs of the cicadellids, *Tapajosa rubromarginata* (Signoret), *Agalliana ensigera*, and *D. maidis* (Virla et al. 2009b; Luft Albarracin et al. in press). The third parasitoid found in both countries was the trichogrammatid *Pseudoligosita longifrangiata,* which was reported to parasitize eggs of Odonata in Brazil (Querino & Hamada 2009) and *D. maidis* in Argentina (Luft Albarracin et al., in press). The remaining egg parasitoids are mostly those species that we find in Argentina. These parasitoids use the corn leafhopper as host, but are also generalists, attacking not only cicadellids but also delphacids.

For instance, the parasitoid *Anagrus flaveolus* attacks eggs of planthoppers such as *Delphacodes kuscheli*, *D. haywardi* Muir, *Delphacodes* sp., *Peregrinus maidis*, *Pissonotus* sp., *Saccharosydne* sp., and *Toya propinqua* (Fieber) (all Delphacidae); *D. maidis, Amplicephalus simpliciusculus* Linnavuori, and *E. obscurinervis*, the last two as factitious hosts (all Cicadellidae) (De Santis et al. 1992; Triapitsyn 1997). *Anagrus miriamae* was reported as a frequent parasitoid of *Delphacodes sitarea* Remes Lenicov et Tesón (Delphacidae) but a rare egg parasitoid of *D. maidis* in Argentina (Triapitsyn & Virla 2004; Luft Albarracin et al., in press). The taxa belonging to the genus *Polynema* Haliday mostly attack cicadellid hosts (Huber 1986). *Oligosita desantisi* Viggiani is a parasitoid of *E. obscurinervis* and *D. maidis* (Virla 2000; Luft Albarracin et al., in press). *Oligosita giraulti* Crawford attacks *Aeneolamia flavilatera* (Urich), *A. lepidior* Fowler, *A. varia* (Fabricius), *Mahanarva posticata* (Stål), *Tomaspis saccharina* Distant, and *Zulia pubescens* (Fabricius) (Cercopidae), and recently was found occasionally parasitizing eggs of the corn leafhopper (De Santis 1979; Luft Albarracin et al., in press). *Zagella nanula* De Santis has also been recently found to attack *D. maidis* (Luft Albarracin et al., in press).

The Jaccard's similarity coefficient obtained for Mexican vs. Argentinian sites (0.23) demonstrates that the number of shared species between the invaded region and the native host region is low. In addition, we found that Mexican sites had lower diversity than Argentinean sites due to the dominance of a few species, as shown by the Shannon diversity index. The equitability of the distribution of individuals among egg parasitoid species was relatively lower for assemblages occurring in the native range of *D. maidis*. Thirteen species of *Dalbulus* occur in Mexico. Nault & De Long (1980) and Nault et al. (1983) proposed that *Dalbulus* leafhoppers may have had a long evolutionary history with maize and its relatives. Heady et al. (1985) showed evidence of species-specific oviposition patterns elucidated while studying 7 different *Dalbulus* species, and these behaviors reinforce an allopatric distribution in these species. We considered the possibility that niche partition in *Dalbulus* species co-existing in

Mexico could derive in the existence of parasitoid species showing high specificity degrees, consequently this could result in the low diversity and richness of egg parasitoids recorded in our study. Unfortunately, there is no information about the egg parasitoids of other *Dalbulus* species occurring in Mexico.

Cornell & Hawkins (1993) predicted that a parasitoid complex attacking an invading host should contain a higher proportion of generalists than those attacking native hosts. In the context of biological control, generalist species are important; sometimes a wide host range is a vital parameter with regard to a natural enemy's quality as a control agent (Salvo & Valladares 1997). Knowledge about the wild hosts of parasitoids may be used to improve biological control programs. Alternative hosts, be they innocuous species feeding on wild plants or other pests on different crops, can help improve the synchrony between parasitoids and their pest hosts, sometimes reducing intraspecific competition in the parasitoid population (Van Emden 1991). The results suggest that the parasitoid complex attacking the corn leafhopper in the studied areas in Argentina is constituted mainly by the generalist species. A possible explanation could be as follows: when *D. maidis* moved to South America, associated with its natural host (corn), some species of generalist egg parasitoids would have discovered and exploited this resource; since this is probably correct, then it is logical to find higher parasitoid diversity and higher richness in the expanded portion of the range of *D. maidis*. In both Mexico and Argentina sites, we found percentages of parasitism higher than 44% on the eggs of *D. maidis*, particularly at low elevations; therefore, these egg parasitoids hold promise as important biological control tools. Further research could be done in order to evaluate this assumption.

A more thorough understanding of the egg parasitoid complex of *Dalbulus maidis*, including population characteristics at different elevations as well as in the proposed host's center of origin versus the southernmost range of its distribution, will serve to improve our understanding of the tritrophic relationships between these parasitoids and the vector of one of the most important diseases of maize in Latin America.

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