Comparison of Fecundity and Body Size of Mexican and Argentinian Populations of Dalbulus maidis (Hemiptera: Cicadellidae)

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ABSTRACT The corn leafhopper, Dalbulus maidis (Delong & Wolcott) (Hemiptera: Cicadellidae), is the most important vector of maize, Zea mays L., pathogens throughout the Americas. This species originated in central Mexico, and the farthest southern latitude of the corn leafhopper’s range is in Argentina. A comparison of reproductive and phenotypic traits between Argentinian and Mexican (native) populations can aid in understanding the adaptation of Argentinian populations of the same species. In this study, we compare the fecundity and body size (wing length and head width) of central Mexican D. maidis populations from low (<1,000-m) and high (>1,000-m) elevations with Argentinian D. maidis populations from low (<1,000 m) and high (>1,000 m) elevations. Argentinian populations from high elevations show higher fecundity than Mexican high elevation populations. Furthermore, Argentinian females from high elevations are larger in body size than Argentinian females from low elevations and Mexican females from low and high elevations.

KEY WORDS Hemiptera, leafhoppers, maize, adaptation of populations

The corn leafhopper, Dalbulus maidis (Delong & Wolcott) (Hemiptera: Cicadellidae), is the most important vector of maize, Zea mays L., diseases throughout the Americas, because it efficiently transmits three plant pathogens: corn stunt spiroplasma (Spiroplasma kunkelii Whitcomb), maize bushy stunt phytodplasma, and maize rayado fino virus (Marafivirus) (Nault 1990). The corn leafhopper is widely distributed throughout the Americas. It is found from southeastern and southwestern United States to Argentina, generally below 1,000-m elevation (Triplehorn and Nault 1985). Although the corn leafhopper prefers to live at low elevations (<1,000 m), it is found in a wide range of elevations on its maize host from sea level to as high as 3,200 m in the Peruvian Andes (Nault et al. 1979). This species evolved in central Mexico (17°–21° N) when maize was first domesticated from its teosinte relative (Nault 1990), the annual teosinte Zea mays ssp. parviglumis Iltis & Doesbly >9,000 yr ago (Matsuoka et al. 2002). The farthest southern latitude of the corn leafhopper’s range is 30° S, in Argentina (Paradell et al. 2001); this country is the most distant from the D. maidis center of origin.

Comparison of traits such as fecundity and body size between populations when are reared in common conditions can enhance the understanding of the adaptation of populations of insects, such as D. maidis. In this study, we compared native corn leafhopper populations from Mexico with corn leafhopper populations from Argentina that probably arrived to South America 1,000–2,000 yr ago. Specifically, the objective of this study was to compare the fecundity and body size of native Mexican D. maidis populations from low (<1,000-m) and high (>1,000-m) elevations with Argentinian D. maidis populations from low (<1,000 m) and high (>1,000 m) elevations.

Materials and Methods

Leafhoppers Collection and Maintenance. The two native populations of D. maidis were collected from two sites in central Mexico, El Grullo (880-m elevation; 19° 50’ N) and Zapopan (1,570-m elevation; 20° 74’ N), in July 2006. They were maintained alive in a rearing room at 25–28°C. The two Argentinian populations were collected from two sites in Argentina, Los Nogales (586-m elevation; 26° 42’ S) and El Mollar (1,943-m elevation; 26° 55’ S), in December 2005. These populations also were maintained in the rearing room under the same conditions as the two Mexican populations. The D. maidis determination was based on the key to the species of Dalbulus (Triplehorn and Nault 1985). Voucher specimens representing the four populations were deposited in the Colección Entomológica at the Universidad de Guadalajara, Jalisco, Mexico. Leafhoppers from all four populations were maintained separately, to avoid inbreeding, on a laboratory maize host (variety Tabloncillo) until experiments started in July 2008. We conducted this study with D. maidis populations from low (<1,000 m) and high (>1,000 m) elevations.
high (>1,000-m) elevations because they exist in the field under different environmental conditions. Low-elevation populations from Mexico and Argentina grow throughout the year on maize, whereas populations from high elevations from Mexico and Argentina are deprived of maize during the dry season.

**Fecundity.** Reproduction experiments began in July 2008. *D. maidis* from the four populations were reared to obtain offspring of the same age. To obtain the offspring, females of the four populations were given an oviposition access period of 3 d to obtain individuals of similar age. The oviposition access period was on maize plants confined in rearing cage, maintained in a rearing room at 25 ± 2°C, 50% RH, and a photoperiod of 12:12 (L:D) h. Once the emerged adults had 2 wk, females were separated and transferred individually in a single leaf cage supplied with a four- to six-leaf–stage Tabloncillo maize plant. This was repeated 100 times per population; consequently, 100 females in total per population were used in this experiment. Single-leaf cages with females inside were held at 25 ± 2°C, 50% RH, and a photoperiod of 12:12 (L:D) h in the rearing room for an period of 5 d. At the end of the 5-d period, each female was removed. Each of the maize leaves exposed to each female was examined to determine the presence or absence of *D. maidis* eggs. If eggs were present on a maize leaf the number of eggs was determined per female. This was done with a stereoscope microscope (Stemi DV4, Zeiss, Mexico D.F., Mexico).

**Body Size.** In July 2008, *D. maidis* females from the four populations were given an oviposition access period of 3 d to produce offspring of the same age. The oviposition access period was on maize plants confined in rearing cage, maintained in a rearing room at 25 ± 2°C, 50% RH, and a photoperiod of 12:12 (L:D) h. Hatched adults were held in the rearing room on maize until they had 4 wk old. Then, females and males of the same age (4 wk old) from the four populations were collected and stored in ethanol at 70% after which their body size was determined. Wing lengths and head widths were determined in 15 females and 15 males per population with a stereoscope microscope. Head width was determined as the distance between the compound eyes, whereas wing length was determined by measuring the overall length of the right forewing.

**Data Analysis.** The data were analyzed with a two-way analysis of variance (ANOVA) (population, Mexican-Argentinian × elevation, low-high) test by using log-transformed data to compare the number of eggs per female oviposited on maize leaves in the four populations and the two elevations. Also, wing length and head width of females and males from the four populations and two elevations were compared using a two-way ANOVA test with log-transformed data. If interaction was not significant, means were separated by least significant difference post hoc comparison (McKillup 2006).

**Results**

**Fecundity.** A change in elevation does not have the same effect on number of oviposited eggs for each of the two countries and a change in population does not have the same effect on oviposited eggs at each elevation (*F* = 9.52; df = 1,117; *P* = 0.003) (Fig. 1). Females from El Grullo (Mexico) oviposited an average of 26 eggs. However, the high-elevation population from Mexico (Zapopan) oviposited few eggs, the average being 13, compared with the high-elevation population from Argentina (El Mollar).

**Body Size.** A change in elevation does not have the same effect in female wing length (*F* = 10.32; df = 1,52; *P* = 0.002) and female head width (*F* = 6.21; df = 1,56; *P* = 0.016) for the two countries and a change in population does not have the same effect in female wing length and female head width. Females from high elevations from El Mollar (Argentina) showed the largest wings (Fig. 2A) and the widest heads (Fig. 3A) compared with females from Zapopan (Mexico).

A change in elevation does not have the same effect in male wing length (*F* = 6.49; df = 1,56; *P* = 0.014) but is has the same effect in male head width (*F* = 3.10; df = 1,56; *P* = 0.083) for the two countries and a change in population does not have the same effect in male wing length but it has the same effect in male head width. Males from El Mollar (Argentina) showed the largest wings (Fig. 2B) and but not the widest heads (Fig. 3B).

**Discussion**

The corn leafhopper is a pest adapted to develop on seasonal maize planted in the wet season in high-elevations habitats, and adult leafhoppers can survive without maize for several months in this type of habitat, which is the most common in Mexico and Argentina, such as Zapopan and El Mollar sites, respectively. However, in a few regions below 1,000 m, such El Grullo site (Mexico) and Los Nogales site (Argen-
tina), maize is available for corn leafhopper adults year-round.

We found that the Argentinian population of the corn leafhoppers from high elevations had higher fecundity and larger body size than the Mexican high-elevation population. High fecundity would be advantageous for the Argentinian population from high elevations because it allows rapid demographic growth. Perhaps this is one of the reasons we find high numbers of corn leafhopper adults at high elevations in Argentina compared with a relatively low number of adults at high elevations in Mexico (G.M.-R., unpublished data).

Oliveira et al. (2004) also showed that *D. maidis* adults from high-elevation (1,628 m) sites in Brazil, have larger body sizes. Body size is related to survival of *D. maidis* adults, especially during the dry winter season. Larger females survive longer than smaller females because larger body size indicates greater storage of energy for survival in *Dalbulus* leafhoppers (Larsen and Nault 1994). At the high elevation of the El Mollar site (Argentina), the lowest temperatures, in the dry winter season, can reach −10°C. In addition, high-elevation corn leafhoppers are deprived of their maize food host for several months each winter. It is likely that *D. maidis* adults have become adapted to survive adverse environmental conditions during the winter, because Virla et al. (2003) reported the collection of *D. maidis* adults during winter at high elevations in Argentina at two sites: Santa Maria (1,957 m) and Amplimpa (2,100 m). Furthermore, Summers et al. (2004) mentioned the finding of this leafhopper during winter and stated that it can survive for long periods in the absence of maize.

Large body size and high fecundity are associated with migration as well. Large females generally produce more eggs and are at an advantage because they can store more reserves and are therefore better equipped to perform migrations. Several studies have found a positive relationship between body size and fecundity in insects, particularly in Hemiptera (Honek 1993). Also, Denno and McCloud (1985) found a significant positive relationship between body size and average daily fecundity. They suggested that habitat-related variation in body size-mediated fecundity in part forms the adaptive basis for migration of the planthopper *Prokelisia marginata* Van Duzee. Also, Rossi and Strong (1991) suggest that for the leafhopper *Carneocephala floridana* Ball, a large body is advantageous because larger adult females have higher oviposition rates than smaller females.

Populations of *D. maidis* that invaded Argentina and occupy high-elevation maize habitats show pheno-
typic adaptations in terms of fecundity and body size traits. Adaptation was expected for populations in the high-elevation habitats where *D. maidis* has had to survive locally or migrate or both, because of the low temperature and deprivation of maize host plants during the winter season. It is likely that phenotypic plasticity contributed to the adaptation of the Argentinian corn leafhopper population to high-elevations maize environments. Phenotypic plasticity, the ability of an organism to express different phenotypes depending on its biotic and abiotic environment (Agrawal 2001), is higher in invasive populations because they encounter different environments during invasion (Lombaert et al. 2008).

The corn leafhopper is specialist on teosintes and maize (Nault 1990). Maize was domesticated from an annual teosinte ~9,000 yr BP in central Mexico (Matuoka et al. 2002); later, maize was used in Central America (7,800–7,000 yr ago) (Dickau et al. 2007); and finally, isotopic and macrobotanical data show that maize arrived 2,000 yr ago to lowlands and 1,000 yr ago to highlands of central western Argentina (Gil et al. 2006). Maize has been dispersed via diffusion or exchange rather than movement of human populations practicing agriculture (Dickau et al. 2007). We hypothesize that maize could be colonized by *D. maidis* adults through this process of maize dispersal, because leafhopper adults are able to migrate and survive for several months without maize. A possible consequence of this long association between maize and *D. maidis* is that the corn leafhopper is broadly distributed throughout Americas. Another interesting result is that the southern extent of both pre-Hispanic maize agriculture and the range of *D. maidis* are the same, because both are localized between 30 and 33°S (Gil et al. 2006, Paradell et al. 2001). Further research is needed to test competing hypotheses concerning the time and means of introduction of *D. maidis* to South America.

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