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Estimation of direct damage to maize seedlings by the corn leafhopper, *Dalbulus maidis* (Hemiptera: Cicadellidae), under different watering regimes

Research Paper

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Abstract

The corn leafhopper *Dalbulus maidis* (Hemiptera: Cicadellidae), a specialist herbivore, is the cause of serious losses in maize yield for its capacity to transmit three important plant pathogens. They are also active phloem feeders, that insert stylets into the plant as they feed. Females place their eggs endophytically, totally inserted in the central midrib or the leaf blades, leaving conspicuous openings in the place where the ovipositor was inserted. In spite of the consequences that feeding and oviposition may have on the water status of the plant and the production of biomass, direct damage caused by the leafhopper has been only scarcely studied. In the present contribution, we measured biomass loss due to direct damage in maize plants under two watering regimes, with water supply *ad libitum* and with a watering restricted regime, emulating the most frequent field conditions. Moreover, we analyzed the effects of increasing densities of the vector on the biomass loss and plant mortality and the effects of females vs males. We observed that a density of 10 insects is sufficient to cause damage to 10-day-old seedlings, even in an *ad libitum* watering regime; however, in drought conditions, damage can be significantly greater, causing plant mortality. Also, females cause more damage than males, due to their oviposition habits.

Introduction

The hemipteran infraorders Cicadomorpha and Fulgoromorpha (*Auchenorrhyncha*) are sap-sucking insects, injuring plants either directly through feeding and oviposition (Nault and Ammar, 1989; Backus *et al*., 2005; Perez Grosso *et al*., 2016) or indirectly through transmission of plant pathogens (Maramorosch and Harris, 1979; Nault, 1997; Weintraub and Beanland, 2006). In several species, these characteristics are aggravated by a high reproductive potential, short life cycle, great adaptability and high rates of dispersion.

Most of the studies on the characterization of direct damage by *Auchenorrhyncha* have been performed on species involved in the induction of hopperburn symptoms, and have dealt with feeding, quantification of probing behavior using the direct current electrical penetration graph (DC-EPG) system, cellular alterations in the feeding site, and occlusion phenomena (i.e. Ogunlana and Pedigo, 1974; Backus *et al*., 2005; Carpane *et al*., 2011; Saeed *et al*., 2018).

Hopperburn is induced by several hopper species (mostly Typhlocybinae in the Cicadellidae) by a dynamic interaction between insect feeding stimuli and complex plant responses; it causes millions of dollars' worth of yield loss and control costs (Backus *et al*., 2005). On the other hand, few studies have quantified direct damages, such as the reduction of biomass, yield, or hydric stress, and most of them were focused on Delphacidae (Noda, 1986; Wilson and Claridge, 1991; Sarao and Bentur, 2018; Goode *et al*., 2019), and a few devoted to Cicadellidae (Cuperus *et al*., 1983; Jones *et al*., 2000; Atakan, 2009; Ersin *et al*., 2017).

In tropical and subtropical America, the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) causes enormous damage to maize (*Zea mays* L.) because it efficiently transmits three important plant pathogens: corn stunt spiroplasma (CSS), maize bushy stunt phytoplasma (MBSP) and maize rayado fino virus (MRFV) (Oliveira *et al*., 1998; Virla *et al*., 2010). In these regions, CSS is one of the most dominant pathogens affecting maize. The highest infection rates have been found in Central America, Peru, Brazil and Argentina, with 100% of the crop plants affected in many maize fields (Virla *et al*., 2004). The importance of CSS and MBSP alternate depending on the cultivated germplasms of maize and/or climatic factors (Oliveira *et al*., 2002). Sabato *et al*. (2020) demonstrated that in Brazil, MBSP is more tolerant than CSS at lower temperatures and is able to express symptoms in a larger number of plants than CSS under these conditions.

Few studies have been conducted on the direct damage caused by *D. maidis* to maize plants. As with other cicadellids, *D. maidis* cause direct damage by feeding and oviposition. As they feed, they insert stylets into the plant, lacerating the mesophyll and parenchyma cells. They are active phloem feeders preferring small and intermediate vascular bundles rather than central veins, but sometimes they probe xylem and parenchymatic tissues (Alivizatos, 1982). *D. maidis* secretes large volumes of honeydew that accumulates and supports the growth of sooty mold fungi (Bushing and Burton, 1974). Females oviposit endophytically inside the plant tissues (Heady and Nault, 1984), cutting the leaf cuticle with the ovipositor valvulae, which contains numerous teeth. The eggs are deposited individually in the central midrib or leaf blades, and a conspicuous opening is left where the ovipositor was inserted (Heady and Nault, 1984; Luft Albarracin *et al.*, 2021).

In USA (California), Bushing and Burton (1974) reported that *D. maidis* causes more damage on late-planted silage maize by extensive feeding on the foliage rather than by transmitting CSS. Waquil (1997) reported that 10-day-old maize plants exposed to a density of 10 adults/plant reduced their canopy by 40% and their root system dry weight by 62%. However, he made no mention of the watering regime used in the assays, nor discriminated between the damage caused by females or males. Drought stress is one of the most adverse factors of plant growth and productivity (Anjum *et al.*, 2011). Due to the importance of this leafhopper in America and considering the very scarce information on the direct damages that it causes to maize crops, we postulate the following hypotheses: (1) herbivory damage would cause drought stress, and the effects would be more notorious on a watering restricted regime, (2) a density of 10 insects per seedling would cause biomass loss, even in an *ad libitum* watering regime, and (3) Due to their ovipositing habits, females would be more injurious than males. Therefore, the aims of our study are to evaluate the effects of *D. maidis* on maize seedlings' biomass under different watering regimens and to determine differences in the levels of damage caused by females and males.

Materials and methods

Insect rearing

Dalbulus maidis colony used in this study was established from individuals collected at Los Nogales, Tucumán, Argentina (S 26°42′, W65°13′, 588 m a.s.l.). The leafhoppers were fed using potted maize plants (landrace sweet white maize 'maizón') within cages built with PVC pipes (50 × 50 × 50 cm) and protected with voile fabric to facilitate catch, prevent escape and avoid accidental parasitism (Coll Araoz *et al.*, 2019). The colony has been maintained in the Biological Control Division (PROIMI-CONICET) laboratory, located in San Miguel de Tucumán, Tucumán, Argentina (S26°48′36″, W65°14′27″, 465 m a.s.l) for several years and new individuals are collected from the field twice a year, during summer, to avoid inbreeding. Only pathogen-free colonies were used in the experiments. Individuals used in all experiments were obtained from established colonies, belonging to the third generation in laboratory rearing, with no symptoms of corn stunt disease in the plants used for rearing; moreover, random PCR analysis for the detection of *S. kunkelii* presence in the leafhoppers were carried out twice a year.

Soil and maize seedlings

The maize plants (landrace sweet white maize) were kept in expanded polystyrene pots, of 250 cm^3 capacity filled with 95 g of dry soil, and were grown from seeds that weighed 0.5 g. The used soil was a typical fine Argiudoll (Pereyra and Fernández, 2018) taken from a surface layer (0–20 cm) of an agricultural land. The initial test of the soil properties indicated: organic matter (2.71%), pH (5.93), total nitrogen (0.160%), nitrates NO_3 (32.3 $kgN\ ha^{-1}$), phosphorous (7.7 ppm) and potassium (1.17 me 100 g^{-1}).

Plants were irrigated with 5 ml of water on the day of planting and with the same volume every two days until the beginning of the assays. All trials were carried out using maize seedlings whose first leaf had the same length as the second leaf in development (from 8 to 9 cm in height, and 10–12 days after emergence). Two experiments were carried out, the first one to verify the effect of insect density on the biomass of maize seedlings, and the second one to assess the levels of damage caused by females and males. Both were done under two different levels of watering: (a) *ad libitum* watering, where the plants were supplied with 5 ml of water daily, and (b) with restricted watering, where the plants received 5 ml of water only on days 0, 5, and 10 after the leafhoppers were introduced. In both levels of watering, the initial soil moisture was ~33%, which was the field capacity of the soil. In the assay with daily watering, soil moisture was maintained between 32 and 33% along the duration of the experiment. In the assay with watering every five days, soil moisture decreased between 17.5 and 18.5% before watering on the fifth day, when a 21–23% humidity was restored after the addition of 5 ml of water. The amount of water provided to the plants was calculated on the basis that the monthly average rainfall does not exceed 100 mm at the time of sowing in the northern subtropical plains of Argentina. Trials were conducted during the summer of 2019.

Influence of insect density

Tests were carried out by exposing four maize seedlings to different vector densities. The tests were performed in glass cages, 20 × 20 × 35 cm, with two lateral windows covered by voile fabric (Fig. 1S). There were four treatments: control (without leafhoppers), low density (10 leafhoppers/plant), medium density (30 leafhoppers/plant) and high density (50 leafhoppers/plant). Five replicates were done for the *ad libitum* watering regimen and four replicates for the restricted watering regimen. Only adults were used, in a proportion of 1:3 males:females. All plants were exposed to leafhoppers for 7 days, after which the leafhoppers were removed. Plants were left isolated for a week after the removal of the leafhoppers. Afterwards, they were carefully removed from the soil under water flow to avoid loss of root material. The aerial parts were separated from the roots with a razor blade and the fresh weights (FW) of the aerial parts were recorded. Then, the aerial parts and roots from each plant were labeled, bagged in paper and dehydrated in an oven at 45°C during 7 days until constant weight. Dry weight (DW) was then recorded.

Influence of leafhopper gender

Individual plants were covered by a plastic cylindrical cage (6.5 cm diam × 26 cm height) with a piece of voile fabric on the top (Fig. 2S) and then exposed to the different treatments.

Figure 1. General appearance of the corn plants exposed for 7 days at different densities of *Dalbulus maidis* and under a regime of watering restriction, one week after taking out the vectors. (a) control, (b) 10 adults/plant, (c) 30 adults/plant, and (d) 50 adults/plant. The assays were carried out in the laboratory, under controlled conditions (25 ± 2°C, 75 ± 10% RH, and 14L:10D light) during the summer of 2019.

There were six treatments; (1) control: with restricted watering and without leafhoppers ($N = 30$); (2) with restricted watering and 10 females/plant ($N = 37$); (3) with restricted watering and 10 males/plant ($N = 33$); (4) with *ad libitum* watering but without leafhoppers ($N = 65$); (5) with *ad libitum* watering and 10 females/plant ($N = 72$); and (6) with *ad libitum* watering and 10 males/plant ($N = 68$).

The leafhoppers used for both experiments were randomly captured from breeding colonies. After release into the cages, insects were counted daily and dead individuals were replaced immediately by specimens of the same sex. Trials were performed in climate-controlled chambers (25 ± 2°C, 75 ± 10% RH, and 14L:10D light). All plants were exposed to leafhoppers for 7 days, after which insects were removed. Plants were left isolated for a week after the removal of the leafhoppers and afterward, they were removed from the soil as described above. The FW of the root and the aerial parts (hereafter canopy) of each plant was immediately recorded, and plants were then dehydrated as described above and the DW was recorded. The water content in each plant was calculated from the difference between the FW and DW.

Experimental design and statistical analysis

For the 'Influence of insect density' assay, we designed an experiment with two factors: the first factor, 'insect density', had four levels (0, 10, 30, and 50 leafhoppers/plant) while the second factor, 'watering amount', had two levels (*ad libitum* watering and restricted watering). Due to the restrictions in the aleatorization procedure, a mixed model was used for DW data analysis: aleatory effects were used for the factor 'replicate/cage' and fixed effects for the density of insects in each cage and the watering regimen. We fitted a quadratic model to our data and calculated the determination coefficient (R^2) between the vector density and DW of the canopy or root as previously described by Waquil (1997).

In the 'Influence of vector gender' assay, raw data means were compared with one-way ANOVA ($P < 0.05$). The means of canopy FW of plants under the restricted watering regimen were compared with ANOVA after normalization to log-normal distributions. Homogeneity of variance and normality were checked using Bartlett's and Shapiro–Wilk tests, respectively. If ANOVA assumptions were not met, the Kruskal–Wallis test was performed using XLSTAT® 19.6.

Voucher specimens of *D. maidis* were deposited in the Instituto de Entomología, Fundación Miguel Lillo (San Miguel de Tucumán, Tucumán, Argentina) (IMLA).

Results

During the experiments, we never observed hopperburn symptoms in plants exposed to the corn leafhopper. The symptoms observed in the most affected plants corresponded to those typical described for significant water stress (fig. 1).

Influence of insect density

No mortality occurred in the plants that received *ad libitum* watering and had 0 or 10 leafhoppers/plant, but plant mortality was observed in the rest of the treatments. At the highest leafhopper density (50 individuals/plant), a high mortality of plants was observed after 7 days of exposure to the leafhoppers: 40% and 56.2% for those watered *ad libitum* and with restricted watering, respectively (Table 1).

Biomass loss was less severe in an *ad libitum* watering regime and this was corroborated for every leafhopper density analyzed. In both watering regimes, there was a corresponding reduction in FW and DW of the canopy and DW of the roots (Table 1).

Both the watering regimen and the insect density influenced the DW of maize plants (fixed effects: $F = 8.155$, df 1_{33}, $P = 0.007$, $F = 30.679$, df 1_{33}, $P < 0.0001$, respectively). With a density of 10 insects, there was a greater effect of leafhopper density on

Table 1. Effect of different density of *Dalbulus maidis* on maize biomass under different watering regimens: percentage of seedlings mortality and percentage of biomass loss of the exposed plants relative to the control plants.

Watering regime	Insect density (number of plants)	% seedlings mortality	% canopy loss FW (±SE)	% canopy loss DW (±SE)	% roots loss DW (±SE)
Ad libitum	10 (20)	0	38.83 (±12.26)	24.91 (±6.62)	25.83 (±5.93)
	30 (20)	10.0	64.50 (±7.67)	38.01 (±4.48)	36.22 (±6.54)
	50 (20)	40.0	75.61 (±7.87)	45.96 (±5.74)	40.63 (±3.03)
Watering restriction	10 (16)	12.5	64.62 (±9.06)	55.66 (±16.49)	18.35 (±15.43)
	30 (16)	25.0	80.67 (±2.75)	61.44 (±11.54)	20.13 (±14.79)
	50 (16)	56.2	86.24 (±5.86)	68.58 (±9.72)	34.55 (±14.47)

FW, fresh weight; DW, dry weight.
The assays were carried out in the laboratory, under controlled conditions (25 ± 2°C, 75 ± 10% RH, and 14L:10D light) during the summer of 2019.

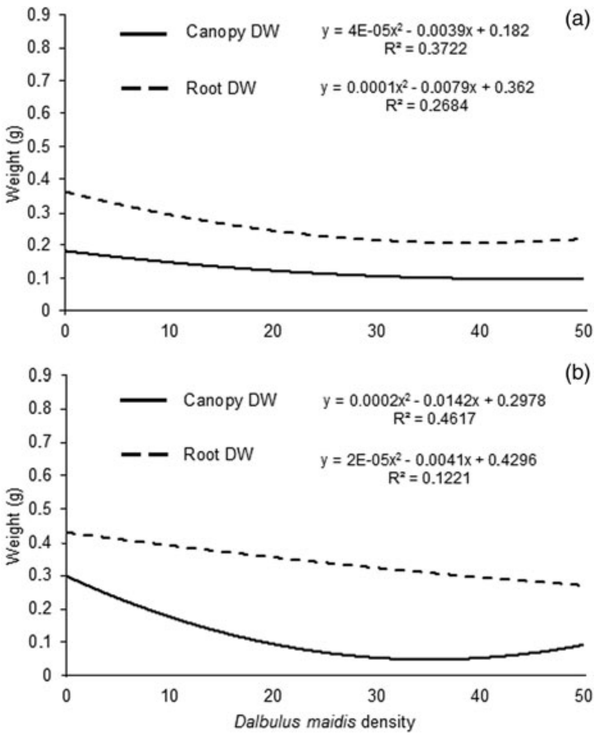

Figure 2. Relationship between the dry weight (DW) of maize seedlings (canopy and roots) exposed to different densities of *Dalbulus maidis*. Adjustments curves of the quadratic relation and the corresponding coefficient of determination (R^2) are given. (a) *ad libitum* watering regime, (b) restricted watering regime. The assays were carried out under controlled laboratory conditions (25 ± 2°C, 75 ± 10% RH, and 14L:10D light) in the summer of 2019.

DW ($F = 20.309$, df 1_{15}, $P = 0.0004$) than the watering regimen ($F = 3.186$, df 1_{15}, $P = 0.094$).

When adjusting the data to a quadratic relationship between the vector density and the canopy DW and roots DW, we only found a relatively acceptable relationship for the canopy DW of the treatment with restricted watering (R^2: 0.46) (fig. 2). In the remaining treatments, the adjustments were poor, with determination coefficients below 0.40.

Influence of vector gender

Under the *ad libitum* watering regimen, plants exposed to 10 leafhoppers of different gender did not show noticeable differences in their canopy FW ($F = 2.29$, df = 2_{102}, $P = 0.097$), although the plants exposed to females were lighter (fig. 3a). In contrast, under the restrictive watering regime, the canopy FW of plants exposed to vector females was significantly lighter than that of the control plants ($F = 3.21$, df = 2_{97}, $P = 0.045$) (fig. 3b).

When the DW was considered, there was a significant reduction in the canopy DW of the exposed plants independent of leafhopper gender with a density of 10 females or males in both watering regimes, *ad libitum* ($K = 22.99$, $P < 0.001$) and restricted ($K = 18.22$, $P < 0.001$) (fig. 3c, d). Females had a greater effect on canopy DW, particularly in a water-restricted regime; relative to control plants, those exposed to females had a 53.84% (±SE, 4.43) reduction in canopy DW compared to a 33.59% (±5.92) reduction caused by males. This effect was also noticeable in *ad libitum* watering conditions: a 46.63% (±3.65) reduction in canopy DW in plants exposed to females vs a 28.97% (±8.64) in plants exposed to males. However, although noticeable and biologically relevant, using a significance level of $P < 0.05$ there were no statistical differences between the canopy reduction in plants exposed to females and males.

The effect of biomass loss was less evident in the roots. There was a significant root biomass loss in plants exposed to the females in the *ad libitum* watering regimen ($F = 10.96$, df = 2_{102}, $P < 0.001$) (fig. 3e). Interestingly, there was not a significant reduction in root biomass in watering restricted plants, independently of the vector gender ($F = 0.36$, df = 2_{97}, $P = 0.697$) (fig. 3f). No plant mortality was recorded during the course of this experiment.

There were no significant differences in the water content of the plants (FW-DW) under the *ad libitum* watering regimen ($K = 3.24$, $P = 0.198$) (2.52 g ± 0.15 for the control plants, 2.10 ± 0.17 for those with females, 2.14 ± 0.17 for those with males). However, under a restricted watering regimen, plants subjected to females had significantly less water content (0.80 g ± 0.10) than the control plants (1.17 ± 0.15) and those exposed to the males (1.13 ± 0.12) ($K = 7.43$, $P = 0.024$).

Discussion

The results of our study showed that, in the early stages of plant development, a density of 10 adult leafhoppers per plant can significantly damage the crop, even when water is freely available. If small plants are subjected to water stress, then attack by *D. maidis* can also lead to significant plant mortality, reducing crop stand. Direct damages are not only associated with the extraction of

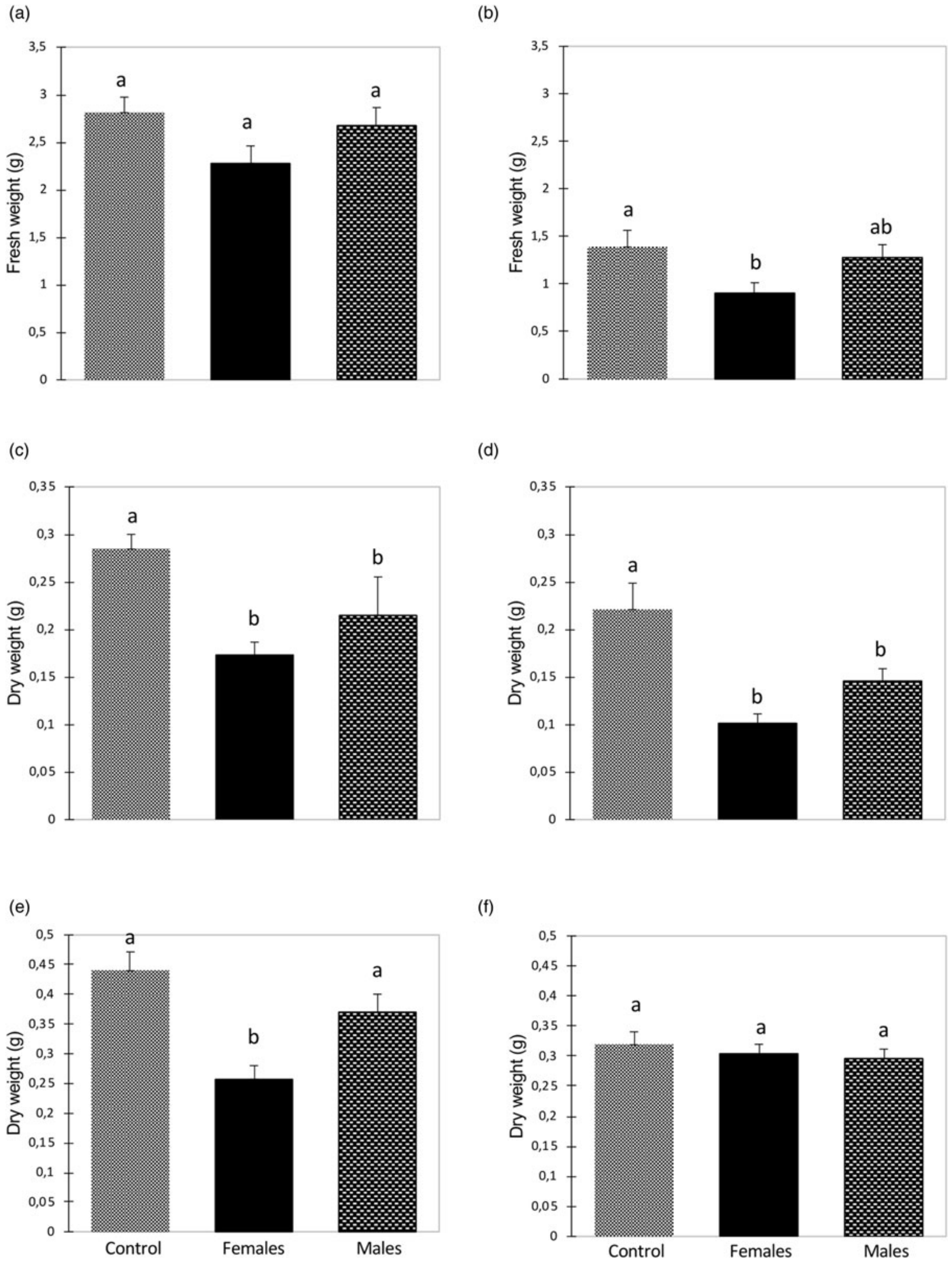

Figure 3. Biomass of control maize plants (without insects) and plants exposed to either 10 females or 10 males *Dalbulus maidis*, under two watering regimens. (A) water *ad libitum* fresh weight of aerial parts. (b) water restriction fresh weight of aerial parts. (c) water *ad libitum* dry weight of aerial parts. (d) water-restriction dry weight of aerial parts. (e) water *ad libitum* dry weight of roots. (f) water restriction dry weight of roots. Different letters indicate significant differences ($P < 0.05$) among gender. The assays were carried out under controlled laboratory conditions (25 ± 2°C, 75 ± 10% RH, and 14L:10D light) in the summer of 2019.

sap, but also with water loss in the tissues due to the injuries caused by females during oviposition. Our results showed that good water availability allowed the plants to better withstand the attack of the leafhopper.

Bushing and Burton (1974) and Waquil (1997) are the only two previous works that refer to the direct damage caused to maize by *D. maidis*. They stated that the corn leafhopper is capable of causing serious yield losses. But they made no mention that feeding by this leafhopper did not produce hopperburn, and that plants may die from their attack. Bushing and Burton (1974) affirmed that feeding damage was more important than damage by transmitted diseases, and that the quality of silage maize was affected by sooty mold resulting from the large volumes of honeydew secreted by the leafhopper. Waquil (1997), working with maize seedlings, showed that one-, five-, and 10 adults/plant confined on 15-day-old plants for one week caused little feeding damage; however, significant damage was seen on 10-day-old plants. Neither study indicated that plant mortality occurred, nor did they examine the relationship between leafhopper damage and the level of irrigation. We showed that seedlings grown under a restricted watering regimen, which emulated the field conditions in the north of Argentina, and exposed to 10–50 leafhoppers, exhibited mortality rates ranging from 12 to 56%. On the other hand, plants irrigated daily showed mortality only when they were exposed to very high leafhopper densities (30 and 50 adults/plant), with a range of 10–40%, respectively. The highest densities used in the assays (30 and 50 individuals/plant) are unlikely to occur in the field 10–15 days after the emergence of the plant; but in late plantings it is possible to observe up to 10 adults/plant in that phenological stage (Waquil, 1997; Virla & Luft Albarracin, personal observation).

Good water availability allowed maize plants to better withstand leafhopper attack. In our trials, we observed that plants exposed to the leafhoppers and subjected to restricted watering showed evident symptoms of drought stress. Drought stress in maize plants affects several morphological and physiological characteristics, including senescence, reduction of foliar area, chlorophyll content, root elongation, stomatal closure, membrane integrity, osmotic adjustment of water relations, and photosynthetic activity (Moussa and Abdel-Aziz, 2008; Anjum *et al.*, 2011; Curá *et al.*, 2017). In nature, drought stress impacts the growth and yield of corn crops; the severity of the symptoms depends on different factors such as genotype, developmental stage, and duration of the stress (Anjum *et al.*, 2011). We observed that, depending on the situation, not all of the plants subjected to leafhopper attack could overcome the stresses due to drought and water deficiencies.

When we compared the effect of the watering regime with the effect of herbivory, analyzing only the data of the control plants and those exposed to 10 insects per plant, herbivory affected DW more than water restriction. Insect density had a very marked effect on the percentage of biomass loss, both of the canopy and the roots. At the lowest vector density (10 adults/plant), the DW loss of the seedlings' canopy reached 25% under an *ad libitum* watering regimen and 56% under a restricted watering regimen. Waquil (1997) found that 10 leafhoppers/plant reduced 40% of the canopy DW and 62% of the root DW but did not indicate the level of irrigation provided. Notably, our findings differ in the measured root DW because we observed a much lower biomass loss than that found by Waquil (1997); in an *ad libitum* watering regime roots dry weight was reduced by only 26% (36.2% lower than that reported by Waquil) and, surprisingly, only 18% in the watering restricted regimen (43.6% less than reported by Waquil). In addition, Waquil (1997) found a quadratic relationship between corn leafhopper infestation density with canopy and root DW of 10-day-old plants (R^2: 0.44 for canopy DW, and R^2: 0.55 for root DW). We only found a relatively acceptable quadratic relationship between insect density and the canopy DW weight when seedlings were maintained under a restricted watering regime (R^2: 0.46).

In general, the water stress of the plants was much more evident when they were exposed to females. The water content of the canopy in plants exposed to leafhoppers was less than control plants, and this difference was substantially greater in the treatment with restricted water supply. The canopy FW and DW, and root DW of attacked plants were generally lower in those exposed to females compared to those exposed to males. But the greatest differences were observed when the plants were poorly watered. The main reason for this is because plants exposed to males suffered damage only due to feeding (punctures plus sap extraction) while plants exposed to females, were damaged not only by feeding, but also by the oviposition, as they lay eggs endophytically. The plants thus showed abundant open wounds that allowed a constant and uncontrollable loss of water from its tissues. Our findings contrast with the observations made by Alyokhin *et al.* (2001) and Avanesyan *et al.* (2019), who studied the damage to different plants caused by *Sophonia orientalis* (Matsumura), the two-spotted leafhopper. They stated that oviposition damage in leaf mid-veins resulted in the death of distal tissue, but it is unlikely that oviposition alone can cause significant damage to affected plants and the major problem was caused by feeding.

In our study, there was no significant reduction in the root biomass (as DW) of plants exposed to leafhoppers under a restricted watering regimen, regardless of the leafhopper gender. As was mentioned, the effect of the attack of *D. maidis* was barely noticed in roots dry weight in water-restricted plants in both experiments. This fact could be explained by the mode of action of the phytohormone abscisic acid (ABA). As a physiological response to water deficit, plants close their stomata, a process that is regulated by ABA, which is synthesized mainly in the leaves (Mittelheuser and Van Steveninck, 1969; Geiger *et al.*, 2011). One of the most noticeable effects of ABA is the inhibition of growth in most plant tissues, but in contrast to the inhibitory effect on shoot growth, increased levels of ABA in plants experiencing stressful conditions promote root growth (McAdam *et al.*, 2016). These differential changes in growth by ABA are thought to be an adaptive response to water stress, increasing the allocation of biomass to roots and thereby the effectiveness of root water uptake (Creelman *et al.*, 1990).

In summary, our results indicate that *D. maidis* causes substantial biomass loss in maize seedlings, even in the absence of disease. The levels of damage are significantly influenced by the amount of water available for the plant, and in drought conditions damage can be significantly greater, causing plant mortality. Also, due to oviposition activities, females are more injurious than males and can cause more damage.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485321000079.

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