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# Olfactory Response and Host Plant Feeding of the Central American Locust *Schistocerca piceifrons piceifrons* Walker to Common Plants in a Gregarious Zone

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**Abstract**
The Central American locust (CAL) *Schistocerca piceifrons piceifrons* Walker is one of the most harmful plant pests in the Yucatan Peninsula, where an important gregarious zone is located. The olfactory response and host plant acceptance by the CAL have not been studied in detail thus far. In this work, the olfactory response of the CAL to odor of various plant species was evaluated using an olfactometer test system. In addition, the host plant acceptance was assessed by the consumption of leaf area. Results showed that the CAL was highly attracted to odor of *Pisonia aculeata.* Evaluation of host plant acceptance showed that the CAL fed on *Leucaena glauca* and *Waltheria americana*, but not on *P. aculeata* or *Guazuma ulmifolia*. Analysis of leaf thickness, and leaf content of nitrogen (N) and carbon (C) showed that the CAL was attracted to plant species with low leaf C content.

## Introduction

The Central American locust *Schistocerca piceifrons* Walker (Orthoptera: Acrididae) is a harmful phytophagous species that induces significant damages to cropped species in Central America (Harvey 1983, Barrientos *et al* 1992, Hernández *et al* 2013). The Central American locust has two subspecies: *Schistocerca piceifrons piceifrons* found from Mexico to North Costa Rica and *Schistocerca piceifrons peruviana* which inhabits Perú, Ecuador, Colombia, Venezuela, Panamá, and Trinidad and Tobago (Barrientos *et al* 1992). The Yucatan Peninsula in Mexico has an important gregarious zone for *Schistocerca piceifrons piceifrons* (Central American locust (CAL)), where formation of swarms and damage to various crops are frequent; in particular, losses of corn crops have large impact on local communities as this grain is one of the main sources of food (Contreras & Magaña 2013). In other areas of Mexico and Central America, the CAL has also caused significant losses in sorghum, wheat, beans, peas, palms, bananas, sugarcane, and castor oil plants (Harvey 1983, Barrientos *et al* 1992).

The breeding areas, known as gregarious zones, where CAL is permanently found, the environment, and vegetation play a key role on sustaining feeding of nymphs, formation of swarms, and outbreaks of adults (Harvey 1983). The vegetation in the gregarious zone in the Yucatan Peninsula is composed of weedy pasture, small mixed cultivations, and secondary regrowth of mixed plants, where *Waltheria americana*, *Cassia biflora*, *Guazuma ulmifolia*, and various species of grasses are abundant (Barrientos *et al* 1992).

Food selection by acridids generally involves two processes: attraction from a distance and food acceptance (feeding). In attraction, the olfactory and visual stimuli play a significant role, while in food acceptance, the olfactory receptors and tarsal/palp contact are critical. In addition, food selection is highly influenced by both physical and chemical properties of plant leaves (Chapman 1990). Food preference in the CAL is also dependent on its developmental status, for example, CALs in solitarious phase feed only on limited number of plant species, while in the gregarious phase, they are less selective for food (Latchininsky 2010).

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In locusts, behavioral phase change to gregarization is mediated primarily by direct tactile contact of hind femur among individuals (Hägele & Simpson 2000, Simpson *et al* 2001). Endocrine changes have been also implicated in gregarization, particularly the role of the biogenic amine, serotonin, has been well documented (Anstey *et al* 2009). In addition, there is also evidence that food distribution and nutritional quality can also influence phase change. When the distribution of the vegetation is patchy, locusts are more active, experience higher levels of crowding, and become more gregarious (Despland *et al* 2000). Change in the threshold of gregarization occurs according to the cover, and status of the vegetation, low cover, and dry vegetation lead to a low-density threshold of gregarization, probably due to high probability of individuals to touch each other (Cisse *et al* 2013). Regarding food quality, a detailed study using synthetic food treatments with near-optimal, dilute, and unbalance diets found that gregarization was most pronounced in the dilute diet treatment, owing to increased activity (Despland & Simpson 2000).

To contribute to the knowledge on attraction/feeding behavior of the CAL, the present work was carried out to evaluate the olfactory response and the host plant acceptance using common plants found in the gregarious zone of the Yucatan peninsula.

## Material and Methods

### *Insects*

Young adults (60–75 days old) of the CAL in *transciens congregans* phase that occurred in small patches (12–30 locusts/100 $m^2$) were collected by entomological nets in ranches of the municipalities of Tizimín, Buctzotz, and Cenotillo in the state of Yucatán. Insects were collected in September, when the first generation of the cycle occurs (Hernandez *et al* 2013). Adults were maintained in cages (50 × 50 × 50 cm) made of wood frame and metallic mesh walls. Cages were kept in a conditioned room with a photoperiod of 12L:12D and temperature of 32 ± 2°C at day and 27 ± 2°C at night. Insects were fed ad libitum with fresh leaves of elephant grass *Pennisetum purpureum* and maize *Zea mays*.

### *Selection of plant species*

Plant species commonly found in the gregarious zone of the Yucatan Peninsula (Arellano *et al* 2003) were selected for evaluation, which included *Citrus sinensis* (Rutaceae), *Manihot esculenta* (Euphorbiaceae), *G. ulmifolia* (Sterculaceae), *Viguifera dentata* (Compositae), *Pisonia aculeata* (Nyctaginaceae), *W. americana* (Sterculaceae), *Cassia wilsonii* (Fabaceae), *Leucaena glauca* (Fabaceae), *Piscidia communis* (Fabaceae), *Sabal yapa* (Arecaceae), *Sida acuta* (Malvacea), and *Azadirachta indica* (Meliaceae).

### *Olfactory response bioassay*

Olfactory response of the CAL to each plant species was evaluated in a dynamic combined Y and T glass olfactometer as described for behavioral responses by Seidelmann *et al* (2000). Briefly, warm air current was purified by activated charcoal filter and humidified with water. Air current was split into two streams and drawn through two arms of the Y-shaped test funnel (4-cm diameter) at 2 L/min/arm. Air current flow passed through a small tube that contained the odor sources. For the right arm was 2 g of triturated fresh leaves and for the left arm was clean air (odor-free air). Both arms were connected to the main funnel that contained in the central part a T-shape inlet through which the CALs were individually introduced. Once the individual had been introduced into the main funnel, it was allowed to habituate for 20 s and the following reactions were recorded: no choice (the CAL remained in the main funnel), avoiding the triturated plant odor (the CAL moved downstream to the exit), full attraction (the CAL moved upstream with the final choice to move directly to the triturated plant odor), or no attraction (the CAL moved upstream with the final choice to move to the clean air). Each individual was observed for a maximum of 3 min to record the reaction (Seidelmann *et al* 2000, 2005). The percentage of individuals that did not make a choice was low (<5%), and these individuals were not included in the analysis. The device was dismantled and washed every five to six replicates (insects), and fresh triturated leaf sample was placed. Likewise, the device was rotated through 180° on the horizontal axis to control for any effect of side bias.

All insects used for this assay were 60–75-day-old females starved for 18 h prior to the test. The experiments were carried out from 9:00 to 12:00 h; the room temperature was 29 ± 2°C and 70–80% relative humidity. For the evaluation, 1-day assessment only included plants from the same species. We evaluated five to six CAL groups for each treatment (plant species). Each CAL group consisted of 18–30 insects/plant/day. For the analysis, data from all groups were combined. The total numbers of replicates (insects) evaluated were for *Pisonia aculeata*, 100; *L. glauca*, 141; *G. ulmifolia*, 156; *W. americana*, 100; *Sabal yapa*, 105; *A. indica*, 100; *Citrus sinensis*, 118; *P. communis*, 100; *Cassia wilsonii*, 94; *M. esculenta*, 121; and *V. dentata*, 100.

### *Feeding bioassay*

For host plant acceptance, no choice feeding bioassay was carried out with the plant species that significantly attracted

the CAL from the olfactometer test. Plants were prepared as described by Begna & Fielding (2003) with some modifications. Briefly, plants were established into plastic growing pots (0.2 m diameter × 0.4 m depth) that contained regular soil. Each pot received 2.5 g of the fertilizer Triple 17 (17-17-17 nitrogen-phosphorus-potassium; Nutrigarden, Qro, Mexico). Plants were watered two to three times a week. Plants were obtained from a variety of sources: For *L. glauca* and *G. ulmifolia*, seeds were sown directly in the pots; for *Pisonia aculeata*, woody cuttings collected in the field were rooted and maintained in the pots for 50 days; and for *W. americana*, cuttings collected in the field were set in the pots 5 days prior to use. For the latter two species, sexual reproduction was difficult, but vegetative propagation was successful. For the feeding bioassay, plant leaves were harvested and immediately offered to the CAL. Leaf consumption was recorded in a per cage basis.

To know the density of CAL per cage that consumed a significant amount of food for the feeding experiments, a preliminary bioassay was carried out using *Z. mays*, a common host plant for the CAL in the Yucatan Peninsula (Barrientos *et al* 1992). For such purposes, maize leaves were placed in cages and groups of two, four, or six individuals were introduced. Percentage of leaf area consumed for 24 h by the groups of CAL was calculated as the difference in leaf area ($cm^2$) of food in the cages with the CAL (experimental group) versus cages without CAL (control group). Data showed that compared to the control group, groups of two or four individuals showed low consumption of leaves. In contrast, the group of six individuals consumed approximately 50% of the leaf area offered. The bioassay for feeding preference was then performed using groups of six individuals.

For the feeding bioassay, females were starved for 18 h and groups of six individuals were confined into each cage as previously described. Four replicates (cages) were used for each plant species. Approximately, 12 g of fresh weight of plant leaves per cage were offered to the CAL for 24 h (experimental cage), whereas a similar amount of leaves was deposited in a cage with no presence of the CAL (control cage). Mean leaf area for the leaves offered to the CAL (2 g/ individual) in the cages were 22 $cm^2$ for *Pisonia aculeata*, 35.8 $cm^2$ for *G. ulmifolia*, 15.7 $cm^2$ for *L. glauca*, and 45 $cm^2$ for *W. americana*. To determine the leaf area consumed by the CAL for 24 h, the leaf area of the experimental cages was subtracted from the leaf area of the control cages. Quantification of leaf area was carried out as described by Bakr (2005). Briefly, areas of leaves were digitalized in an image scanner (HP LaserJet, Model M1132) and the JPG files exported to the software "Compu Eye, Leaf & Symptom Area." Leaf areas were then determined as comparing the size of the scanned leaves with a given known area.

### *Analysis of leaf thickness and leaf content of nitrogen and carbon*

Leaf thickness was determined indirectly by calculating the specific leaf area (SLA, $cm^2\ g^{-1}$) (Hunt 1978, Poorter 1999). Briefly, leaves of each plant species were excised and dried at 75°C for 72 h. Subsequently, the areas of dry leaves were measured using the software Compu Eye, Leaf & Symptom Area as previously described. Dry weight of leaves was measured in an electronic scale (Ohaus Scout Pro, Ohaus USA). For analysis, means were obtained from 20 replicates (leaves).

To determine the content of N and C, excised leaves were washed with distilled water containing 5% neutral detergent (Extran® MA02 5%) and subsequently rinsed with distilled water alone. Leaves were left at room temperature to eliminate the excess of water and subsequently placed in paper bags and dried at 45°C for 72 h. Nitrogen content of samples was determined by Kjeldahal method (digestion, distillation, and titration). Briefly, organic nitrogen was converted to ammonium at 370°C; subsequently, the sample was alkalinized with NaOH. The quantification of the amonuium (nitrogen) present in the simple is determined by titration (Nielsen 2010). Carbon content of leaves was determined in a carbon analyzer (Schimadzu TOC-5000A TOC analyzer). Briefly, the sample underwent combustion through heating to 680°C. It decomposed and was converted to carbon dioxide. The carbon dioxide generated was cooled and dehumidified and then detected by a nondispersive infrared sensor. The concentration of total carbon in the sample was obtained through comparison with a calibration curve formula (Fagbenroa & Oyeleyea 1999). For analysis, means of N and C content of leaves were obtained from four replicates.

### *Statistical analysis*

The olfactometer behavioral test was analyzed in contingency table as described by Seidelmann *et al* (2000) and Infante & Zárate (2003) using $\chi^2$ procedure in SigmaStat 11® ($\alpha < 0.01$, 3° of freedom). Data of host plant acceptance were analyzed by Student's *t* test, where comparisons were made between a cage with host plant plus insects and a cage with the same host plant with no insects. The experiments to evaluate leaf traits were set in a complete randomized design. For leaf traits, analyses of variance and Tukey's mean comparison were performed. Correlation between the leaf traits and host plant attraction/acceptance was carried out with linear regression analysis. All analyses were performed in InfoStat (www.infostat.com.ar). Prior to run, data in percent were transformed to arcsine [$y$ = arcsine (square root $x$/100)]. This transformation stabilizes variance and normalizes proportional data (Sokal & Rohlf 1994).

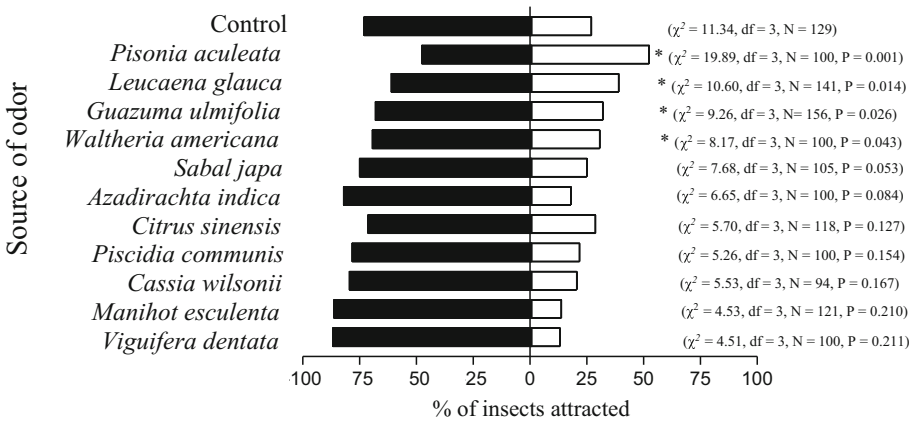


Fig 1 Olfactory response of *Schistocerca piceifrons piceifrons* to odors of plant species commonly found in the gregarious zone of the Yucatan Peninsula. The *bars* indicate the proportion of individuals that was attracted to the odor source that consisted of macerated leaves (*white section*) and the proportion of individuals that made other choice (*black section*). In control trials, the macerated leaves were absent from the right arm of the olfactometer. Significant attraction of *Schistocerca piceifrons piceifrons* to the odor source is indicated by *asterisk* (contingency tables analysis, $\chi^2$ test, $n = 94–156$, $p < 0.05$).

## Results

### *Olfactory response bioassay*

The olfactory test showed that the CAL responded differently to the plant species evaluated as a source of odor. Contingency table analysis showed that the CAL was highly attracted to *Pisonia aculeata* ($\chi^2 = 19.89$, $df = 3$, $n = 100$, $p = 0.001$). The CAL was also somewhat attracted to *W. americana* ($\chi^2 = 8.17$, $df = 3$, $n = 100$, $p = 0.043$), *G. ulmifolia* ($\chi^2 = 9.26$, $df = 3$, $n = 156$, $p = 0.026$), and *L. glauca* ($\chi^2 = 10.60$, $df = 3$, $n = 141$, $p = 0.014$). In contrast, the CAL was not attracted to *Sabal yapa*, *A. indica*, *Citrus sinensis*, *P. communis*, *Cassia wilsonii*, *M. esculenta*, and *V. dentata* (Fig 1).

### *Feeding bioassay*

Host plant acceptance test showed that the CAL had differential responses to the evaluated plant species. The CAL consumed 39 to 46% of leaf area offered of *L. glauca* ($t_6 = 3.59$, $p < 0.01$) and *W. americana* ($t_6 = 5.2$, $p < 0.05$), whereas no significant consumption of leaves of *Pisonia aculeata* and *G. ulmifolia* was observed (Fig 2).

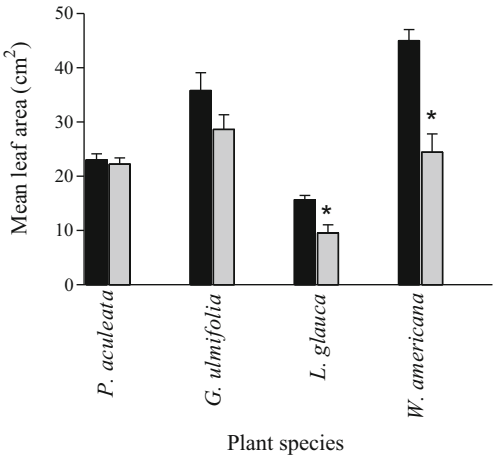


Fig 2 *Schistocerca piceifrons piceifrons* feeding on leaves of plant species that were selected from the olfactory response test. Leaf area was measured before and 24 h after placing leaves in the cages. Control cages contained no individuals (*black bars*) and experimental cages contained six individuals (*gray bars*). Significant difference from the control is indicated by *asterisk* (*t* test, $n = 4$, $p < 0.05$).

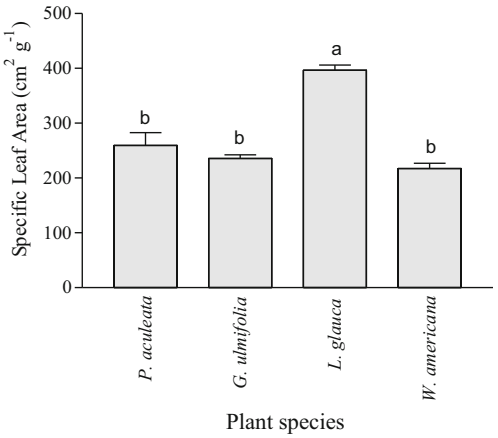


Fig 3 Leaf thickness of plant species evaluated in the feeding test. Higher values of specific leaf area (+standard error) represent lower leaf thickness. *Bars* with different *letters* are statically different (Tukey test, $n = 20$, $p < 0.05$).

Table 1 Average (±standard error) contents of nitrogen (*N*) and carbon (*C*), and C/N ratio in leaves of plants that attracted *Schistocerca piceifrons piceifrons*.

| Plant species | N content (%) | C content (%) | C/N ratio |
|---|---|---|---|
| *Waltheria americana* | 2.7 ± 0.25 b | 47.0 ± 0.39 a | 17.4 |
| *Leucaena glauca* | 4.1 ± 0.15 a | 47.2 ± 0.39 a | 11.6 |
| *Guazuma ulmifolia* | 2.1 ± 0.14 b | 46.5 ± 0.39 a | 21.9 |
| *Pisonia aculeata* | 2.4 ± 0.39 b | 39.7 ± 0.39 b | 16.5 |

Means with different letters within the same column are significantly different (Tukey test; $p < 0.05$; $n = 4$).

Table 2 Correlation coefficient (*R*) and *p* values of plant leaf eliciting olfactory response in *Schistocerca piceifrons piceifrons* and host plant feeding.

| | Attraction | Feeding |
|---|---|---|
| Thickness | −0.00 ($p = 0.99$) | −0.22 ($p = 0.27$) |
| C content | −0.97 ($p = 0.02$) | 0.57 ($p = 0.42$) |
| N content | 0.19 ($p = 0.80$) | 0.54 ($p = 0.12$) |
| C/N ratio | −0.16 ($p = 0.83$) | − 0.14 ($p = 0.85$) |

*Analysis of thickness, nitrogen, and carbon content in leaves*

Leaf thickness was evaluated as a function of the specific leaf area (SLA, leaf area/leaf mass). A lower SLA value would be indicative of a thicker leaf. Leaves of *L. glauca* showed significant lower thickness than those of *G. ulmifolia*, *Pisonia aculeata*, and *W. americana* ($F_{3, 76} = 33.9$; $p < 0.05$) (Fig 3).

The content of N in leaves was significantly different among plant species ($F_{3,12} = 12.2$; $p < 0.01$). *Leucaena glauca* had the highest values for this variable. In contrast, *W. americana*, *G. ulmifolia*, and *Pisonia aculeata* showed the lowest content of N in leaves (Table 1). The C content in leaves was significantly different among plant species ($F_{3, 12} = 85.8$; $p < 0.01$). The C content in leaves of *W. americana*, *L. glauca*, and *G. ulmifolia* was significantly higher than that of *Pisonia aculeata* (Table 1). Calculated values for C/N ratios were higher in *G. ulmifolia*, *Pisonia aculeata*, and *W. americana*, relative to that of *L. glauca* (Table 1).

For a more detailed view of the possible influence of leaf traits on the CAL olfactory response and host plant acceptance, correlation analysis was performed. In the analysis of leaf traits and olfactory response, a significant negative correlation was observed between C content and the CAL attraction ($R = -0.97$; $p = 0.02$), whereas no correlation was found between the CAL attraction and thickness, N content, or C/N ratio of leaves. No correlation was observed between the leaf traits and host plant acceptance ($R = -0.14$ to 0.57, $p > 0.05$; Table 2).

## Discussion

Attraction and acceptance are two key aspects of the interaction between phytophagous insects and host plants. A wide range of insect behavioral response are associated to attraction and food choosing; especially the olfactory system plays critical role to assure suitable nutrition resource for survival and reproduction (Hansson & Anton 2000, Reddy & Guerrero 2004, Cunningham 2012, Beyaert & Hilker 2014). In this experiment, we found that the CAL was highly attracted to odors of *Pisonia aculeata* and also attracted to *L. glauca*, *W. ulmifoia*, and *W. americana*. The response of the CAL might have been initially guided by leaf volatiles, where safe sources of food with no toxic compounds could be found. At first glance, plants that attracted the CAL were expected to be highly accepted as source of food. However, feeding test did not fully support this inference, as *Pisonia aculeata* that highly attracted the CAL was not significantly consumed. In addition, only two sources of odor (*L. glauca* and *W. americana*) out of three that somewhat attracted the CAL were significantly consumed. These results suggest that the interaction between the CAL and potential host plants is affected by two distinct elements, one related to olfactory response and another related to food acceptance. In the first case, plant volatiles may play an important role, whereas in the second case, leaf traits, like physical characteristics and the presence of antinutritional compounds, may be determinant.

As previously mentioned, we observed that *Pisonia aculeata* as source of odor highly attracted the CAL, but leaves of this plant were not a feasible source of food. To our knowledge, no reports were found on volatiles emitted by *Pisonia aculeata* that attract phytophagous insects, but a broader overview of its family (Nyctaginaceae) suggests that various genera of this family possess a wide variety of volatile compounds, including monoterpenoids and sesquiterpenoids, aromatics (both benzonoids and phenylpropanoids), and aliphatic compounds, as well as lactones and nitrogen-bearing compounds that are involved in the attraction of phytophagous insects (Levin *et al* 2001). *Pisonia aculeata* is an evergreen thorn bush commonly used as refuge for the CAL in the gregarious zone. The CAL might have been attracted by volatiles of this plant that provide protection against natural predators. Migration to thorn bushes to avoid predation has been also observed in other species of acridids, like *Hieroglyphus perpolita* (Uvarov) (Orthoptera: Acrididae), which has been observed moving to thorn bushes rather than other plants when disturbed. This behavior has been associated to a strategy of insects to protect themselves from enemies (Sultana & Wagan 2010). Finally, insect protection by a thorn bush has also been well documented in the relation between ants and acacias (Janzen 1966).

Factors that affect feeding in phytophagous insects when in contact with theirs host plants include physical defense (morphological traits), chemical compounds (secondary metabolites and digestibility reducing proteins), and antinutritive enzymes. We believe that plants, like *Pisonia aculeata* and *G. ulmifolia* that attracted the CAL when used as source of odor but were not consumed when used as source of food, might contain antinutritional or toxic compounds. In this regard, related species to *Pisonia aculeata* have high content of saponins in their leaves, compounds that are considered antifeedant, molt disturbant, growth regulator, and toxic (Lavaud *et al* 1996, De Feo *et al* 1998, De Geyter *et al* 2007, Chaieb 2010). Similarly, in *G. ulmifolia*, precocene I, a major chemical constituent of leaves, is a toxic compound that causes changes in physiology and morphology of insects (Arriaga *et al* 1997, Farazmand & Chaika 2011). The presence of these potentially harmful compounds may explain why the CAL did not consume leaves of these plants.

Physical and chemical properties of leaves can act also as lines of defense and affect insect attraction and host plant acceptance (Chapman 1990, War *et al* 2012). In general, phytophagous insects need food sources with appropriate content of N, C, and other mineral elements to ensure growth and egg production (Meloni *et al* 2011). Previous studies have documented that acridids generally feed on vegetation that has high N content (Loaiza *et al* 2011, Joern *et al* 2012). Positive effects of N content of leaves on acridids fitness include faster development, higher survivorship, and higher reproduction rate (Jonas & Joern 2008, Van Huis *et al* 2008). In contrast to what has been reported in literature, in the present work, we found no evidence that the CAL feeds on leaves with higher N content.

In the present study, we observed that the CAL was highly attracted to odor of leaves with lower C content, but no correlation was observed between C content or C/N ratio of leaves and host plant acceptance. These results are not in agreement with the general knowledge that points out that the C content is a key element for food choice in insects; a decrease in herbivore damage has been observed when host plant have high C/N ratio (Knepp *et al* 2005). Carbon in leaves is critical in the formation of cell walls and lignin, and production of phenolic substances and consequently in the suitability of food choice by phytophagous insects (Paré & Tumilson 1999, Poorter 2002).

In summary, this is the first report on the study of interaction between the CAL and common plants found in the gregarious zone of the Yucatan Peninsula. We observed that the CAL was attracted to odor of *Pisonia aculeata* and fed only on *L. glauca* and *W. americana*. The CAL was highly attracted to odor of leaves with low C content. There was no correlation between leaf traits and the host plant acceptance by the CAL.

Study of the CAL interaction with various species of plants commonly found in the gregarious zone of the Yucatan Peninsula showed that this phytophagous was highly attracted to *Pisonia aculeata* leaf odor but did accept this plant as source of food. The CAL fed on *L. glauca* and *W. americana*. Correlation between attraction/host plant acceptance and leaf traits showed that the CAL was attracted to odor of leaves with low C content, and no correlation was found between the traits of plant leaves and host plant acceptance.

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