Implications of Antibiosis and Antixenosis in Four Plant Species Against *Oligonychus punicae* (Trombidiformes: Tetranychidae)[1]

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Abstract Oviposition and feeding of herbivorous arthropods influence the plant-arthropod interaction and determine the success in colonization and establishment on their host plant. The avocado brown mite, *Oligonychus punicae* Hirst (Acari: Tetranychidae), causes severe damage to several crops due to its feeding. This study proposed to evaluate the resistance mechanisms of *Moringa oleifera* Lamarck (Moringaceae), *Phaseolus vulgaris* L. (Fabaceae), *Persea americana* Miller (Lauraceae), and *Rosa hybrida* L. (Rosaceae) to the attack by avocado brown mite under laboratory conditions. The study was conducted under laboratory conditions at 28 ± 1°C and 70–80% relative humidity (RH), with a photoperiod of 12:12 h (light: dark). *Oligonychus punicae* females showed no preference to oviposit on *M. oleifera* (2.10 ± 0.05 eggs/female/day) compared with *R. hybrida* (2.77 ± 0.06), *P. americana* (2.73 ± 0.08), and *P. vulgaris* (3.05 ± 0.08). Females showed a preference to feed on *P. vulgaris* compared with other host plants. Avocado brown mite recorded the lowest values in *r* (0.5990 d^{-1}) on *M. oleifera* foliage square. *Moringa oleifera* was the most resistant to *O. punicae*, whereas the most susceptible host plant was *P. vulgaris*. These results indicate possible resistance of *M. oleifera* to the attack of *O. punicae* and that those responses might be due to antibiosis and antixenosis.

Key Words avocado brown mite, host plant resistance

The avocado brown mite, *Oligonychus punicae* Hirst (Acari: Tetranychidae), is found around the world, mainly in countries in the neotropical region, including Brazil, Chile, Colombia, Guatemala, and Mexico (Migeon and Dorkeld 2024, Peña et al. 2013). This mite feeds on 121 species of host plants (Migeon and Dorkeld 2024). In Mexico, *O. punicae* is an important pest in avocado crops (Peña et al. 2013). Mites feed on the upper surface of the leaf, causing leaf bronzing and a reduction in photosynthetic activity by more than 50%, which can result in losses in avocado yield up to 20% (Castañeda-Cabrera et al. 2022, Maoz et al. 2011).

Control of the avocado brown mite mostly depends on the use of chemical pesticides, but tetranychid mites such as *O. punicae* have a short life cycle, high reproductive rate, and arrenotic reproduction and, thus, can quickly develop resistance to these synthetic compounds (Van Leeuwen et al. 2015).

Avocado brown mite can develop and reproduce on a wide range of host plants and under a variety of climatic factors (Ferraz et al. 2020, 2021; Vásquez et al. 2008). For example, Ferraz et al. (2021) evaluated the behavior of *O. punicae* on *Eucalyptus tereticornis* Smith (Myrtaceae) discs at different temperatures ranging from 21 to 37°C. They determined that *O. punicae* performs better between 25 and 29°C than at other temperatures. Vásquez et al. (2008) reported that the performance of *O. punicae* was better on the Chenin Blanc cultivar of grapevine, *Vitis vinifera* L., when compared with other cultivars. Ferraz et al. (2020) found that optimal development for avocado brown mite was on *E. tereticornis* than on *E. pellita* F. Mueller, *E. brassiana* S.T. Blake, *E. grandis* W. Hill Ex Maiden (Myrtaceae), and *Corymbia citriodora* L.A.S. Johnson (Myrtaceae). The biology and demographic parameters of *O. punicae*, such as fecundity, survival rate, and total developmental time (egg-adult), may vary in response to changes in host plant species, temperature, secondary metabolites, and anatomical features of leaves (Ferraz et al. 2020, 2021; Vásquez et al. 2008).

Plant-arthropod interactions are influenced by both the interactions among plants and arthropod feeding and the relationship among plants and arthropods oviposition (Hilker and Meiners 2011). Egg laying by herbivorous arthropods on their host plants is the first and most important event in their interactions because it determines the establishment of a new generation (Hilker and Meiners 2011, Kim et al. 2012, War et al. 2018). Furthermore, the deposition of eggs by herbivorous arthropods on their host plants is a warning sign of future larval herbivory (Hilker and Meiners 2011, Kim et al. 2012). On the other hand, the process of colonization and establishment of a species that inhabits new favorable environments occurs with low population densities, exhibiting exponential growth in a short period (Carey 1993, Smith and Smith 2015).

On the other hand, the response of the plants to the attack of a phytophagous mite can be recorded through various mechanisms such as antixenosis, antibiosis, tolerance, or combinations of these. Antixenosis occurs when a resistant plant is absolutely rejected or accepted by a herbivorous arthropod as a host plant due to the non-preference as a food resource and ovipositional substrate caused by biophysical or allelochemical factors present in the plants. Antibiosis occurs when a plant negatively affects the survival, growth, and fecundity of an herbivorous arthropod, caused by bioactive compounds present in the resistant host plants. Tolerance is a polygenic trait that allows a plant to resist, repair, or recover from damage caused by the herbivorous arthropod (Smith 2005, Smith and Clement 2012). This research aimed to assess antibiosis and antixenosis as resistance mechanisms in four plant species (*Moringa oleifera* Lamarck [Moringaceae], *Persea americana* Miller [Lauraceae], *Rosa hybrida* L. [Rosaceae]), and *Phaseolus vulgaris* L. [Fabaceae]) to the attack by avocado brown mite under laboratory conditions.

Materials and Methods

Brown avocado mite colony. A mite colony was started with biological material from the Plant Physiology Laboratory, Faculty of Engineering and Sciences,

Autonomous University of Tamaulipas. The mite population was increased by placing females and males on bean plants (*P. vulgaris*) under greenhouse conditions at 29 ± 4°C and 80 ± 10% relative humidity (RH).

Collection and preparation of plant material. Three host plants (*M. oleifera*, *P. americana*, and *R. hybrida*) and *P. vulgaris* were used to evaluate feeding damage, oviposition, mite mortality, and mite population growth of *O. punicae* (Migeon and Dorkeld 2024). All plants were grown under field conditions.

Mature leaflets of *M. oleifera* (30) and *R. hybrida* (15) and leaves of *P. vulgaris* (10) and *P. americana* (2) were collected and transported in resealable plastic bags inside a cooler with gel packs at a temperature of 5 ± 2°C to the Physiology Laboratory of the Faculty of Engineering and Sciences of the Autonomous University of Tamaulipas. The transfer time of the plant material to the laboratory was between 15 and 30 min, depending on the host plant location. The selected leaves and leaflets were clean, that is, without the symptoms of fungi, bacteria, and any damage. However, the plant material was washed for 2 min wash with 1.5% sodium hypochlorite solution. Leaflets and leaves were then cut into 2-cm^2 squares.

Experimental design. Oviposition rate and the percentage of damage caused by feeding of *O. punicae* females were evaluated using a host plant leaf square of 2 cm^2. Each square was placed abaxial surface downward on cotton saturated with water and placed in a Petri dish (5 cm diam.). Twenty females in the teleiochrysalis stage (2 d old) and 20 adult males were placed on each foliage square of each host plant. Males were removed 24 h later. Once the females began ovipositing, each was allowed to lay eggs during the first 5 d of the oviposition period, after which we recorded the number of eggs laid (Gotoh et al. 2004). The assay was conducted under laboratory conditions at 28 ± 1°C and 70–80% relative humidity (RH), with a photoperiod of 12:12 h (light: dark). To ensure the freshness of the leaf squares of each tested host plant, individuals were transferred to new leaf squares every 2 d. Six randomly selected foliage squares of each host plant were assigned to one of four groups, one group for each host plant species. One foliage square of each host plant served as a replicate to establish six replicates per group or 24 in total.

The occurrence of antixenosis was based on two criteria: (1) *O. punicae* did not lay eggs and (2) non-feeding. The number of eggs laid per female on every foliage square of each host plant species was counted using a dissecting microscope (UNICO Stereo and Zoom Microscopes ZM180, Princeton, NJ). Feeding damage was estimated visually on each foliage square using a foliage damage index proposed by Nachman and Zemek (2002), where 0 = 0% damage (no feeding damage) and 5 = 81% to 100% feeding damage (e.g., a dense mark caused by feeding). The number of eggs laid per female and the percentage of feeding damage were recorded at 24 (day 1), 48 (day 2), 72 (day 3), 96 (day 4), and 120 h (day 5).

Antibiosis was determined by mite population growth rate and mite mortality. The growth rate (r, day^{-1}) was calculated using the formula, $r = (1/t) \times \ln(Nt/N0)$, where Nt is the final number of eggs, larvae, and live adults of *O. punicae* at time t (days, [equal to 5 d]), N0 is the number of females mites at time 0 (initial cohort = 20). The calculated r provides information on the short-term population growth patterns (Carey 1993). If $r = 0$, the mite population numbers do not change, whereas, if $r > 0$ or $r < 0$, the mite population increases or decreases over time, respectively

(Smith and Smith 2015). Mortality was measured by the mean percentage of dead (drowned) individuals outside the foliage square, using the formula, $(\Sigma di/n) \times 100$, where di is the number of individuals drowned and n is the number of individuals on the foliage square. Mite mortality was recorded each day for 5 d.

We also recorded, on the fifth day, the number of *O. punicae* larvae because the hatch time of a single *O. punicae* egg is 4.4 to 4.7 d on grapevine leaf discs at 27°C, 80 ± 10% RH, and a photoperiod of 12:12 h (Vásquez et al. 2008). Furthermore, hatching time on discs of 6 species of eucalyptus plants is 5.03 to 5.27 d at 25 ± 2°C, 70 ± 10% RH, and a photoperiod of 12:12 h (Ferraz et al. 2020), while the required time for an *O. punicae* egg to hatch is 3.70 ± 0.04 d on *E. tereticornis* at 29°C, 70 ± 10% RH, and 12:12 h of photoperiod (Ferraz et al. 2021).

Statistical analysis. The data (number of laid eggs, dead mites, and the percentage of damage by feeding *O. punicae* females) was analyzed using analysis of variance of repeated measurements (ANOVArm). The number of larvae and the growth rate (r, day^{-1}) were analyzed using one-way ANOVA and in both cases, the significant differences were analyzed with LSD's multiple range comparison test. The SAS/STAT software was used for all analyses (SAS Institute, Inc. 2002).

Results

Antixenosis. The number of *O. punicae* eggs laid per female differed significantly among the host plants tested ($F = 127.32$; df = 3, 20; $P < 0.0001$), among the observation times ($F = 54.13$; df = 4, 80; $P < 0.0001$), and the host × time interaction ($F = 14.37$; df = 12, 80; $P < 0.0001$). The number of eggs laid on *P. vulgaris* was significantly higher (3.05 eggs/female) and significantly lower on *M. oleifera* (2.10 eggs/female) (LSD's test, $P < 0.0001$) (Table 1). These differences indicate possible *M. oleifera* resistance to the oviposition of avocado brown mites compared to *P. vulgaris*, and these responses might be due to antixenosis.

The feeding damage of *O. punicae* differed significantly among the host plants ($F = 338.30$; df = 3, 20; $P < 0.0001$), among the observation times ($F = 1281.35$; df = 4, 80; $P < 0.0001$), and the host×time interaction ($F = 5.15$; df = 12, 80; $P < 0.0001$). Damage was significantly greater and less on *P. vulgaris* (28.73%) and *M. oleifera* (15.20%), respectively (LSD's test, $P < 0.0001$) (Table 2). Thus, these discrepancies indicate a possible resistance of *M. oleifera* to damage caused by female avocado brown mite feeding compared to *P. vulgaris* and the other host plants, and these responses might be due to antixenosis.

Antibiosis. Growth rate (r, day^{-1}) of *O. punicae* differed significantly among the host plants ($F = 98.60$; df = 3,20; $P < 0.0001$). The highest mean (±SD) r of *O. punicae* was observed with *P. vulgaris* (0.6884 ± 0.01), while the lowest was with *M. oleifera* (0.5990 ± 0.01) (Fig. 1). This indicates that *M. oleifera* is more resistant to the development of avocado brown mite than *P. vulgaris*, and these responses might be due to antibiosis.

The number of dead *O. punicae* differed significantly among the host plants ($F = 14.89$; df = 3, 20; $P < 0.0001$), among the observation times ($F = 24.83$; df = 4, 80; $P < 0.0001$), and the host×time interaction ($F = 1.95$; df = 12, 80; $P = 0.0398$). In general, the largest mean percentage of dead mites per day was observed on *M. oleifera* (8.33%) and the lowest on *P. vulgaris* (1.67%). Therefore, these results

Table 1. Mean number of eggs laid per female/day of *Oligonychus punicae* on four plant species.

Host Plant	Number of Eggs*					General Average
	24 h	48 h	72 h	96 h	120 h	
Moringa oleifera	1.82 ± 0.20c	2.22 ± 0.18c	2.21 ± 0.17c	1.92 ± 0.13c	2.35 ± 0.08b	2.10 ± 0.23c
Persea americana	3.22 ± 0.52b	2.72 ± 0.19b	2.53 ± 0.17b	2.12 ± 0.13b	3.03 ± 0.15a	2.73 ± 0.42b
Phaseolus vulgaris	3.72 ± 0.18a	3.22 ± 0.19a	2.87 ± 0.17a	2.42 ± 0.15a	3.02 ± 0.15a	3.05 ± 0.42a
Rosa hybrida	3.10 ± 0.13b	3.00 ± 0.15a	2.98 ± 0.08a	2.31 ± 0.10ab	2.45 ± 0.12b	2.77 ± 0.31b
General Average	2.96 ± 0.76A	2.78 ± 0.42B	2.65 ± 0.34C	2.20 ± 0.22D	2.71 ± 0.34BC	

* Means (± SD) within columns and rows followed by different lowercase and uppercase letters, respectively, are significantly different ($P < 0.05$; ANOVArm and LSD test).

Table 2. Mean percentage feeding damage of *Oligonychus punicae* females to foliage square of four plant species.

Host Plant	Percentage of Damage*					General Average
	24 h	48 h	72 h	96 h	120 h	
Moringa oleifera	6.00 ± 0.89c	9.50 ± 1.38c	14.33 ± 1.03c	19.67 ± 1.21d	25.50 ± 1.04d	15.20 ± 6.82d
Persea americana	8.00 ± 0.89b	11.67 ± 2.73b	18.00 ± 0.89b	25.00 ± 0.89b	30.33 ± 1.03b	18.60 ± 7.74b
Phaseolus vulgaris	15.833 ± 2.13a	21.67 ± 1.75a	29.67 ± 1.97a	34.83 ± 1.17a	41.67 ± 1.75a	28.73 ± 8.64a
Rosa hybrida	7.00 ± 0.89b	11.00 ± 0.89b	18.00 ± 0.89b	23.00 ± 0.89c	28.00 ± 0.89c	17.40 ± 7.13c
General Average	9.20 ± 4.15E	13.45 ± 5.19D	20.00 ± 6.02C	25.62 ± 5.85B	31.62 ± 6.19A	

* Means (±SD) within columns and rows followed by different lowercase and uppercase letters, respectively, are significantly different ($P < 0.05$; ANOVArm and LSD test).
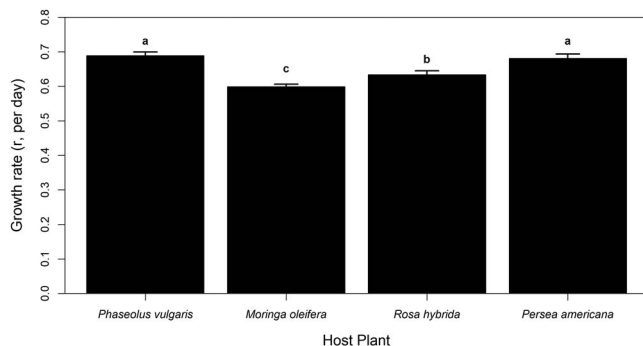
Fig. 1. Population growth rate of *Oligonychus punicae* on four tested plants.

indicate the possible resistance of *M. oleifera* compared to other host plants to attack by *O. punicae* (Table 3), this response might be due to antibiosis.

Hatched eggs. The number of *O. punicae* eggs that hatched was significantly higher on *P. vulgaris* (36.17 larvae) than on *P. americana* (31.67 larvae), *R. hybrida* (28.00 larvae), and *M. oleifera* (16.00 larvae) ($F = 55.28$; df = 3, 20; $P < 0.0001$). The percentage of hatched eggs was significantly higher on *P. americana* (98.54%) and *P. vulgaris* (97.31%) than on *R. hybrida* (90.38%) and *M. oleifera* (88.07%) (Table 4). This indicates that the *O. punicae* eggs oviposited during the first 24 h were affected by the *M. oleifera* host plant. These eggs are expected to hatch on the fifth day after oviposition.

Discussion

The deposition of eggs is the beginning of the attack by herbivorous arthropods. Furthermore, the eggs laid by phytophagous arthropods indicate future damage to the plant since the larvae hatched from those eggs will cause damage due to their feeding. However, the survival of the progeny from those eggs requires a host plant that provides sufficient food for the following stages of development (Hilker and Fatouros 2015). The mean ($\pm$ SD) number of eggs laid by *O. punicae* females was greater on *P. vulgaris* (3.05 ± 0.08) than on *P. americana* (2.73 ± 0.08), *R. hybrida* (2.77 ± 0.06), and *M. oleifera* (2.10 ± 0.05), suggesting that plants influence the ovipositional behavior and biology of the avocado brown mite. Other studies have shown that *Oligonychus* spp. fecundity is related to the species and variety of the host plant. Ferraz et al. (2020) reported that the total fecundity *O. punicae* was higher on *E. tereticornis* (44.75 ± 22.89 eggs/female) than on *E. grandis* (22.80 ± 11.09), *E. brassiana* (18.44 ± 8.99), *E. pellita* (13.35 ± 9.11), *E. urophylla* (8.45 ± 4.40), and *C. citriodora* (5.45 ± 3.71). Vásquez et al. (2008) documented the daily egg production of *O. punicae* on six grape cultivars and found that the daily oviposition rate was higher on Tucupita cultivar (2.82 ± 2.42 eggs/female/day) than on Red Globe (2.72 ± 1.91), Chenin Blanc (2.16 ± 1.99), Sauvignon (2.15 ± 1.41), Villanueva (1.79 ± 0.94), and Sirah (0.94 ± 0.95) cultivars. Yao et al. (2019) reported that litchi cultivars (*Litchi chinensis* Sonn [Sapindaceae]) affect the number of eggs oviposited per female of

Table 3. Mean percentage mortality of *Oligonychus punicae* on foliage squares of four plant species at different times.

Host Plant	Mortality*					General Average
	24 h	48 h	72 h	96 h	120 h	
Moringa oleifera	0.00 ± 0.00a	3.33 ± 5.16a	6.67 ± 5.16a	15.00 ± 5.47a	16.67 ± 8.16a	8.33 ± 7.61a
Persea americana	0.00 ± 0.00a	0.00 ± 0.00a	1.67 ± 1.67a	3.33 ± 2.11c	6.67 ± 2.11c	2.33 ± 0.79c
Phaseolus vulgaris	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	3.33 ± 5.16c	5.00 ± 5.47c	1.67 ± 3.50c
Rosa hybrida	0.00 ± 0.00a	1.67 ± 4.08a	3.33 ± 5.16a	10.00 ± 6.32b	13.33 ± 5.16b	5.67 ± 6.18b
General Average	0.00 ± 0.00E	1.25 ± 3.38D	2.91 ± 4.64C	7.91 ± 7.21B	10.42 ± 7.51A	

* Means (±SD) within columns and rows followed by different lowercase and uppercase letters, respectively, are significantly different ($P < 0.05$; ANOVArm and LSD).

Table 4. Mean number of hatched eggs following oviposition by *Oligonychus punicae* on four species of plants during the first 24 h.

Host Plant	Hatched Eggs*	Percentage of Eggs Hatched*
Moringa oleifera	16.00 ± 1.79d	88.07 ± 1.56b
Persea americana	31.67 ± 4.96b	98.54 ± 1.63a
Phaseolus vulgaris	36.17 ± 1.83a	97.31 ± 0.13a
Rosa hybrida	28.00 ± 1.095c	90.38 ± 3.28b

* Means (±SD) are presented. Different letters following the means indicate significant differences ($P < 0.05$; ANOVA and LSD).

Oligonychus litchii Lo & Ho (Prostigmata: Tetranychidae) with *O. litchii* ovipositing more on the litchi cultivar Nuomici (64.84 ± 3.57 eggs/female) than on Sanyuehong (38.55 ± 2.34), Feizixiao (22.30 ± 1.59), and Baili (14.78 ± 1.66) cultivars. Chaaban et al. (2012) reported the daily fecundity of *Oligonychus afrasiaticus* (McGregor) (Acari: Tetranychidae) when fed fruits of five date palm (*Phoenix dactylifera* L. [Arecaceae]) cultivars and sorghum leaves (*Sorghum* sp.). They found that fecundity of *O. afrasiaticus* was greater on sorghum leaves (2.00 ± 1.3 eggs/female/day) than on Deglet Noor cultivar (1.5 ± 0.4), Kentichi (0.9 ± 0.5), Bessr (0.9 ± 0.4), Alig (0.7 ± 0.3), and Deglet Noor pinnae (0.7 ± 0.2). Roknuzzaman et al. (2020) found that *Oligonychus biharensis* (Hirst) (Acari: Tetranychidae) lays more eggs on country bean (*Lablab purpureus* L.) (1.67 ± 0.06 eggs/female/days) than on mung bean (*Vigna radiata* L. [Wilczek]) (1.28 ± 0.01 eggs/female/days). It is, therefore, likely that *O. punicae* females lay a greater number of eggs on *P. vulgaris* than on *P. americana*, *R. hybrida*, and *M. oleifera* which is likely due to the influence of biotic and abiotic factors. Biotic factors include differences among *Oligonychus* species, nutritional quality, morphological and chemical features in different host plant species and varieties, and abiotic factors, including adapting specific mite species to the local climate and host plants, handling methods, and observation time intervals (Ferraz et al. 2020, Roknuzzaman et al. 2020, Vásquez et al. 2008).

Feeding damage caused by *O. punicae* females differed significantly among host plants. *Moringa oleifera* and *P. vulgaris* were the host plants that suffered the least and the greatest damage, respectively, caused by feeding of the avocado brown mite. Plants produce various biochemical compounds (alkaloids, flavonoids, terpenes, and phenols) to defend themselves or avoid attack by phytophagous arthropods. These secondary metabolites have acaricidal activity, which generates antixenotic and antibiotic effects on these arthropods. *Moringa oleifera* may present phytochemicals such as alkaloids, coumarins, flavonoids, phenols, and tannins in its leaves (Heinz-Castro et al. 2021). These phytochemicals are substances with insecticidal and acaricide action (Hamza et al. 2016, Heinz-Castro et al. 2021, Ojo et al. 2013). Koul (2016) and Singh et al. (2021) mentioned that bioactive compounds such as alkaloids, coumarins, terpenes, and phenols adversely affect feeding herbivorous arthropods. Hence, these phytochemicals may explain the low feeding damage rate of *O. punicae* when fed *M. oleifera*.

In this study, the number of *O. punicae* hatched eggs oviposited in the first 24 h was less on *M. oleifera* than on other host plants. Furthermore, the mortality percentage of female brown avocado mites was higher on the same host plant species, indicating that this plant has a toxic effect on the eggs and females of *O. punicae* females and, hence, a negative effect on the growth rate (*r*) of the avocado brown mite. Hilker and Meiners (2011) mentioned that low humidity due to dry air and closed plant stomata and gas concentrations in the host plant leaf boundary layer can cause desiccation of eggs. Hence, this may explain the low growth rate of *O. punicae* when fed *M. oleifera* compared to other host plants. In addition, many factors influencing the population growth of spider mites, including the nutritional value of the host plant, environmental factors, and feeding inhibitions caused by the different morphological and physiological characters of host plants (Roknuzzaman et al. 2020). The growth rate estimated the process of colonization and establishment in new environments for *O. punicae*, which had exponential growth ($r > 0$), characteristic of populations inhabiting favorable environments at low population densities (Smith and Smith 2015).

Female mite feeding and oviposition on beans in comparison to avocado, rose, and moringa. Using the same host plant in the test as for the mite rearing could induce changes in the responses of the adult females of *O. punicae* on the other host plants in comparison to the mites that experienced in the pre-adult stages on the plants of beans, suggesting memory conditioning in *O. punicae*. Thorpe (1939) described this as preimaginal conditioning. More studies are required to determine if this behavior is due to preimaginal conditioning. Arthropods with preimaginal experiences can learn the characteristics of a high-quality food resource and, as adults, females with retention of this learning quickly locate an oviposition site suitable for larval development (Barron and Corbet 1999).

In conclusion, the results of these tests show that the host plant *M. oleifera* presents possible resistance to the attack of *O. punicae* females and that those responses might be due to antibiosis and antixenosis, causing a lower oviposition, lower feeding damage, a low population growth rate, higher mortality, and lower number of hatched eggs as compared to *P. vulgaris*, *P. americana*, and *R. hybrida*. While promising, further research is required, including the morphological and biochemical characters of plants to correlate them with their observed antibiotic and antixenotic effects on *O. punicae*. Furthermore, to have a clear and systematic image of the specific age at birth (m_x) and survival (l_x) of the *O. punicae* population on tested plants, both for females and males must be analyzed in detail, the development time from egg to adult, the pre- and post-oviposition, oviposition periods; total and daily fecundity and its demographic parameters.

Acknowledgments

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