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Source: Florida Entomologist, 89(2) : 127-134

Published By: Florida Entomological Society

URL: [https://doi.org/10.1653/0015-4040\(2006\)89\[127:HSBOLA\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2006)89[127:HSBOLA]2.0.CO;2)

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HOST SELECTION BEHAVIOR OF *LEPTOPHOBIA ARIPA*
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ABSTRACT

Host selection and egg laying behavior of wild populations of the mountain white butterfly, *Leptophobia aripa* (Boisduval), was observed in the presence of a group of host plants (*Brassica oleracea* L. var. *capitata*) of varying quality. Host variation was generated by manipulating three crop management variables: fertilization, water, and light. *Leptophobia aripa* was not indifferent to host quality variation, and showed great ability to evaluate and discern among a group of hosts. A sigmoidal relation was found between egg laying and host plant size. The latter was probably perceived through the host's diameter, or other physical and chemical characteristics related to this attribute. More detailed studies are necessary in order to understand which cues this insect uses to locate its host and which other attributes it evaluates upon deciding to lay eggs. This understanding could allow for the development of agro-ecological alternatives in controlling this insect, considered to be a crop pest in some regions of Mexico and Central America.

Key Words: mountain white butterfly, *Brassica oleracea*, host plant selection, host quality

RESUMEN

Se observó el comportamiento de selección y oviposición de poblaciones silvestres de *Leptophobia aripa* (Boisduval) ante un conjunto de plantas hospederas (*Brassica oleracea* L. var. *capitata*) de distintas calidades, generadas mediante cambios en tres condiciones de manejo del cultivo: fertilización, riego y luz. Su comportamiento no fue indistinto a las diferentes calidades de hospedera, sino que obedeció a una compleja selección. Mostrando una gran capacidad para evaluar y discriminar entre el conjunto de hospederas. Se encontró una relación altamente no lineal entre la oviposición y el tamaño de la planta, probablemente percibida a través del diámetro de la hospedera, o por otras características físicas y químicas relacionadas con este atributo. Son necesarios estudios más detallados que contribuyan a entender cuáles son las señales que este insecto usa para localizar su hospedera y que otros atributos evalúa al tomar la decisión de ovipositar. Esto permitiría desarrollar alternativas agroecológicas para su control, dado que en algunas regiones de México y Centroamérica se le considerar como plaga.

Translation provided by the authors.

All herbivorous insects show some degree of host selectivity. Most adult holometabolous species must select an appropriate host for larval growth and survival (Bernays & Chapman 1994). Under natural conditions, insects confront many external stimuli, their own internal physiological stimuli, and a series of environmental constraints (Visser 1986; Bernays & Chapman 1994; Badenes et al. 2004). This makes it very difficult to discern the relative importance to the insect of chemical, visual, and mechanical stimuli from host and non-host plants (Schoonhoven et al. 1998; Hooks & Johnson 2001). However, it is generally assumed that the host selection process in specialist insects is governed primarily by volatile chemical signals, later by visual stimuli, and finally by

non-volatile chemical signals (Hern et al. 1996; Hooks & Johnson 2001).

Female butterflies reject many potential hosts when searching for egg laying sites. They demonstrate a hierarchy in host preferences, discriminating among plant species, among genotypes, among individuals with different phenological and physiological conditions, and even among plant parts, although not all discriminate at the finer scales (Thompson & Pellmyr 1991; Bernays & Chapman 1994). However, this knowledge is derived from studies of very few insect species (Bernays & Chapman 1994; Schoonhoven et al. 1998). Furthermore, there may be significant behavioral differences within a family, among species of the same genus, or even among different

populations of the same species (Jones 1977; Singer & Parmesan 1993; Reich & Downes 2003).

To this date, there are no studies on host selection behavior of the mountain white butterfly, *Leptophobia aripa* (Boisduval). This insect is a multivoltine species with overlapping generations. Females lay masses of 15 to 80 eggs (Bautista & Vejar 1999). The mountain white butterfly specializes in the family Brassicaceae, and it is an important pest of Brassica crops in Southeastern Mexico, Central America, and the Caribbean (CATIE/MIP 1990, Santiago et al. in press). However, it is not known which plant physiological stage is best suited for oviposition of *L. aripa*. In the case of cultivated plants, crop management choices may determine the quality of the plant as a host (Andow 1991).

The objective of the present study was to observe the egg laying behavior of *L. aripa* in host plant patches (*Brassica oleracea* L. var. *capitata*) of different qualities.

MATERIALS AND METHODS

The experiment was established in the Valley of San Cristóbal de Las Casas Chiapas, México (2,113 m.a.s.l.; C(w₂)(w); García 1973) within the cabbage production area of the Highlands of Chiapas. Cabbage plants of the variety Copenhagen Market were started in seed beds. Twenty five days after germination, each seedling was transplanted to a black plastic bag (20 cm high by 15 cm in diameter). The bag contained a 1:1 proportion of clay-loam forest soil and sand.

Sixty four plants were prepared. These were divided into eight groups of eight plants each, and placed in a greenhouse. In order to generate different host qualities, each group was submitted to one of eight treatments for 40 days. These treatments consisted of all possible combinations of two fertilization levels, two watering levels, and two photosynthetically active radiation (PAR) levels (Table 1). Nitrogen fertilization was equivalent to 100 kg Ha⁻¹, the most common dose ap-

plied to cabbage in the study zone (Santiago et al. in press). Treatments were irrigated with high or low water treatments every four and eight days, respectively, from August 1 to September 20, 2002. Accumulated irrigations (326 and 183 mm, respectively) were roughly equivalent to the high (320 mm) and low (195 mm) average cumulative rainfalls during the same period, to be found within the cabbage production zone where *L. aripa* was studied (Cervantes 1997).

Sixty five days after germination, the bagged plants were moved to an open field 200 m from a cabbage field to promote visits from wild populations of *L. aripa*. The 64 bags were randomly distributed in a square pattern without contiguous repetitions (Hurlbert 1984), with 50 cm between plants. Watering treatments were continued throughout the time of the plants' exposure to *L. aripa*.

For five days, *L. aripa*'s flights during host location and egg laying behavior were observed (for 1 h per day between 10 a.m. and 2 p.m.) and this information was recorded. A total of 28 individuals were observed from the time they entered until they left the group of host plants. The behavior of 8 females (that actually laid eggs during the five recorded hours) was classified into four types of acts: linear flight, turning flight, landing and egg laying. Each behavioral act was recorded on an experiment layout map.

The cabbage plants were reviewed daily in the afternoon (5 to 5:30 p.m.) for 11 days, and the number of eggs laid per plant during 9 h of exposure (8 a.m. to 5 p.m.) was recorded. After being counted, the eggs were carefully removed with a damp flannel cloth, in order to avoid hatching and to minimize visual or chemical stimuli from the eggs which could inhibit egg laying of conspecific females (Bernays & Chapman 1994). Hilker & Meiners (2002) reported for *Pieris brassicae* (L.) that egg removal might not completely eliminate such stimuli. However, in this study, *L. aripa* laid eggs repeatedly on most plants from which previously laid eggs were removed.

TABLE 1. DESCRIPTION OF FACTORS AND LEVELS FOR THE TREATMENTS. EACH LEVEL OF A FACTOR WAS COMBINED WITH BOTH LEVELS OF THE OTHER TWO FACTORS.

Factors	Level 1	Level 2
Nutrient (N)	N1: Without fertilizer.	N2: Foliar fertilizer (20% N - 30% P - 10% K - 1.6% micronutrients) at a dose of 12.5 g per plant. N dose equivalent to 100 kg Ha ⁻¹ . Applied 15 days after transplanting.
Water (W)	W1: Watered with a total of 3,240 ml over a period of 51 days. Equivalent to 183 mm of rainfall from August 1 to September 20.	W2: Watered with a total of 5,760 ml over a period of 51 days. Equivalent to 326 mm of rainfall from August 1 to September 20.
PAR(L)	L1: Mesh shade which eliminated 64% of the photosynthetically active radiation inside the greenhouse.	L2: 100% of the photosynthetically active radiation inside the greenhouse.

Each afternoon after sampling, the group of plants was enclosed with greenhouse plastic in order to prevent them from receiving rain water and additional butterfly visits.

Eighty two days after planting, the height and diameter of plants were measured, and above ground biomass was harvested to determine fresh weight per plant. Also, a 2-cm² leaf sample was taken from each plant for determining the foliar nitrogen and chlorophyll concentrations with standard methods (AOAC 1999).

The experiment was designed to relate oviposition to host plant management treatments, assuming that the latter produce variation in host plant parameters that are relevant for egg-laying behavior (Myers 1985; Hern et al. 1996; Hooks & Johnson 2001). To check this assumption, we also explored to what extent such variation was actually produced by treatments. Nutrient, water, and light treatment effects on plant height, diameter, above-ground fresh weight, leaf nitrogen concentration, and leaf chlorophyll concentration were analyzed with three-factor ANOVAs (Underwood 1997).

Because egg laying counts did not meet assumptions of normality due to numerous zero counts (Underwood 1997), statistical analysis was performed by logistical regression (Agresti 1996).

A step-wise multiple linear regression analysis was carried out between the number of eggs laid and the five parameters measured for each plant. A non-linear regression model was fitted between the number of eggs laid and that factor best explaining the egg-laying pattern observed in the linear model. Factors discarded in the linear model were proven to be non significant for the non-linear model as well. The non-linear regression model was fitted and selected with the program TableCurve™ 2D (AISN Software, Inc. 1994). The statistical software SPSS version 10.0.5 (1999) was used for the remaining analyses.

RESULTS

When a female *L. aripa* entered the host plant patches, on average 64% of behavioral acts were turning flights over the potential hosts, possibly for recognition and evaluating purposes. Landing on the host comprised 12% of behavioral acts. Egg laying was always preceded by a turning flight. Linear flights also were observed. The latter alternated with turning flights and landings. Sixty percent of linear flights were over lesser-quality hosts (e.g., non-fertilized plants). A typical search behavior in egg-laying *L. aripa* females is shown in Fig. 1, which shows that the butterfly flew over almost the entire group of plants and selectively laid eggs on up to four different highest-quality hosts.

The logistical regression model (maximum likelihood test: $\chi^2 = 14.001$, $df = 3$, $P = 0.003$) showed a greater probability of oviposition on fertilized plants (N2) than on non-fertilized plants

(N1) ($\chi^2_{\text{Wald}} = 4.163$, $df = 1$, $P = 0.041$). There was a marginally greater egg laying probability for plants which received more watering (W2) than on those which were watered less (W1) ($\chi^2_{\text{Wald}} = 3.212$, $df = 1$, $P = 0.073$). The probabilities of laying eggs on plants with a greater (L2) and lesser (L1) PAR availability were not different ($\chi^2_{\text{Wald}} = 0.965$, $df = 1$, $P = 0.326$) (Fig. 2).

None of the interactions among the three factors was significant: Nutrient \times Watering ($\chi^2_{\text{Wald}} = 0.288$, $df = 1$, $P = 0.591$). Nutrient \times PAR ($\chi^2_{\text{Wald}} = 0.039$, $df = 1$, $P = 0.843$). Watering \times PAR ($\chi^2_{\text{Wald}} = 0.088$, $df = 1$, $P = 0.767$). Nutrient \times Watering \times PAR ($\chi^2_{\text{Wald}} = 0.021$, $df = 1$, $P = 0.885$).

Nutrient, watering, and PAR caused significant variation in physical and chemical plant parameters evaluated in this study (Tables 2 and 3). Fertilized plants (N2) were taller, had a greater diameter, greater fresh weight, greater nitrogen concentration, and greater chlorophyll concentration than non-fertilized plants (N1). Plants receiving more water (W2) had a greater diameter and greater fresh weight, but similar height, nitrogen concentration, and chlorophyll concentration as compared to less watered plants (W1). Plants exposed to greater PAR availability (L2) were the shortest, had a smaller diameter, less fresh weight, greater nitrogen concentration, and similar chlorophyll concentration as compared to plants with less available PAR (L1). (Some of these effects of PAR reduction were possibly caused by better soil humidity conservation in shaded bags).

Significant Nutrient \times Watering interactions were found for plant weight and crown diameter. These plant parameters did not respond to nutrient addition at low watering levels, but responded strongly at high watering levels (Table 2). Significant Nutrient \times PAR interactions were found for nitrogen concentration.

The step-wise multiple linear regression analysis determined that fresh weight is the parameter that best explains variation in the number of eggs laid per plant ($R^2 = 0.61$, $df = 59$, $F = 90.731$, $P < 0.0005$). The other four attributes evaluated proved to be non-significant (diameter, $P = 0.248$; height, $P = 0.245$; chlorophyll, $P = 0.615$; nitrogen, $P = 0.779$). When fresh weight was not included in the analysis, the only parameter selected as significant was diameter ($R^2 = 0.39$, $df = 59$, $F = 36.782$, $P < 0.0005$). Again, the other three parameters were not significant (height, $P = 0.905$; chlorophyll, $P = 0.718$; nitrogen, $P = 0.743$).

A non-linear regression model was fitted between fresh weight and number of eggs per plant. The best among biologically reasonable models was a sigmoidal function. This function shows an abrupt increase in the response variable when the fresh weight of the plant exceeds a threshold, estimated for this study to be between 30 and 40 g (Fig. 3).

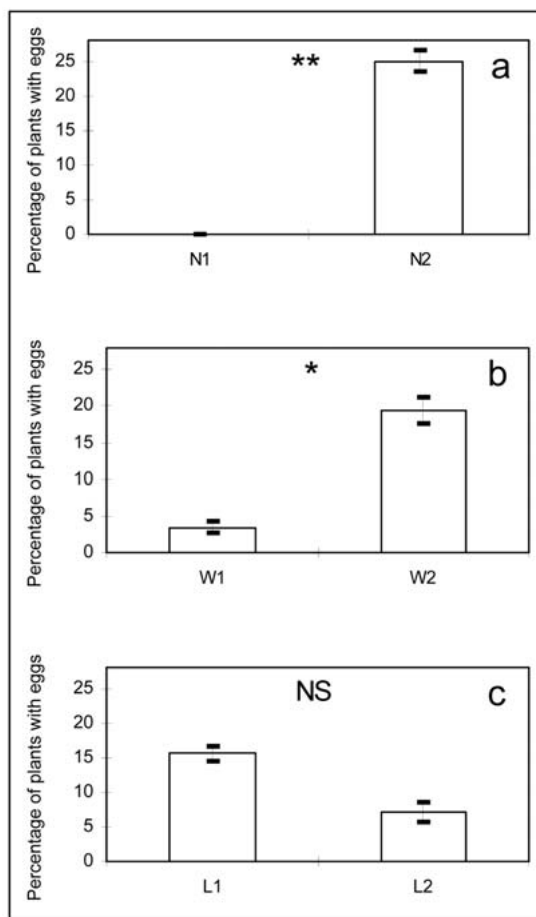


Fig. 2. Average percentage of cabbage plants on which *L. aripa* laid eggs (taken from 11 samples). a) N1: non fertilized plants, and N2: fertilized plants (** $P < 0.05$). b) W1: plants with less watering, and W2: plants with more watering (* $P < 0.1$). c) L1: plants with lesser PAR availability, and L2: plants with greater PAR availability. Error bars: ± 1 SE.

grew under conditions of greater soil humidity. In this study, host size, probably perceived as foliar crown diameter, was the plant parameter factor associated to host preference by *L. aripa*. Host size increased significantly when both nutrient addition and high watering levels were present. Other plant parameters commonly modified by management (Chen et al. 2004), such as volatiles that act as cues and/or stimulate oviposition, were not studied and cannot be ruled out.

No single host management factor or host parameter has explained selection by Pieridae, and the importance of different factors varies and remains controversial. One of the species most closely related to *L. aripa* is *Pieris rapae* (L.), whose egg laying behavior has been widely stud-

ied, but remains controversial. For instance, Root & Kareiva (1984) reported that *P. rapae* follows a random flight host search, and lays eggs without discriminating quality factors. Renwick & Radke (1983) found that *P. rapae* was not attracted by volatile host cues. They also found that host size and form were not important in egg laying behavior. Radcliffe & Chapman (1966) did not find a correlation between plant size and *P. rapae*'s egg laying preference. They concluded that color or chemical stimuli could be determining factors in host choice. In contrast, other authors have demonstrated that *P. rapae*'s flight and egg laying patterns are modified by factors such as plant size, phenology, species, humidity content, nutrients, leaf color and plant chemistry (Jones 1977; Latheef & Irwin 1979; Myers 1985; Andow et al. 1986; Jones et al. 1987; Hern et al. 1996; Hooks & Johnson 2001).

Another related species is *Pieris virginiensis* (Edwards). Flight and egg laying patterns of *P. virginiensis* are very similar to those of *P. rapae*. Their flight is markedly linear; they widely disperse their eggs, and leave behind apparently attractive hosts. Their egg laying behavior does not respond to host-plant size (Cappuccino & Kareiva 1985).

Egg laying behavior observed for *L. aripa*, unlike that reported for *P. rapae* and *P. virginiensis*, did respond to plant size. We found a sigmoidal relation, as would be expected with species that lay eggs in masses and confront host quality heterogeneity (Roitberg et al. 1999). Perhaps *L. aripa* perceived size through the host's foliar crown diameter, as this was the second most important plant parameter explaining host selection.

Host selection by *Leptophobia aripa* also could have occurred through other size-related physical and chemical characteristics not evaluated in this study. These signals could play an important role in other ecological interactions. For example, *Pieris napi* (L.) uses *Arabis gemmifera* (Mastum.) as a plant host. This plant species grows covered by neighboring vegetation, and for this reason is a host of inferior quality (in nutritional content and biomass), but it allows *P. napi* to avoid parasitism by the *Cotesia glomerata* (L.) wasp and the *Epicampocera succincta* (Meigen) fly (Ohsaki & Sato 1999).

Fertilization and watering treatments also could have modified the plant's chemical composition; in the case of members of Brassicaceae family, it could modify glucosinolate concentrations (Myers 1985; Mewis et al. 2002; Chen et al. 2004). These secondary metabolites are produced by the plants as a chemical defense (Renwick & Radke 1983; Lambdon et al. 2003; Müller et al. 2003). Specialized insects sometimes use these compounds as chemical cues, and even incorporate them into their body and use them to defend against predators and parasitoids (Messchendorp et al. 2000; Mewis et al. 2002). Several crucifer insects are known to have glucosinolate detoxification and sequestration mechanisms (Wadleigh &

TABLE 2. SUMMARY OF RESULTS FROM THREE-FACTOR ANOVAS TESTING THE EFFECTS OF NUTRIENT (N), WATER (W), AND PAR (L) ON PLANT HEIGHT, DIAMETER, ABOVE-GROUND FRESH WEIGHT, LEAF NITROGEN CONCENTRATION, AND LEAF CHLOROPHYLL CONCENTRATION. TEST OF SIGNIFICANT *P* VALUES < 0.05 ARE IN BOLD.

Source	<i>df</i>	Height		Diameter		Weight		Nitrogen		Chlorophyll	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
N	1	1.6	14.9	619.1	38.0	30.7	41.2	0.2	11.9	2.3	13.5
W	1	0.4	3.7	377.5	23.2	10.1	13.6	0.0	0.1	0.2	1.2
L	1	1.6	14.8	691.5	42.5	24.9	33.4	0.2	9.0	0.3	1.8
NXW	1	0.1	0.6	258.6	15.9	5.2	7.0	0.1	2.8	0.0	0.1
NXL	1	0.4	4.0	23.0	1.4	1.6	2.1	0.2	9.0	0.0	0.0
WXL	1	0.3	2.7	30.9	1.9	2.5	3.4	0.0	0.6	0.3	1.5
NXWXL	1	0.3	3.1	55.8	3.4	2.9	3.9	0.0	0.4	0.0	0.2
Error	52	0.1		16.3		0.7		0.0		0.2	

TABLE 3. MEAN (± 1 SE) OF PLANT HEIGHT, DIAMETER, ABOVE-GROUND FRESH WEIGHT, LEAF NITROGEN CONCENTRATION, AND LEAF CHLOROPHYLL CONCENTRATION FOR EACH FACTOR LEVEL.

Factor	Height	Diameter	Weight	Nitrogen	Chlorophyll
N1	7.9 (0.5)	12.3 (0.9)	8.0 (1.2)	4.0 (0.1)	0.5 (0.1)
N2	11.2 (0.7)	19.6 (1.3)	37.7 (5.5)	4.6 (0.2)	0.9 (0.1)
W1	8.7 (0.6)	13.3 (1.0)	12.5 (2.0)	4.3 (0.2)	0.7 (0.1)
W2	10.2 (0.7)	17.9 (1.4)	30.6 (5.6)	4.3 (0.1)	0.6 (0.1)
L1	10.7 (0.5)	18.9 (1.0)	28.2 (4.8)	4.1 (0.1)	0.8 (0.1)
L2	8.1 (0.7)	12.0 (1.3)	14.5 (3.9)	4.5 (0.2)	0.6 (0.1)

Yu 1988). Müller et al. (2003) did not find glucosinolate sequestration in *P. rapae* and *P. brassicae*; the case for *L. aripa* still needs to be studied.

Another manner in which *L. aripa* could be attracted to larger plants is that observed in *P. brassicae*. This species, like *L. aripa*, tends to lay eggs

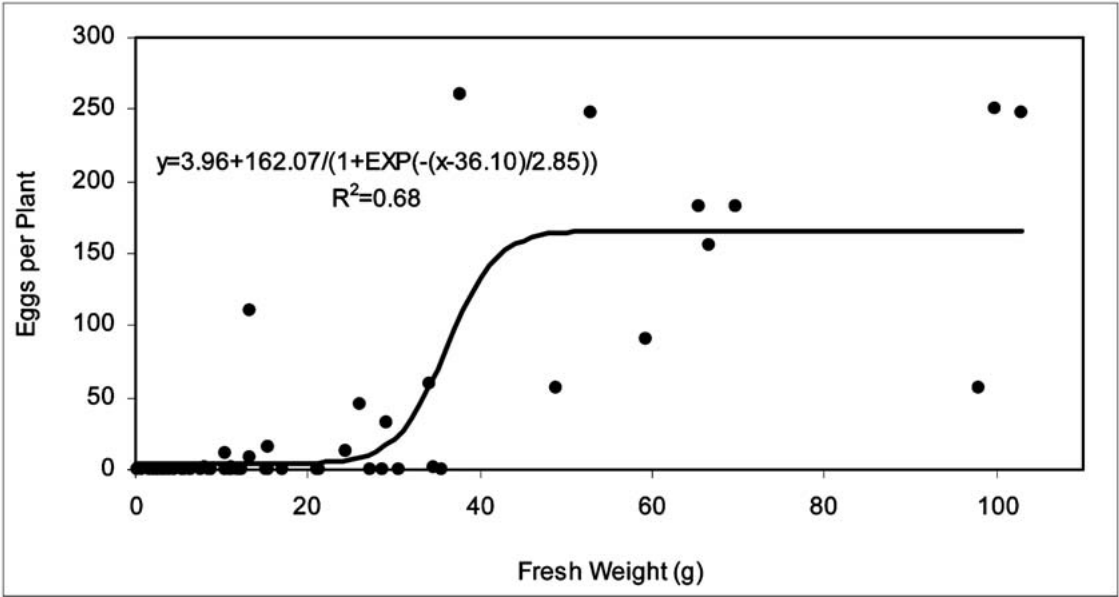


Fig. 3. Non-linear regression between fresh weight of cabbage plants and number of eggs laid by *L. aripa* per plant throughout 11 days of exposure. ($R^2 = 0.68$, $df = 59$, $F = 39.934$, $P < 0.001$).

in large masses when locating large-size hosts with abundant leaves (Stamp 1980; Le Masurier 1994). The aggregate lifestyle and conspicuous coloration of its larvae may provide a defense against predators and parasitoids (Stamp 1980; Le Masurier 1994).

In many cases, insect egg laying behavior results from balancing among factors which include minimizing parasitic and predatory risk, selecting the most nutritious host, avoiding intra-specific competition for food, and maximizing egg laying (Myers 1985; Ohsaki & Sato 1999). The insect internally weighs the various stimuli and inhibitors perceived through visual, chemical, and mechanical signals (Thompson & Pellmyr 1991; Hern et al. 1996).

Leptophobia aripa's searching and egg laying behavior observed in this study demonstrates its capacity to evaluate and discriminate among a group of hosts. Egg laying preference associated to host size has also been found for *P. brassicae* but not for *P. rapae*, *P. virginensis* and *P. napi*. This confirms that related species may have significantly different behavior (Jones 1977; Singer & Parmesan 1993; Reich & Downes 2003).

Leptophobia aripa is a pest for Brassicaceae crops in some regions of Mexico and Central America. Producers in the region have adopted fertilizers and pesticides rather recently (Santiago et al. in press). Agroecological alternatives to heavy agrochemical use are desirable. Our findings suggest that nutrient addition to well-watered plants significantly increases plant weight (as expected) and, beyond a plant weight threshold, it also increases oviposition. It is important to study to what extent increased oviposition affects larval survival and growth, and cabbage head damage. Other plant parameters such as production of cue volatiles need to be investigated and their relation with plant size established. It is also important to study tradeoffs between plant size, cabbage head value, and crop damage caused by *L. aripa*, as well as the capacity of alternative management strategies (e.g., intercropping and moderate organic fertilization) to improve tradeoffs.

ACKNOWLEDGMENTS

We thank Carlos V. Pérez Rodríguez and Juan Colazo López for technical support in the field, and Juan J. Morales López and Jesús Carmona de La Torre for chemical analysis. This study was supported by a grant from Fundación Produce Chiapas, A. C., and by a graduate scholarship from CONACYT to JASL. We also thank two anonymous reviewers for useful and constructive comments.

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