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INTERACCIONES TRÓFICAS ENTRE *Eretmocerus eremicus* (HYMENOPTERA: APHELINIDAE) Y *Trialeurodoes vaporariorum* (HEMIPTERA: ALEYRODIDAE) EN TOMATE Y PIMENTÓN[1]

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RESUMEN

La comprensión de las interacciones multitróficas entre parasitoides, plagas y plantas hospederas es importante para el desarrollo de alternativas de manejo agroecológico que potencien el restablecimiento de funciones ecosistémicas. En este estudio se realizaron experimentos de laboratorio para determinar la influencia del tomate (*Solanum esculentum*; cv. Moneymaker) y el pimiento dulce (*Capsicum annuum;* cv. Goldenwonder y Yolowonder) en la aptitud y parasitoidismo del *Eretmocerus eremicus* atacando a *Trialeurodes vaporariorum*. El tamaño del parasitoide, medido por la longitud de la tibia posterior, se correlacionó con el tamaño de las pupas del huésped como un indicador de aptitud. No se observó efecto significativo por cultivar en la longevidad de los parasitoides emergidos, en la tasa de emergencia y en la mortalidad de la etapa de inmaduros. Sin embargo, las plantas hospederas influyeron en el tiempo de desarrollo (días) y la proporción de sexos de los parasitoides. La tasa de crecimiento de la población del parasitoide era mayor que la de *T*. *vaporariorum*. La mosca blanca de los invernaderos *T*. *vaporariorum* se observó alimentándose del tomate cv. Moneymaker y el pimiento dulce cv. Goldenwonder, fue un hospedero igualmente adecuado para especímenes de *Er*. *eremicus*, lo que convierte a este parasitoide, en un agente de control biológico con potencial en un sistema de cultivo de tomate/pimiento dulce.

Palabras clave: Aptitud demográfica, Interacciones tritróficas, control biológico.

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TROPHIC INTERACTIONS BETWEEN *Eretmocerus eremicus* (HYMENOPTERA: APHELINIDAE) AND *Trialeurodoes vaporariorum* (HEMIPTERA: ALEYRODIDAE) GROWING ON TOMATO AND GREENPEPPER PLANTS

ABSTRACT

Understanding multitrophic interactions between parasitoids, pests, and host plants is important for the development of agro-ecological management alternatives that enhance the restoration of ecosystem functions. Laboratory experiments were conducted to determine the influence of tomato (*Solanum lycopersicum*; cv. Moneymaker) and sweet pepper (*Capsicum annuum*; cv. Goldenwonder and cv. Yolowonder) on the fitness and parasitisation of the *Eretmocerus eremicus* attacking *Trialeurodes vaporariorum*. Parasitoid size, as measured by hind tibia length, was correlated with host pupae size as a fitness indicator. No significant cultivar effect was observed on the longevity of the emerged parasitoids, on the rate of emergence and on immature mortality. However, the host plants did influence development time (days) and sex ratio of the parasitoids. The population growth rate of the parasitoids was observed to be higher than that of *T. vaporariorum*. *T. vaporariorum,* feeding on the tomato cv. Moneymaker and the sweet pepper cv. Goldenwonder, was an equally suitable host for *Er. eremicus* specimens, which makes this parasitoid a promising biocontrol agent in a tomato/sweet pepper mix-cultivation system.

Key words: Demographic fitness, tritrophic interactions, biological control.

INTRODUCTION

The greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) is one of the most important vegetable pests (Perring et al., 1993; Byrne et al.,1990; Gonzalez and Santamaria, 2015). *This insect pest* is native to America, particularly the United States (USA) and northwestern Mexico. It is distributed in tropical and semi-tropical regions of the world (Myartseva et al., 2010), where it is parasitized by diverse natural enemies (García-Guerrero et al., 2018); adults and immature are phloem feeders and can contribute to reduce productivity by directly consuming transportable carbohydrates, nitrogen and other nutrients. Moreover, they produce large amounts of honeydew on the leaf, on which sooty moulds occasionally develop with a resultant reduction in leaf photosynthesis (Byrne et al., 1990; Gonzalez and Santamaria, 2015).

The parasitoid *Eretmocerus eremicus* has shown its potential as a biological control agent of the greenhouse whitefly (De Barro et al., 2000), and it is recommended for use by commercial companies (*e.g.* Koppert Biosystems, Bioplanet, Biobest). Furthermore, Greenberg et al. (2002), indicate that *Er. Eremicus* (Hymenoptera: Aphelinidae) is very efficient in attacking the two important whitefly pest species: *T. vaporariorum* and *Bemisia tabaci*. Similarly, Aliaga (2013) reported from Perú *Er. eremicus attacking Trialeurodes variabilis* feeding on yuca plants (*Manihot esculenta* L.). In Panama *Eretmocerus* had been reported by Rusell (1962), Carreiro (1994) and Ferguson (1994). More recently, Bernal (2001) reported *Eretmocerus* as the most abundant species for tomato under field condition in Azuero. Gonzalez et al. (2009), reported this parasitoid feeding on *Bemisia* and *Trialeudores vaporariorum* at Los Santos, Capira and Boquete districts in Panama. Eggs are deposited underneath whitefly nymphs at the leaf surface, and 1st instars penetrate the underside of the host upon eclosion. Parasitoid larvae completely consume the contents of the host before pupation (Gerling et al., 1990; Foltyn and Gerling,1985).

Eretmocerus have developed a special type of ectoparasitism. They oviposit under the host and their eggs are protected between the leaf and the host. Thereafter, they enter the host but induce it to form a capsule that allows them to remain functionally external to both the host's blood cells and to cellular defence mechanisms. The capsule remains intact during the first and much of the second larval instars. During that time, the whitefly nymph disintegrates with just a few tissues remaining. When the capsule breaks up, and the parasitoid larva becomes fully exposed to the host's body fluids, these are scarcely able to invoke effective defensive mechanisms. Thus, by ovipositing under a young host instar, *Eretmocerus* avoids the disadvantages of ectoparasitism by ovipositing under the host and developing within it, and of endoparasitism by living within a capsule that protects it from host defences (Gerling, 1966).

The effective implementation of biological agents for whitefly management relies on the feasibility of augmenting parasitoids in a whitefly-affected crop. Efficient mass rearing and release of parasitoids is dependent on our knowledge of the nature of agroecosystems and the principles by which they work (León and Altieri, 2010). One very important aspect of this is the deep understanding the plant-herbivore-parasitoid interaction. The study of the parameters of life of parasitoids is also important because of the possibility of combining more than one of these natural enemies in the biological control strategy of the same insect pest (Qiu et al., 2005).This is a research topic that has received a lot of attention in the past, yet research with respect to the strategies (*e.g.* host selection) used by different parasitoids with different life histories and studies on the effect of the integration of agroecological practices on the performance of the production system are growing rapidly (Vásquez and Fernández, 2008; Altieri and Nicholls, 2007).

Large hosts are supposed to be of better quality, as they are believed to contain more resources than small ones (Charnov, 1982). However, host size may not always be indicative of host quality at the time of parasitisation. The influence of host size on parasitoid development may differ between idiobont and koinoboiont parasitoids. According to Waage's (1982) hypothesis: "size dependent sex ratios are to be anticipated in idiobiont parasitoids which oviposit in non-growing stages (*e.g.* eggs and pupa) or which paralyse their hosts prior to oviposition (many larval parasitoids), but not in koinobiont parasitoids which oviposit and develop in growing host stages (egg-larval or larval parasitoids) for which host size is not a good predictor of larval resources". However, King (1989) stated that Waage's hypothesis is not true for all koinobionts.

Since the effective implementation of biological agents for whitefly management relies on the feasibility of augmenting parasitoids in a whitefly-affected crop trough understanding the plant-herbivore-parasitoid interaction, the present study focuses on the effect of host quality of *T. vaporariorum* feeding on sweet pepper (poor quality host plant) or tomato (intermediate quality host plant). This is a common mix cropping system at horticultural farms in the highlands of the Chiriquí province.

MATERIALS AND METHODS

Whitefly and parasitoid species

Adult whiteflies, *Trialeurodes vaporariorum* were reared in a wooden cage (50cm×50cm×56cm) on tomato plants (*Solanum lycopersicum* L. cv. Moneymaker). From this rearing, adult whitefly (20 females:20 males) from zero to seven days old were transferred and confined to the undersides of leaves of the host plants cultivars (sweet pepper *Capsicum annuum* cv. Goldenwonder and cv. Yolowonder; and tomato cv. Moneymaker) using clip cages of 2,5 cm diameter and were allowed to ovoposit for 24 h.

After these time all the whiteflies were removed with an aspirator and the host plants were transferred and maintained at the laboratory of Entomology (IDIAP, Chiriquí), in a climatic chamber at 22 ± 1° C and 50% RH with a 12:12 h light:dark photoperiod until the nymphs had developed in to the 2^{nd} instar.

Parasitoid pupae *Er. eremicus* used in this experiment were obtained from Koppert Biological Systems BV, through its distributor Agrobio NCS based in Costa Rica. Cardboards of parasitoids pupae were located in petri dishes to allow emergence of both females and males. Newly emerged adult females were allowed to mate individually with an individual male inside a gel capsule (20 mm long x 7 mm diameter).

Effect of sweet pepper and tomato on the quality of whitefly and its parasitoid Er. eremicus

Three plants of each cultivar were infested with whitefly as described above. About 35 second instars whitefly nymphs were offered to the parasitoid and superfluous whiteflies nymphs were removed. Subsequently, one mated female parasitoid (1 d old) was released and confined with the nymphs in a large (3,5 cm diameter) clip cage at 22° C. After 24 h, the parasitoid females were removed. Ten percent of the total nymphs offered were dissected and checked for parasitoid eggs. All of the remaining nymphs were allowed to complete their development. When the parasitized nymphs had changed colour from light to dark, they were counted daily until emergence. This allowed the number of successfully parasitized hosts to be determined. The percentage of parasitized nymphs was calculated from the total number of nymphs used per female. The percentage of emerged parasitoids was calculated only from hosts that could be identified as parasitized. After emergence, the puparia from parasitized and non-parasitized individuals that had developed on each plant cultivar were measured. Longevity of each emerged adult parasitoidwas measured by daily checking the vials in which adult parasitoids were held as unfed individuals. Upon death, parasitoid adults were frozen for posterior measurement of the hind tibia length.

Statistical tests: Differences were tested for significance with ANOVA, Mann-Whitney U test or the Chi Square test, all at the 5%-probability level.

A one-factor analysis of variance (ANOVA) was used to examine the effect of plant species on the total immature development time, and longevity of males and females of *Er. eremicus*. When the ANOVA result indicated a significant difference, the means were compared with the Least test (LSD; α = 0,05).

Calculation of demographic parameters: The net reproduction rate (Ro), the average generation time (T), the intrinsic rate of natural growth (r_m) were calculated using the two equations of Andrewarta and Birch (1954) where r_m 1 = (In Ro1) / T1 and r_m2 = (In Ro2) / T2 The survival of each stage was calculated using the following formula:

Equal stage survival = N° individuals enter stage (i + 1) / N° individuals enter stage i) × 100

RESULTS AND DISCUSSION

Effect of sweet pepper and tomato on the quality of whitefly and its parasitoid

The development time of immature male parasitoids varied significantly for the tested cultivars. Males from the sweet pepper cv. Goldenwonder had the longest development time. The pooled male and female development period of different cultivars were 22,09 d; 22,64 d and 23,82 d for sweet pepper cv. Goldenwonder, tomato cv. Moneymaker and sweet pepper cv. Yolowonder, respectively, and the differences between cultivars were significant (P<0,05; Table 1). Wasps emerging from hosts feeding upon the sweet pepper cv. Yolowonder took more than one day longer to complete development than wasps emerging from hosts on the sweet pepper cv. Goldenwonder and tomato cv. Moneymaker.

Table 1. Immature development time in days of *Eretmocerus eremicus* on *Trialeurodes vaporariorum* and on three different cultivars at 22° C.

Host plant	Mean ± se [1/]	*n*	*CV* (%)	Min – Max
Tomato – cv. Moneymaker	22,64 ± 0,06**a**	497	0,26	17 – 28
Sweet pepper – cv. Goldenwonder	22,09 ± 0,27**b**	59	1,21	19 – 28
Sweet pepper – cv. Yolowonder	23,82 ± 0,23**c**	69	0,94	21 – 30

[1/] Different letters in a column indicate significant differences; ANOVA with LSD (P<0,05).

The longevity of unfed female *Er. Eremicus* was not influenced (P<0,001) by the host plant on which *T. vaporariorum* had developed (Table 2). Few parasitoid females emerged from whiteflies on the sweet pepper cultivars and so the data might not be representative, nevertheless, as reported by Vet et al. (1980), data of intrinsic rate of increase for *Er. eremicus* feeding on *T. vaporariorum* on sweet pepper are extremely varied.

The longevity of unfed males differed significantly between the three cultivars (Table 2), being longest on the sweet pepper cv. Goldenwonder and shortest on the sweet pepper cv. Yolowonder.

Table 2. Mean of males and female's longevity (days) of unfed *Eretmocerus eremicus* emerging on *Trialeurodes vaporariorum* feeding on three different cultivars.

Host plants	Mean ± s.e[1/]	*n*	CV (%)	Min - Max
	Females			
Tomato – cv. Moneymaker	2,12 ± 0,05 **a**	129	2,36	0 - 3
Sweet pepper– cv. Goldenwonder	2,43 ± 0,29 **a**	7	11,9	1 - 3
Sweet pepper– cv. Yolowonder	2,09 ± 0,21 **a**	11	10,5	1 - 3
	Males			
Tomato – cv. Moneymaker	1,72 ± 0,04 **a**	212	2,3	1 - 3
Sweet pepper– cv. Goldenwonder	2,15 ± 0,15 **b**	33	6,9	1 - 4
Sweet pepper– cv. Yolowonder	1,47 ± 0,21 **c**	37	14,3	1 - 3

[1/] Within each row (host's food plant) different letters in a column indicate significant differences. ANOVA with LSD (P<0,05).

Basic life history parameters and demographic parameters of *Er. eremicus* are shown in Tables 3 and 4. *Trialeurodes vaporariorum*was an equally suitable host for *Er. eremicus* specimens feeding on the tomato cv. Moneymaker and the sweet pepper cv. Goldenwonder as host plant. *Eretmocerus eremicus* developed faster, had a lower immature mortality, and a greater longevity on whiteflies on the sweet pepper cv. Goldenwonder than on the sweet pepper cv. Yolowonder. The sex ratio was significantly different for both sweet pepper cultivars species (χ^2 =0,84; P=0,66).

Table 3. Life history parameters of *Eretmocerus eremicus* developing on different host plants.

	Tomato cv. Moneymaker	Sweet pepper cv. Yolowonder	Sweet pepper cv. Goldenwonder
Parameter	**Mean**	**Mean**	**Mean**
% Emergence rate	81,3 **a**	77,8 **a**	71,9 **a**
% Immature mortality	18,6 **a**	22,1 **a**	19,6 **a**
Sex ratio (males: females)	0,41 **a**	0,3 **b**	0,3 **b**

Within each column (host's food plant) different letters in a column indicate significant differences (P<0,5).

The χ^2 analysis of percentage of emergence in this experiment revealed non-significant differences (P=0,66) for the host plants studied.

Table 4. Demographic parameters of *Eretmocerus eremicus* on tomato and sweet pepper as host's food plants.

Parameter	**Tomato cv. Moneymaker**	**Sweet pepper cv. Yolowonder**	***Sweet peppe*** **cv. Goldenwon**
Ro = net reproduction	43,82	43,13	36,55
T = generation time	27,64	27,09	28,82
r_m = intrinsic rate of increase	0,142	0,133	0,130

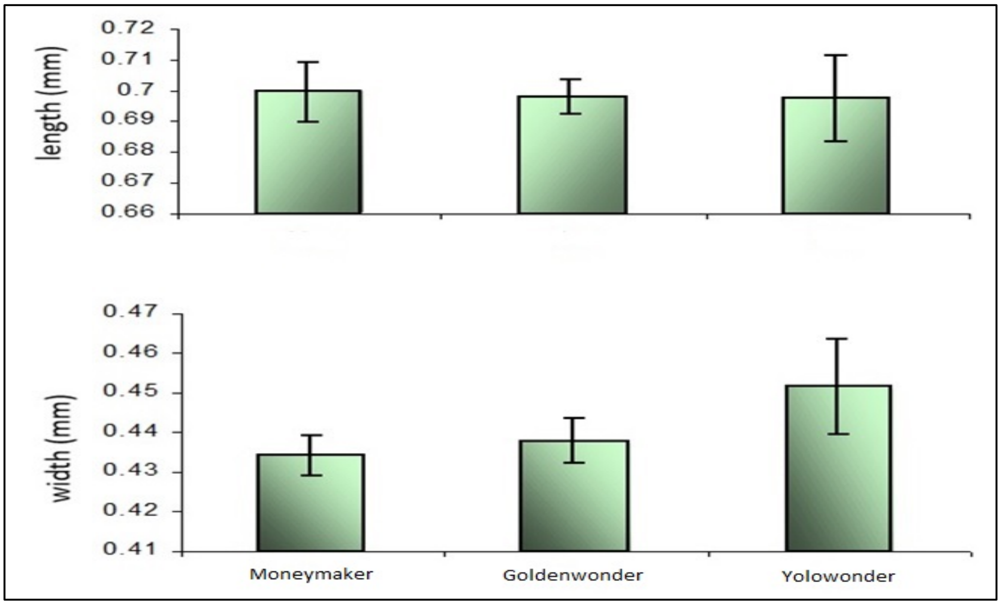

Figure 1. Width and length of the puparium after parasitoid adult emergence per each cultivar (Moneymaker; Goldenwonder, Yolowonder).

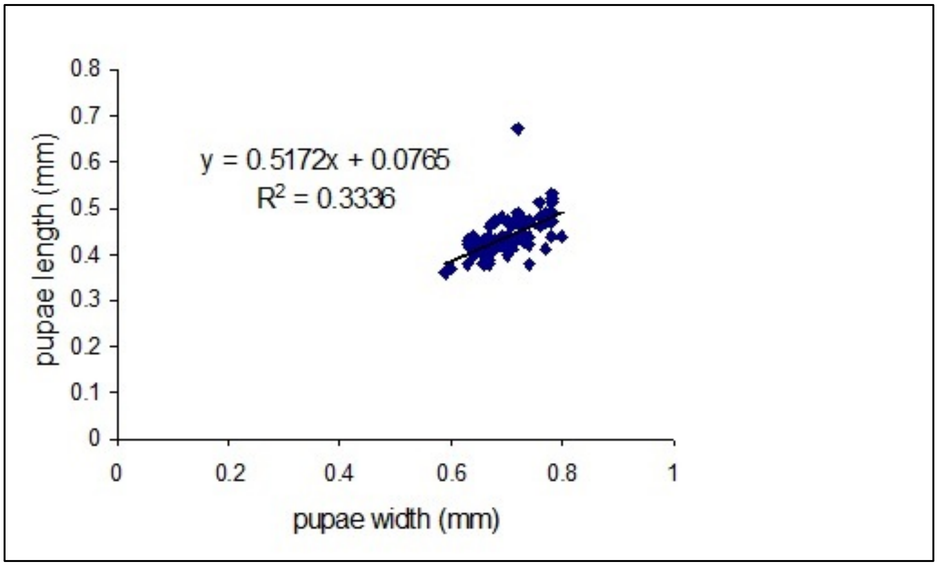

Figure 2. Effect of *Eretmocerus eremicus* tibia length on puparium length: width ratio measured after emergence.

A positive correlation was observed between length and width size (Figures 2). The data of hind tibia length for parasitoids that developed in hosts on the three types of host plant investigated is given in Table 5. No significant host-plant effect was observed on the tibia length of adult parasitoids studied under laboratory conditions.

Table 5. Effect of host's food plant on the tibia length of *Eretmocerus eremicus.*

Host plant	Mean ± se[1/](mm)	N	CV(%)	Min	Max	Range
Tomato- cv Moneymaker	0,241 ±0,002 **a**	70	0,97	0,20	0,28	0,08
Sweet pepper– cv.Goldenwonder	0,245 ± 0,003 **a**	36	1,25	0,20	0,27	0,07
Sweet pepper– cv.Yolowonder	0,247 ± 0,003 **a**	19	1,19	0,23	0,26	0,03

[1/] Within each row different letters indicate significant differences. ANOVA with LSD (P>0,05).

The current study on tritrophic-interactions established that sweet pepper as the host plant slightly affected some of the life history parameters of the parasitoid *Er. eremicus,* but the host plant did not influence the population development of the parasitoid, as well as the size of the hind tibia of the parasitoids emerging from *T. vaporariorum.* These results agree with the conclusions reported by other authors (van Lenteren and Noldus, 1990; Thomas, 1993; Shah and Liu, 2013) about host quality of the sweet pepper upon *T. vaporariorum.*

Eretmocerus eremicus developing in the larval stages of *T. vaporariorum* feedingon sweet pepper, performed least well on the cultivar Yolowonder. However, performance of *Er. eremicus* on the sweet pepper cultivar Goldenwonder was much better than that on tomato. Within the genus *Eretmocerus*, differences in performance of parasitoids have previously been reported by Powell and Bellows (1992) and De Barro et al. (2000), working with *Bemisia* as host. The first authors compared development of parasitoids on cotton (*Gossypium hirsutum*) and cucumber (*Cucumis sativus*), and, De Barro et al. (2000), reported a host plant effect on *Eretmocerus* spp., with a suitability gradient from most suitable to least suitable as follows: cotton, hibiscus (*Hibiscus* sp.), rockmelon (*Cucumismelo*), soybean (*Glycine max*), and tomato.

Plant effects on another aphelinid group have been reported by Heinz and Parrella (1994). These authors reported differences in host feeding, parasitism, and total number of nymphs killed among four parasitoid species (*Encarsia Formosa* Gahan, *En. luteola* Howard, *En. pergandiella* Howard, and *En. transvena* Timberlake), and on two different poinsettia cultivars (*Poinsettia pulcherrima*). Greenberg et al. (2002), investigated the effect of different tomato cultivars on two *Eretmocerus* species, *Er. eremicus* and *Er. mundus*, and reported no significant differences for these characteristics. Interestingly, they observedsize differences for *Eretmocerus* species when reared on *T. vaporariorum* and *B. tabaci*. Both, *Er. eremicus* and *Er. mundus*, were larger when they had developed on *T. vaporariorum* than on *B. tabaci*. Regarding other groups of biological control agents, our findings agree with those of van Huis and de Rooy (1998) who studied the effect of leguminous plant species on *Callosobruchus maculatus* and its egg parasitoid *Uscana lariophaga*. They observed higher mortality and longer development in the eggs of *C. maculatus* on the legume that was less favourable for the development of *C. maculatus*. While Orr and Boethel (1986), reported that plant antibiosis can influence the biology over four trophic levels.

When looking at the fitness parameters, this study demonstrated that *T. vaporariorum* nymph size did not vary when this whitefly feeds on the evaluated sweet pepper or tomato and agree with the results reported by Greenberg et al. (2002). This might be the reason why there was no influence on the parasitoids hind tibia length, and why *T. vaporariorum* was an equally suitable host for *Er. eremicus* specimens feeding on the tomato cv. Moneymaker and the sweet pepper cv. Goldenwonder as host plant.

Positive significant correlation between tibia length and puparium ratio agree with those studies on which size alone was a significant longevity predictor (Hooker et al., 1987) in the eulophid studied parasite. Sagarra et al. (2001), observed in laboratory conditions that parasitoid size, as measured by left hind tibia length, was positively correlated with several indicators of the parasitoid fitness (longevity, mating preference, fecundity, reproductive longevity, progeny emergence, and sex-ratio).

Regarding to the longevity of the adults, our results were similar to those reported by Hanan et al. (2010), who observed a life span of 2,5~5,5 days without food source. Data from the present study showed that unfed females lived longer (2,02~2,43 days) than unfed males (1,47~2,15 days). This can be interpreted as an adaptation to ensure that the parasitoids live for longer if hosts are unavailable, so that they have more time to search for their hosts and therefore a greater chance of producing progeny.

On the other hand, strong female sex bias in the parasitoid offspring from sweet pepper cultivars was reported on this study. This agrees with Islam and Copland (1997) report on that the proportion of male parasitoids decreased with the increasing host size and showed significant linearity. Biological data indicate maternal manipulation of the offspring sex ratio of parasitoid wasps in response to host size. From this it can be predicted that a greater proportion of females will be laid in large hosts (King, 1989). However, the extremely high mortality experienced by the host on sweet pepper plant might mask the offspring sex ratio. Experimental studies have shown that, for hymenopteran parasitoids, host size at oviposition is often a reliable indicator of host suitability for parasitoid development (Visser, 1994; Sagarra, 2001). Large hosts contain more resources for parasitoid development than small hosts; and therefore in terms of parasitoid fitness are assumed to be qualitatively superior (Waage's host size dependent theory). However, King

(1989) suggests that in koinoinbiont species with wide host-species size ranges, there will not be a selection pressure for females to manipulate offspring sex ratio in response to host size unless females can discriminate between host species or host species do not overlap in the size of susceptible instars.

Published data of intrinsic rate of increase for *Er. eremicus* feeding on *T. vaporariorum* on tomato and sweet pepper are extremely varied (Vet et al., 1980). Values reported here are comparable within the range reported by Koopert (2002) working at 25° C on *Er. mundus* and *B. tabaci* as host, who reported a r_m of 0,192 for tomato and 0,198 for sweet pepper, with survival rates of 73% and 64%, respectively. In our study we observed smaller values for the r_m (0,142) for tomato and [0,131 (cv. Yolowonder) - 0.131(cv. Goldenwonder)] sweet pepper with survival rates of 81,3% for tomato cv. Moneymaker, and 77,8% for sweet pepper cv. Yolowonder and 71,9% for sweet pepper cv. Goldenwonder.

Despite the difference reported in life history parameters, the intrinsic rate of increase observed for *Er. eremicus* developing in nymphs of *T. vaporariorum* feeding on tomato and sweet pepper was still greater than that of their host (Gonzalez et al., 2018). Good control of whitefly on sweet pepper may be possible because this is an extremely poor host plant for whitefly (both larvae and adult) but conditions for the parasite are rather good as the leaves are smooth and the wasp is hardly hampered by obstacles(van Lenteren et al.,1977). Although with smooth leaves, the margin of the nymph fits well with the leaf surface making it more difficult for the wasps to oviposit under the nymph (Headrick et al., 1996; De Barro et al., 2000; Cetintas and McAuslane, 2009). This information would be useful for development rearing strategies of whitefly parasitoids, and biological control of the species of whiteflies using *Eretmocerus*.

As a starting point for understanding how parasitoids respond as larvae to host quality constrains in a tomato sweet pepper mix cropping system, the results obtained in this study indicate that biological control of *T. vaporariorum* on tomato and sweet pepper might be possible under protected cultivation. In addition, these findings will aid scientific understanding of tritrophic interactions in nature and agricultural field systems under the scope of agroecological reconversion of conventional production systems based on the habitat diversification andagroecological pillar. The optimal function of agroecosystems depends on the spatial-temporal designs that promote synergies between above and below ground key biodiversity components, which in turn determine the expression of ecological processes such as pest regulation, nutrient cycling and productivity.

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