BioControl
DOI 10.1007/s10526-014-9625-4

Biology and life history of *Tamarixia triozae*, a parasitoid of the potato psyllid *Bactericera cockerelli*

Patricia Rojas · Esteban Rodríguez-Leyva · J. Refugio Lomeli-Flores · Tong-Xian Liu

Received: 8 February 2014 / Accepted: 23 September 2014

Abstract *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) is an important parasitoid of the potato psyllid, *Bactericera cockerelli* Sulc (Hemiptera: Triozidae). We quantified the biology and life table parameters of *T. triozae* parasitizing *B. cockerelli* nymphs under laboratory conditions (26 ± 2 °C, 60 ± 10 % RH and 14:10 [L:D] h). Parasitoid developmental times were 1.5, 3.5, 5.7 days for eggs, larvae and pupae respectively, with an average of 12.0 days from egg to adult emergence. Female pupae took 0.4 day longer to develop than male pupae. Adult females lived 19.9 ± 4.5 days and had a 1.9 ± 0.8 days preoviposition period. Each female laid an average of 165.4 ± 45.2 eggs during her lifetime. The net reproductive rate (R_0), generation time (T), intrinsic rate of increase (r_m), doubling time (DT) and the finite rate of increase (λ) were 130.9, 18.72, 0.26, 2.7, and 1.3 respectively. The potential for the use of *T. triozae* as a biological control agent of *B. cockerelli* is discussed.

Keywords *Bactericera cockerelli* · Biological control · Eulophidae · Native natural enemy

Handling Editor: Dirk Babendreier.

P. Rojas · E. Rodríguez-Leyva (✉) ·
J. Refugio Lomeli-Flores
Posgrado en Fitosanidad, Entomología y Acarología, Colegio de Postgraduados, Carretera Mexico-Texcoco Km. 36.5, Montecillo, 56230 Texcoco, Estado de Mexico, Mexico
e-mail: esteban@colpos.mx

T.-X. Liu
Key Laboratory of Applied Entomology, Northwest A&F University, Yangling 712100, Shaanxi, China

Introduction

The potato psyllid, *Bactericera cockerelli* Sulc (Hemiptera: Triozidae), is thought to have originated in North America and was first described from specimens collected in Colorado, USA (Sulc 1909). During the 1930s and 1940s it was reported sporadically as a pest in Utah, Idaho, Colorado, Wyoming and also in some locations in Mexico (Richards 1928; Pletsch 1947). Currently *B. cockerelli* remains only an occasional pest in protected and field crops in Canada (Ferguson and Shipp 2002; King 2014), but is considered one of the most noxious pests of tomatoes (*Solanum lycopersicum* L.) and potatoes (*Solanum tuberosum* L.) in many states in the USA (Liu and Trumble 2004, 2006, 2007; Munyaneza et al. 2007, 2008; Hansen et al. 2008; Butler and Trumble 2011, 2012), North and Central Mexico (Pletsch 1947; Leyva-López et al. 2002; Munyaneza et al. 2007; Garzón-Tiznado et al. 2009; Butler and Trumble 2012), and most recently as an invasive pest species in New Zealand (Teulon et al. 2009).

Bactericera cockerelli causes damage directly during feeding: the saliva of nymphs is toxic to the

Published online: 01 October 2014

host plant and the honeydew excreted encourages the growth of sooty mould. However, the greatest economic damage occurs because *B. cockerelli* is a vector of zebra chip disease (ZC), a devastating disease of potatoes in Texas and the northern states of Mexico (Munyaneza et al. 2007, 2008). ZC is associated with a bacterium, *Candidatus Liberibacter psyllaurous* (also known as *Ca. L. solanacearum*) (Hansen et al. 2008; Liefting et al. 2008; Lin et al. 2008; Crosslin and Munyaneza 2009). The role of this insect as a vector of ZC is well known on tomato, potato and pepper (*Capsicum annuum* L.) (Leyva-López et al. 2002; Munyaneza et al. 2007; Hansen et al. 2008; Liefting et al. 2008; Gao et al. 2009; Garzón-Tiznado et al. 2009; Camacho-Tapia et al. 2011).

Management of *B. cockerelli* is challenging due to its high reproductive rate and cryptic location on the abaxial leaf surface (Yang and Liu 2009; Butler and Trumble 2012). Growers rely on the application of insecticides as the primary *B. cockerelli* control strategy on potato and tomato (Yang et al. 2010). However, intensive use of broad-spectrum insecticides is often costly and known to destroy natural enemy populations, leading to insecticide resistance and environmental contamination, and resulting in secondary pest outbreaks (Doutt and Smith 1971; Pimentel 2005). Extensive use of synthetic insecticides on food crops is of great concern to the general public, policy makers and agricultural communities alike (van Driesche and Bellows 1996). For this reason, the development of integrated pest management (IPM) programmes, that include the use of natural enemies, are encouraged for control of *B. cockerelli*. The use of entomopathogenic fungi against *B. cockerelli* is under development and may have some potential (Sanchez-Peña et al. 2007; Lacey et al. 2009, 2011; Butler and Trumble 2012). Two primary parasitoids of *B. cockerelli* nymphs have also been reported: *Methaphycus psyllidus* Compere (Encyrtidae) and *Tamarixia triozae* (Burks) (Eulophidae) (Compere 1943; Pletsch 1947; Jensen 1957). *Tamarixia triozae* has been collected from field and greenhouse populations of *B. cockerelli* nymphs in Mexico and USA (Pletsch 1947; Jensen 1957; Johnson 1971; Lomeli-Flores and Bueno 2002; Tong-Xian Liu personal observation) and is recorded as the most important parasitoid of *B. cockerelli* in Guanajuato, Mexico (Lomeli-Flores and Bueno 2002) and Oaxaca, Mexico. In Oaxaca high levels of parasitism (70–80 %) were found in fields where insecticides had not been used extensively (Bravo and López 2007).

Some preliminary observations of the biology of *T. triozae* have been made on different host plants and indicate that *T. triozae* is a primary solitary ectoparasitoid with a life cycle lasting approximately 14 days (Pletsch 1947; Johnson 1971). However, to better estimate the potential of *T. triozae* as a biological control agent of *B. cockerelli*, more detailed studies on biology and population parameters (life tables) are required, and this was the aim of this study.

Materials and methods

Insect and plant cultures

In October 2008 approximately 150 *T. triozae*-like adult parasitoids were collected from Salvatierra, Guanajuato State, Mexico (20°12′49″ LN, 100°52′49″ LO) and a further 200 from Texcoco, Mexico State, Mexico (19°29′49″ LN, 98°53′49″ LO). A subsample from each collection were identified as *T. triozae* by J. R. Lomeli-Flores and voucher specimens were deposited in the Biological Control Collection, Colegio de Postgraduados. The parasitoids were pooled and maintained for several generations on fourth or early fifth instar *B. cockerelli* nymphs that had been reared on tomato plants (*Solanum lycopersicum* L.) in mesh cages (60 × 80 × 60 cm), under greenhouse conditions, at the Colegio de Postgraduados in Texcoco, Mexico State.

In February 2009, 200 specimens from this initial colony were sent to the Vegetable IPM Laboratory at Texas AgriLife Research & Extension Center, Weslaco, Texas, USA where their life history attributes were determined experimentally. *Tamarixia triozae* were maintained on *B. cockerelli* nymphs on tomato plants (var. "Florida Lanai") in rearing chambers at 26 ± 1 °C, 60 ± 10 % RH and a 14:10 (L:D) h photoperiod. Experimental evaluations of life history attributes were made under the same abiotic conditions. Tomato plants were grown in plastic pots (15 cm in diameter) on Metro-Mix growing substrate (Grace Sierra, Horticultural, Milpitas, CA, USA), and fertilized after transplanting with 2 g of 12:8:6 (N:P:K) fertilizer every other day prior to use.

Longevity of *T. triozae* adults

Longevity of male and female *T. triozae* adults that were either provided with a source of carbohydrate or

excluded from a carbohydrate source was determined. Forty female and 40 male parasitoids were collected from the main colony eighteen hours after emergence, and caged individually in plastic vials (2.2 cm in diameter and 5.4 cm long). Half the individuals of each sex were provided with small drops of diluted honey (94 %) every 48 h (treatment with carbohydrate). The remaining individuals received no honey (treatment without carbohydrate). All individuals were provided with water every 12 h on the cotton wool plug that sealed each plastic vial. The cotton wool plug was replaced every three days to prevent the growth of mould and the mortality of *T. triozae* individuals was recorded daily.

Life cycle

Early fifth instar *B. cockerelli* nymphs (n = 75) were transferred, using a fine camel-hair brush, to each of five expanded tomato leaves (n = 375 *B. cockerelli* nymphs in total), the petioles of which were inserted into plastic vials of tap water within a 1 l plastic cup that served as a parasitoid oviposition cage. The cup was maintained in the vertical position and sealed at the top (4 cm in diameter) with an organdy screen. Twenty five *T. triozae* females from the colony were introduced into the oviposition cage and allowed to oviposit for 3 h (9h00 to 12h00). After this time the parasitoids were removed and each psyllid nymph was observed under a stereomicroscope for the presence of parasitoid eggs (Olympus SZ30). Nymphs with a single parasitoid egg were selected but, to ensure sufficient replication, nymphs with more than one parasitoid egg were also selected and the excess eggs removed to leave one egg per nymph. Two parasitized nymphs were transferred to each leaflet of new tomato leaves (3–5 leaflets per leaf = 6–10 nymphs per leaf), the petioles of which were placed in water-saturated cotton wool wrapped in aluminum foil to maintain turgidity. Each tomato leaf was incubated in a Petri dish (14 cm in diameter) with a 4 cm diameter ventilation hole in the lid covered with an organdy screen. Approximately 100 parasitized nymphs, each one identifiable as an individual, were incubated in this way and observed every 8 h until all wasps had developed into adults.

At each observation point any mortality and the life stage on the parasitoid was recorded as either egg, larva or pupa. The parasitoids developed beneath the host nymph and so, to avoid disturbance and the potential for mortality, we did not identify the prepupal stage as has been done for other ectoparasitoids (Chien et al. 1991; Morales-Ramos and Cate 2002). Once the pupal stage was attained, sections of leaf supporting each pupa were excised and each pupa was incubated individually in Petri dishes over wet paper towels until adult emergence. The sex of adult wasps was determined once they emerged.

Oviposition behaviour and fecundity

Replicate pairs of male and a female *T. triozae* were incubated individually in oviposition arenas comprised of Petri dishes (9.0 cm in diameter and 1.2 cm in depth) containing psyllid nymphs on tomato leaves and a honey solution (95 %). Female longevity, oviposition rate and sex ratio of parasitoid progeny were determined.

Each oviposition arena had a 0.8 cm diameter sealable hole on one side through which parasitoids could be introduced and two further ventilation holes (1.0 cm diameter) sealed with an organdy screen. Young leaflets were detached from tomato leaves (40 day old plants), and placed in water-saturated cotton wool and their petiole wrapped with parafilm and taped to the base of the oviposition arena. Using a fine camel-hair brush, early fourth and fifth instar *B. cockerelli* nymphs were transferred to the leaflets for presentation to parasitoids. A few drops of honey solution were placed inside the arena and then a single pair of *T. triozae* was introduced, of which the females were less than 20 h of age. Each couple were allowed to forage for 24 h after which time they were transferred to a new oviposition arena containing another cohort of nymphs on tomato leaflets and the process was repeated daily until the *T. triozae* female died. On the first day of the experiment, 12 *B. cockerelli* nymphs per day were presented to each pair of parasitoids but once oviposition started this was increased to 24 *B. cockerelli* nymphs per day to ensure there were more than sufficient hosts for both feeding and oviposition. The number of parasitoid eggs laid and the number of nymphs parasitized were recorded daily. Parasitized nymphs were then incubated to allow the parasitoid progeny to develop through their entire life cycle. The developing progeny were examined every 24 h under a stereomicroscope and mortality and sex of the progeny at adulthood determined.

Data from female parasitoids that died within the first five days or that did not oviposit were excluded from the analysis. If the male wasp died before the female then it was replaced with another one. Overall, data from 18 replicate pairs were collected and analysed.

During the experiment we also made 50 qualitative observations of oviposition behaviour while females were attacking and laying eggs on the host. On each occasion we spent only 5 min observing and made a purely descriptive note of what we observed. Additionally, photographic images of 20 *T. triozae* eggs less that 8 h after oviposition were taken under a microscope (Olympus SZH10 Research Stereo, Japan) and measured using an eyepiece graticule.

Data analysis

We used a Student's *t* test to compare the overall longevity of parasitoids provided with honey solution with those that were not provided with honey solution, and also between the sexes. The length of time at the egg, larval and pupal stage, and the overall developmental time of *T. triozae* were also compared between the sexes using Student's *t*-tests. Means and SD were calculated for the duration of each life stage and the values for age specific survivorship, beginning with one day-old eggs, and age specific fecundity for females were used to develop a life table. The life table parameters of *T. triozae* were calculated using the Birch (1948) method. The net reproductive rate (R_0), the generation time (T), the intrinsic rate of increase (r_m), the doubling time (DT), and the finite rate of increase (λ) were estimated using the computer programme of Maia et al. (2000) in the software package SAS (SAS Institute 2000). This programme included a Jackknife test to estimate confidence levels for all parameters (Maia et al. 2000).

Results

Longevity

Male and female parasitoids provided with honey solution lived significantly longer than those without honey solution. Specifically, honey-fed females lived 46.6 ± 10.1 days compared with 1.7 ± 0.6 days ($t_{38} = 19.9$; $p < 0.0001$) without honey, and honey-fed males lived 37.9 ± 10.5 days compared with 2.4 ± 0.7 days ($t_{38} = 15.2$; $p < 0.0001$) without honey. Honey-fed females lived significantly longer than honey-fed males ($t_{38} = 2.68$; $p = 0.0108$). Interestingly, honey fed-females that were offered nymphs for oviposition in the fecundity experiment only lived for 12 to 29 days (average 19.9 ± 4.5 days).

Life cycle

The development of 107 eggs was recorded, but only the data from individuals that developed successfully to the adult stage (86 females and 14 males) are reported. The incubation period as eggs lasted an average of 1.5 days, and there was no significant difference between the sexes ($t_{98} = 0.99$; $p = 0.3239$) (Table 1). Larval developmental time was not significantly different between males and females ($t_{98} = -1.38$; $p = 0.1699$). However the developmental time spent as pupae and the overall developmental time was significantly different between males and females: females spent significantly longer as pupae (5.7 days) than males (5.4 days) ($t_{98} = 3.61$; $p = 0.0005$), even though the difference was lower than one day. The overall developmental time of females (12.0 days) was longer than males (11.6 days) and the difference was significant ($t_{98} = 3.60$; $p = 0.0005$), even though the difference was again lower than one day and

Table 1 Development time (day ± SD) of *Tamarixia triozae* eggs, larvae and pupae parasitizing *Bactericera cockerelli* on tomato under laboratory conditions [26 ± 1 °C, 60 ± 10 % RH and 14:10 (L:D) h]

Sex	N	Egg	Larva	Pupa	Total development time
Males	14	1.48 ± 0.09	3.39 ± 0.21	5.39 ± 0.40	11.64 ± 0.5
Females	86	1.49 ± 0.05	3.49 ± 0.26	5.73 ± 0.31**	12.02 ± 0.34 **
Average	100	1.49 ± 0.06	3.48 ± 0.26	5.71 ± 0.73	11.99 ± 0.38

** Only the length of time spent as pupae, and the total development time, were significantly different between the sexes ($t_{98} = 3.61$; $p = 0.0005$)

largely explained by the difference in time spent at the pupal stage (Table 1).

Oviposition behaviour and fecundity

The qualitative observations we made on oviposition behaviour of *T. triozae* add some basic information to that reported by Pletsch (1947) and Johnson (1971). From our observations we consider that *T. triozae* is an idiobiont parasitoid because, even though *B. cockerelli* nymphs can feed and move for a short while after being parasitized, they were unable to advance to the next instar. Before *T. triozae* females laid an egg onto fourth or early fifth instar *B. cockerelli* nymphs they were observed to paralyse the nymph using their ovipositors. Eggs were deposited on the ventral surface of nymphs, mostly between the coxae of the first or second pair of legs, but occasionally between the thorax and abdomen and even on the rostrum. Under the laboratory conditions used, *T. triozae* females usually laid more than one egg per host, although only one larva usually reached the adult stage.

The preoviposition period of female *T. triozae* that had mated within a few hours of emergence, was short, between one and three days (average 1.9 ± 0.8 days). Of the 18 mated females we evaluated, 33.3 % laid eggs on the first day, 38.8 % on the second day and 27.7 % on the third day. Newly deposited *T. triozae* eggs were small, shiny, translucent white, oblong and 0.184 ± 0.017 mm in length by 0.08 ± 0.007 mm in width (n = 20). The eggs were typically hymenopteriform and covered with a mucilaginous substance.

The life-time fecundity varied from 12 to 29 days (average 19.9 ± 4.5 days). Females laid an average of 165.4 ± 45.2 eggs (range 98–279) over their lifetime and the sex ratio favoured females (86 %). Fecundity was age dependent: the majority of females began to lay eggs when they were three days old, and there was an egg-laying peak between the ages of 6 and 15 days. The mean number of eggs laid per day per female over their lifetime was 7.7 ± 3.9 (range 0–14), and the maximum number of eggs per day was 19. Superparasitism was common under laboratory conditions, and each female parasitized between 85 and 241 nymphs (average 143 ± 40.3) during her lifetime but it was evident that, after day 15, oviposition declined rapidly (Fig. 1).

Survivorship and life table parameters

The survival rate of *T. triozae* from egg to adult was 92 %. The l_x (age-specific survival rate) remained above 83.3 % for almost 13 days before sharply declining from 72.2 % at 17 days to 0 by 29 days. Actually only two females were still alive at day 24 and only one female was still alive at day 29 (Fig. 1). The net fecundity rate (m_x) and the number of eggs produced per original individual at each age or age specific maternity ($l_x m_x$) are shown in Fig. 2. The net reproductive rate (R_0), generation time (G), intrinsic rate of increase (r_m), doubling time (*DT*), and the finite rate of increase (λ) were 130.9, 18.7, 0.26, 2.7, and 1.3 days, respectively (Table 2).

Discussion

Tamarixia triozae is an important native parasitoid of *B. cockerelli* in North America (Pletsch 1947; Jensen

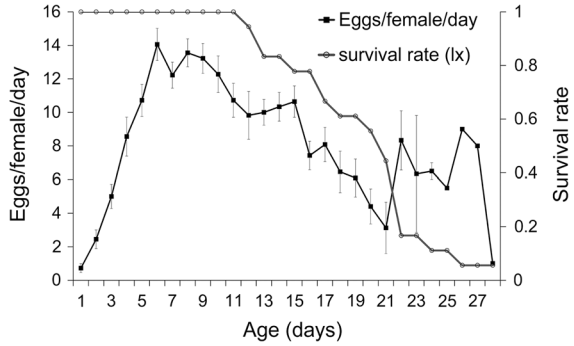

Fig. 1 *Tamarixia triozae* age-specific survivorship (l_x), and fecundity (eggs per female per day ± SD) under laboratory conditions at 26 ± 1 °C, 60 ± 10 % RH and 14:10 (L:D) h

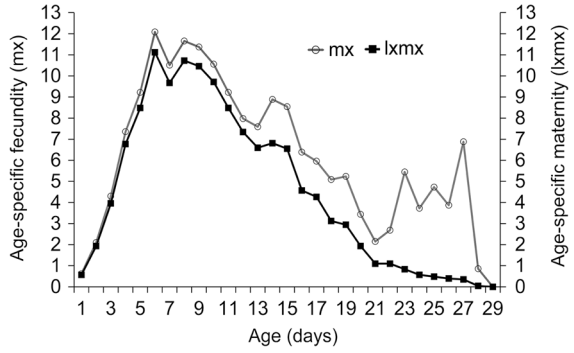

Fig. 2 *Tamarixia triozae* net fecundity rate (m_x), and age-specific maternity ($l_x m_x$) calculated under laboratory conditions at 26.7 ± 1 °C, 60 ± 10 % RH and 14:10 (L:D) h

Table 2 Life table parameters calculated for *Tamarixia triozae* reared on *Bactericera cockerelli* on tomato in comparison with its host reared on two host plants under laboratory conditions [26.7 ± 2 °C, 75 ± 5 % RH and 14:10 h (L:D) h]

Parameters	*Tamarixia triozae* parasitizing *B. cockerelli* on tomato	*Bactericera cockerelli*	
		Eggplant	Pepper
Net reproductive rate (R_0)	130.9 (113.1–148.7)	84.5 (56.4–112.7)	59.0 (29.6–88.4)
Intrinsic rate of increase (r_m)	0.260 (0.25–0.27)	0.110 (0.106–0.114)	0.087 (0.076–0.098)
Mean generation time (T), day	18.7 (17.8–19.7)	40.5 (38.2–42.9)	46.8 (37.9–55.7)
Doubling time (DT) day	2.7 (2.6–2.8)	6.3 (6.1–6.5)	7.9 (6.9–8.9)
Finite rate of increase (λ) day	1.3 (1.2–1.3)	1.1 (1.11–1.12)	1.1 (1.08–1.10)

Data for *B. cockerelli* were taken from Yang and Liu (2009). In both studies life table parameters and confidence levels (95 %,) were calculated using the SAS programme of Maia et al. (2000) with Jacknife estimations

1957; Bravo and López 2007). Before this study there was only basic information on parasitoid biology and none of the detailed studies necessary to determine the potential of *T. triozae* as a biological control agent against *B. cockerelli.*

In general, the life cycle and oviposition behaviour of *T. triozae* was similar to other eulophid species in the same genus such as *T. radiata* (Chien et al. 1991, 2001; Gómez-Torres et al. 2012). Observations on adult and larval behaviour of *T. triozae* allowed us to confirm that it behaved as other solitary, idiobiont and synovigenic ectoparasitoids that use host-feeding to acquire protein for egg production (Clausen 1972; Jervis and Kidd 1986). It was established recently that honey-fed *T. triozae* females were able to host-feed on an average of 181 nymphs of *B. cockerelli* and laid 130 eggs during their life span (30 days) (Cerón-González et al. 2014).

It is well known that a source of carbohydrates, usually a honey or sugar solution, is important to increase survival, longevity and reproductive capacity of parasitoids in laboratory culture (Wäckers et al. 2008; Sandanayaka et al. 2009). This was confirmed for *T. triozae* where neither sex survived longer than three days in the absence of a honey solution. The reproductive capacity of *T. triozae* is an important biological characteristic of the parasitoid, and it was optimal only when females were allowed access to a honey solution, making the provision of a carbohydrate source, potentially in the form of nectar, another characteristic that should be considered when determining and encouraging the biological control capacity of *T. triozae*.

Although the status of *B. cockerelli* as a pest has been reported for decades in USA and Mexico, including most recently its ability as a vector of ZC disease (Leyva-López et al. 2002; Munyaneza et al. 2007; Hansen et al. 2008; Liefting et al. 2008; Crosslin and Munyaneza 2009; Garzón-Tiznado et al. 2009; Camacho-Tapia et al. 2011), detailed evaluation of its population parameters and life table analysis have only recently been published (Yang and Liu 2009). Now we have collected the same information for its native pasasitoid, *T. triozae*, it is possible to compare the two and determine whether *T. triozae* has the potential to regulate populations of *B. cockerelli*. If we compare the data from our study on *T. triozae* on tomato with the data of Yang and Liu (2009) for *B. cockerelli* on eggplant and peppers, which were determined under similar environmental conditions, we can see some interesting trends. The net reproductive rate (R_0), which indicates the number of females per female in a generation was higher for *T. triozae* on tomato than for *B. cockerelli* on eggplant or peppers (Table 2). Furthermore, the intrinsic rate of increase (r_m) was twice as large for *T. triozae* as for *B. cockerelli*, the mean generation time of *T. triozae* was 18.7 days compared with 40 or 46 days for *B. cockerelli* on eggplant and pepper plant respectively, and both the doubling time and the finite rate of increase were higher in the parasitoid than in the pest (Table 2). This suggests that even though the studies were on different host plants, with almost twice the potential for population increase than its host, *T. triozae* has great potential to be an effective control agent of *B. cockerelli*.

Furthermore, in support of its potential for biological control, *T. triozae* has been cited as one of the most abundant parasitoids of *B. cockerelli* in field samples from USA and Mexico (Pletsch 1947; Jensen

1957; Johnson 1971; Lomeli-Flores and Bueno 2002). It mainly parasitizes fourth and early fifth instars of its host, but, if no other food is available it may also parasitize third instars, and it also feeds directly on its host increasing its potential to reduce host populations (Johnson 1971; Cerón-González et al. 2014).

Although the life table data obtained in laboratory studies is only indicative of what might occur in field populations, they clearly indicate the potential of *T. triozae*. This makes it difficult to understand why *T. triozae* has not received more attention since it was first recorded. This may be because, for unknown reasons, under some circumstances parasitism levels can be low despite high populations of *B. cockerelli*. For example, Pletsch (1947) reported 23 % parasitism of *B. cockerelli* by *T. triozae* in one field, but no parasitism in the surrounding areas despite high *B. cockerelli* populations. Similar observations have been made in California, USA where parasitism by *T. triozae* was below 20 % (Butler and Trumble 2012). Johnson (1971) has also reported unexplainable high levels of mortality in pupae of this parasitoid in both the laboratory and field. At the Colegio de Postgraduados, Mexico, we have been rearing *T. triozae* for four years and we have had no problems with pupal mortality in the laboratory or the greenhouse. In addition, our *T. triozae* cultures achieve high parasitism levels (from 60 to 80 %) and only fall during the raining seasons, which we cannot currently explain.

It is possible that one of the reasons for the low parasitism levels reported for *T. triozae* in the field is due to the application of broad spectrum insecticides against *B. cockerelli* as part of the principal control strategy. Working with *T. triozae* Luna-Cruz et al. (2011) and Liu et al. (2012) both identified that this parasitoid is highly sensitive to pesticides. Luna-Cruz et al. (2011) indicated that abamectin and spinosad were the most toxic products for *T. triozae* (IOBC category 3) and imidacloprid (1 l ha^{-1}) prevented parasitoid emergence. We hypothesise that over-reliance on broad-spectrum insecticides is the main reason for low field populations of *T. triozae*.

In summary, we believe that, for the reasons described above, the native parasitoid *T. triozae* is an excellent candidate for biological control of *B. cockerelli*. However, we also believe that a more complete evaluation of the potential of *T. triozae* as a biological control agent of *B. cockerelli* requires additional information on searching behaviour, intraguild predation and development on different host plants. Furthermore, we must also remember that *B. cockerelli* is most important as a vector of *C. Liberibacter psyllaurous* rather than as an herbivore. Because *T. triozae* usually only parasitizes fourth instar nymphs of *B. cockerelli*, having high levels of parasitism may not ensure that the host plants are protected from infection before the nymphs are killed. Nevertheless, the parasitoid *T. triozae* could still be a useful tool within IPM of *B. cockerelli*, particularly in the prevention *B. cockerelli* population build-up on weeds and non-crop host plants. Additionally, it could be used as a biological control agent on crops such as peppers, where the transmission of diseases by the psyllid is less important than it is on potato and tomato.

Acknowledgments Thanks to Yong M. Zhang for her assistance and sharing experiences in insect rearing. E. Rodriguez-Leyva and J. Refugio Lomeli-Flores thank the project INNOVAPYME-CONACYT 154411, Technological development for biological pest control in tomato and chili crops grown in protected environments allotted to Koppert Mexico S.A. de C.V., to fund research about native natural enemies. To the Consejo Nacional de Ciencia y Tecnología (CONACYT, Mexico) for a full master of science scholarship to the first author, and Consejo Mexiquense de Ciencia y Tecnología (COMECYT, Estado de Mexico) for P. Rojas writing thesis scholarship.

References

Birch LC (1948) The intrinsic rate of natural increase of an insect population. J Anim Ecol 17:15–26

Bravo ME, and López LP (2007) Principales plagas del chile de agua en los valles centrales de Oaxaca. Agroproduce, Fundación Produce Oaxaca A.C. 7: 12–15

Butler CD, Trumble JT (2011) New records of hyperparasitism of *Tamarixia triozae* (Burks) by *Encarsia* spp. in California. Pan-Pac Entomol 87:130–133

Butler CD, Trumble JT (2012) The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) life history, relationship to plant diseases, and management strategies. Terr Arthropod Rev 5:87–111

Camacho-Tapia AM, Rojas-Martínez RI, Zavaleta-Mejía E, Hernández-Deheza MG, Carrillo-Salazar JA, Rebollar-Alviter A, Ochoa-Martínez DL (2011) Aetiology of chili pepper variegation from Yurécuaro México. J Plant Pathol 93:1187

Cerón-González C, Lomeli-Flores JR, Rodríguez-Leyva E, Torres-Ruíz A (2014) Fertility and feeding of *Tamarixia triozae* (Hymenoptera: Eulophidae) on potato psyllid *Bactericera cockerelli*. Rev Mex Cienc Agríc 5:893–899

Chien CC, Chu YI, Ku HC (1991) Parasitic strategy, morphology and life history of *Tamarixia radiata* (Hymenoptera: Eulophidae). Chin J Entomol 11:264–281

Chien CC, Chiu SC, Ku SC (2001) Mass rearing and field release of an eulophid wasp, *Tamarixia radiata* (Waters). Food and Fertilizer Technology Center (FFTC), Taiwan Agricultural Research Institute, Taiwan. Technical note 4 p

Clausen CP (1972) Entomophagous insects. Hafner Publishing Company, New York, USA

Compere H (1943) A new species of *Metaphycus* parasite on psyllids. Pan-Pac Entomol 19:71–73

Crosslin JM, Munyaneza JE (2009) Evidence that the Zebra Chip disease and the putative causal agent can be maintained in potatoes by grafting and *in vitro*. Am J Pot Res 86:183–187

Doutt RL, Smith RF (1971) The pesticide syndrome: diagnosis and suggested prophylaxis. In: Huffaker CB (ed) Biological control. Plenum Press, London, UK, pp 3–15

Ferguson G, and Shipp L (2002) New pests in Ontario greenhouse vegetables. Bulletin OILB/SROP [Proceedings of the join IOBC/WPRS working group "Integrated control in protected crops temperate climate" and IOBC/NRS "Greenhouse, nursery, and ornamental landscape IPM working group" at Victoria (British Columbia) Canada, 6–9 May 2002] 25: 69–72

Gao F, Jifon J, Yang X, Liu TX (2009) Zebra chip disease incidence on potato is influenced by timing of potato psyllid infestation, but not by the host plants on which they were reared. Insect Sci 16:399–408

Garzón-Tiznado JA, Cárdenas-Valenzuela OG, Bujanos-Muñiz R, Marín-Jarillo A, Becerra-Flora A, Velarde-Felix S, Reyes-Moreno C, González-Chavira M, Martínez-Carrillo JL (2009) Association of Hemiptera:Triozidae with the disease "permanente del tomate" in Mexico. Agr Téc Méx 35:61–72

Gómez-Torres ML, Nava DE, Parra RP (2012) Life table of *Tamarixia radiata* (Hymenoptera: Eulophidae) on *Diaphorina citri* (Hemiptera: Psyllidae) at different temperatures. J Econ Entomol 105:338–343

Hansen AK, Trumble JT, Stouthamer R, Paine TD (2008) A new Huanglongbing (HLB) species, *Candidatus Liberibacter* psyllaurous, found to infect tomato and potato, is vectored by the psyllid *Bactericera cockerelli* (Sulc). Appl Environ Microbiol 74:5862–5865

Institute SAS (2000) User's guide, version 9. SAS Institute, Cary, USA

Jensen DD (1957) Parasites of the Psyllidae. Hilgardia 27:71–99

Jervis MA, Kidd NAC (1986) Host-feeding strategies in hymenopteran parasitoids. Biol Rev 61:395–434

Johnson TE (1971) The effectiveness of *Tetrastichus triozae* Burks (Hymenoptera: Eulophidae) as a biological control agent of *Paratrioza cockerelli* (Sulc.) (Homoptera: Psyllidae) in north central Colorado. M.S. Thesis. Colorado State University, Fort Collins, Colorado, USA

King C (2014) Serious disease on the horizon? Potatoes in Canada Winter 2013. http://www.bluetoad.com/article/Serious_Disease_On_The_Horizon%3F/1325572/147983/article.html Accessed 12 May 2014

Lacey LA, de la Rosa F, Horton DR (2009) Insecticidal activity of entomopathogenic fungi (Hypocreales) for potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), development of bioassay techniques, effect of fungal species and stage of the psyllid. Biocontrol Sci Technol 19:957–970

Lacey LA, Liu TX, Buchman JL, Munyaneza JE, Goolsby JA, Horton DR (2011) Entomopathogenic fungi (Hypocreales) for control of potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) in an area endemic for zebra chip disease of potato. Biol Control 56:271–278

Leyva-López NE, Ochoa-Sánchez JC, Leal-Klevezas DS, Martínez-Soriano JP (2002) Multiple phytoplasmas associated with potato diseases in Mexico. Can J Microbiol 48:1062–1068

Liefting LW, Perez-Egusquiza ZC, Clover GRG, Anderson JAD (2008) A new "*Candidatus Liberibacter*" species in *Solanum tuberosum* in New Zealand. Plant Dis 92:1474

Lin H, Doddapaneni H, Munyaneza JE, Civerolo EL, Sengoda VG, Buchman JL, Stenger DC (2008) Molecular characterization and phylogenetic analysis of 16S rRNA from a new *Candidatus* Liberibacter strain associated with zebra chip disease of potato (*Solanum tuberosum* L.) and the potato psyllid (*Bactericera cockerelli* Sulc). J Plant Pathol 91:215–219

Liu D, Trumble JT (2004) Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. J Econ Entomol 97:1078–1085

Liu D, Trumble JT (2006) Ovipositional preferences, damage thresholds, and detection of tomato/potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) on selected tomato accessions. Bull Entomol Res 96:197–204

Liu D, Trumble JT (2007) Comparative fitness of invasive and native populations of the potato psyllid (*Bactericera cockerelli*). Entomol Exp Appl 123:35–42

Liu TX, Zhang YM, Peng LN, Rojas P, Trumble JT (2012) Risk assessment of selected insecticides on *Tamarixia triozae* (Hymenoptera: Eulophidae), a parasitoid of *Bactericera cockerelli* (Hemiptera: Triozidae). J Econ Entomol 105:490–496

Lomeli-Flores JR, Bueno R (2002) Nuevo registro de *Tamarixia triozae* (Burks) parasitoide del psílido del tomate *Paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae) en México. Fol Entomol Mex 41:375–376

Luna-Cruz A, Lomeli-Flores JR, Rodríguez-Leyva E, Ortega-Arenas LD, de la Huerta A (2011) Toxicidad de cuatro insecticidas sobre *Tamarixia triozae* (Hymenoptera: Eulophidae) y su hospedero *Bactericera cockerelli* (Hemiptera: Psyllidae). Acta Zool Mex (ns) 27:509–526

Maia AHN, Luiz AJB, Campanhola C (2000) Statistical inference on associate fertility life table parameters using Jacknife technique: computational aspects. J Econ Entomol 93:511–518

Morales-Ramos JA, Cate JR (2002) Laboratory determination of age-dependent fecundity, development and rate of increase of *Catolaccus grandis* (Burks) (Hymenoptera: Pteromalidae). Ann Entomol Soc Am 85:469–476

Munyaneza JE, Crosslin JM, Upton JE (2007) Association of *Bactericera cockerelli* (Homoptera: Psyllidae) with "Zebra chip", a new potato disease in southwestern United States and Mexico. J Econ Entomol 100:656–663

Munyaneza JE, Buchman JL, Upton JE, Goolsby JA, Crooslin JM, Bester G, Miles GP, Sengoda VG (2008) Impact of different potato psyllid populations on Zebra Chip disease incidence, severity, and potato yield. Subtrop Plant Sci 60:27–37

Pimentel D (2005) Environmental and economic costs of the application of pesticides primarily in the United States. Environ Dev Sustain 7:229–252

Pletsch DJ (1947) The potato psyllid *Paratrioza cockerelli* (Sulc), its biology and control. Montana Agr Exp Sta Bull 446:1–95

Richards BL (1928) A new and destructive disease of the potato in Utah and its relation to the potato psylla. Phytopathol 18:140–141

Sanchez-Peña SR, Casas-de-Hoyo E, Hernandez-Zul R, Wall KM (2007) A comparison of the activity of soil fungal isolates against three insect pests. J Agr Urban Entomol 24:43–47

Sandanayaka WRM, Charles JG, Allan DJ (2009) Aspects of the reproductive biology of *Pseudaphycus maculipennis* (Hymenoptera: Encyrtidae), a parasitoid of obscure mealybug, *Pseudococcus viburni* (Hemiptera: Pseudococcidae). Biol Control 48:30–35

Sulc K (1909) *Trioza cockerelli* n. sp. A novelty from North America, being also of economic importance. Acta Soc Entomol Bohemiae 6:102–108

Teulon DAJ, Workman PJ, Thomas KL, Nielsen MC (2009) *Bactericera cockerelli*: incursion, dispersal and current distribution on vegetable crops in New Zealand. N Z Plant Prot 62:136–144

van Driesche RG, Bellows TS (1996) Biological control. Chapman & Hall, New York, USA

Wäckers FL, van Rijn PVJ, Heimpel GE (2008) Honeydew as a food source for natural enemies: making the best of a bad meal? Biol Control 45:176–184

Yang XB, Liu TX (2009) Life history and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on eggplant and bell pepper. Environ Entomol 38:1661–1667

Yang XB, Zhang YM, Hua L, Peng LN, Munyaneza JE, Trumble JT, Liu TX (2010) Repellency of selected biorational insecticides to potato psyllid, *Bactericera cockerelli* (Hemiptera: Psyllidae). Crop Prot 29:1320–1324

Patricia Rojas after finishing her MSc. degree, at the Colegio de Postgraduados, Texcoco, Estado de Mexico, she worked as a technical assistant for a private company (Biobest Mexico). Currently, she is considering the possibility to pursue a PhD.

Esteban Rodríguez-Leyva is a full time professor, lecturing in biological control and IPM courses at the Colegio de Postgraduados, Texcoco, Estado de Mexico. His research focuses mainly on the biology and behavior of natural enemies to assess their potential as biological control agents, and the development of IPM programs based on biological control against indigenous and exotic insect pests.

J. Refugio Lomeli-Flores is a full time professor, lecturing in biological control courses at the Colegio de Postgraduados, Texcoco, Estado de Mexico. His work focuses in identifying and assessing potential biological control agents against agricultural pests in Mexico. He also develops studies to estimate the importance of including biological control agents in national programs against exotic insect pests.

Tong-Xian Liu is a national distinguished professor, and leading expert on entomology at Northwest A&F University, Yangling, Shaanxi, China. He also maintains an important relationship at the Vegetable IPM Laboratory at Texas AgriLife Research & Extension Center, Weslaco, Texas, USA, where he worked as a lecturer for many years. His research focuses mainly in the development of IPM programs against insect pests.