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Low efficiency of four indigenous *Trichogramma* wasp populations, collected from tomato crops, in controlling the invasive pest *Tuta absoluta* in Iran

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Abstract

The tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), has become a major pest in both greenhouse and outdoor tomato crops in Iran since its accidental introduction in 2010. In line with the biological control program of *T. absoluta*, recently developed in Iran, this study investigated the efficiency of four indigenous *Trichogramma* (Hymenoptera Trichogrammatidae) populations to control this pest. Two populations of *Trichogramma brassicae* Bezdenko, i.e. with and without *Wolbachia* Hertig et Burt infection, one population of *Trichogramma evanescens* Westwood, and one population of *Trichogramma principium* Sugonyaev et Sorokina were collected from the *Helicoverpa armigera* (Hubner) eggs in the tomato fields of Isfahan, Iran. The fertility life-table parameters were initially calculated on *Ephestia kuehniella* (Zeller) as a factitious host under laboratory conditions. Accordingly, the highest intrinsic rate of increase, the largest finite capacity for increase, and the greatest net reproductive rate were found in *T. evanescens* and *T. principium* populations, and all of which were positively affected by *Wolbachia* infection in *T. brassicae* population. The parasitism ability of these populations was then evaluated on *T. absoluta* eggs on the tomato leaves. *T. evanescens* showed the highest parasitism ability (26.82%), the rate of which was affected by female age in all populations. The efficiency of these populations was subsequently assessed on a larger scale in cages in the greenhouse under cropping conditions. The highest (7.82%) and lowest (3.17%) parasitism percentages were observed in *T. brassicae*, regardless of *Wolbachia* infection, and *T. principium*, respectively. Because the rates of the parasitism ability recorded from all populations were considerably low (less than 8%), it seems that these indigenous populations could not alone result in efficient control of *T. absoluta*.

Key words: leafminer, biocontrol, egg parasitoid, *Wolbachia*, life table parameter.

Introduction

The tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), is a key pest of tomato in the world, causing large damage to tomato yield through its leaf-mining activity as well as its larval penetration into stems and fruits (Desneux *et al*., 2010; Cocco *et al*., 2015). *T. absoluta* is an invasive species whose spread across the Afro-Eurasian supercontinent rapidly took place after its introduction from South America to Europe in 2006 (Campos *et al*., 2017; Biondi *et al*., 2018). The presence of this pest in Iran dates back to 2010, observed in open and protected tomato crops throughout the country (Baniameri and Cheraghian, 2012). Tomato is one of the most important crops in Iran, cultivated in an area exceeding 177000 hectares, having annual production of over 6.6 million tons (Ministry of Jihad-e-Agriculture of Iran, 2016).

Although *T. absoluta* has largely been controlled by chemical pesticides, *T. absoluta* populations have built up resistance to insecticides (Siqueira *et al*., 2000; 2001; Guedes and Siqueira, 2013; Silva *et al*., 2015; 2016). Moreover, the side effects of these chemical substances on non-target species (Consoli *et al*., 1998; Arno and Gabarra, 2011; Barros *et al*., 2015) have consistently been documented. Other control methods have also been followed, including mass trapping and mating distribution using synthetic sex pheromones (Caparros Megido *et al*., 2013; Cocco *et al*., 2013; Lobos *et al*., 2013). A number of management strategies are currently explored, such as developing resistant varieties (Ecole *et al*., 2001; Leite *et al*., 2001; Pereira *et al*., 2008; Maluf *et al*., 2010) and optimizing fertilizer and water use, both of which have bottom-up effects on life-history traits of the pest (Han *et al*., 2014; Larbat *et al*., 2016).

Another important crop-protection strategy, namely biological control of *T. absoluta*, has been developed based on use of natural enemies in the native range of the pest as well as the newly-invaded regions (Biondi *et al*., 2018). Egg parasitoids, especially *Trichogramma* species (Hymenoptera Trichogrammatidae), have been found to parasitize *T. absoluta* eggs naturally in South America (Desneux *et al*., 2010) and European countries (Biondi *et al*., 2013; Zappalà *et al*., 2013). Other biological control agents, including *Trichogramma pretiosum* Riley (Faria *et al*., 2000; Pratissoli and Parra, 2000; Parra and Zucchi, 2004; Pratissoli *et al*., 2005; Faria *et al*., 2008; Medeiros *et al*., 2009; Ferracini *et al*., 2019), *Trichogramma achaeae* Nagaraja et Nagarkatti (Cabello *et al*., 2009; Vila *et al*., 2010; Cabello *et al*., 2012; Chailleux *et al*., 2012; 2013; Cascone *et al*., 2015), *Trichogramma cacoeciae* (Marchal) (Cherif *et al*., 2013; Zouba *et al*., 2013; Cherif *et al*., 2019), *Trichogramma nerudai* Pintureau et Gerding (Tezze and Botto, 2004), *Trichogramma bourarachae* Pintureau et Babault (Zouba *et al*., 2013) and *Trichogramma euproctidis* (Girault) (El-Arnaouty *et al*., 2014), have successfully been released into tomato greenhouses to control *T. absoluta*. Chailleux *et al*. (2012) studied the ability of several European *Trichogramma* species/strains to control *T. absoluta*. They reported parasitism rates of up to 73% concerning *T. absoluta* eggs in laboratory conditions; the rate of approximately 30% was also recorded in greenhouse cages (Chailleux *et al*., 2012).

In Iran, *Macrolophus caliginosus* Wagner, *Nesidiocoris tenuis* Reuter, *Podisus nigrispinus* (Dallas), *Trichogramma brassicae* Bezdenko, and *Trichogramma pintoi* Voegele, all of which are observed in tomato crops, were reported as potential control agents of *T. absoluta* (Ahmadipour *et al*., 2015; Alsaedi *et al*., 2017; Mirhosseini *et al*., 2019) In addition, *Bacillus thuringiensis* var. *kurstaki* has successfully been sprayed into tomato greenhouses to control *T. absoluta* larvae and the release of *M. caliginosus* is also considered to control the pest (Baniameri and Cheraghian, 2012).

The maternally inherited *Wolbachia* is an α-proteobacteria endosymbiont commonly found in insects, arthropods, and filarial nematodes. *Wolbachia* infection can alter the reproductive characteristics of its host, including incompatibility of cytoplasm, feminization of genetic males, killing of male progeny, and the induction of parthenogenesis (Werren *et al*., 2008). Parthenogenetic induction (thelytoky) has been documented in species having arrhenotokous development, such as *Trichogramma* wasps (Stouthamer *et al*., 1990; Girin and Bouletreau, 1995; Pintureau *et al*., 2000; Braig *et al*., 2002). Since the negative effects of *Wolbachia* infection on host fitness such as reduction of fecundity were reported (Stouthamer and Luck, 1993; Stouthamer *et al*., 1994; We *et al.,* 2016), the success of biological control programs using these wasps can affected by *Wolbachia* infection.

In Iran, *Trichogramma* wasps belonging to various species are being mass-reared and released for the suppression of several lepidopteran pests, such as *Chilo suppressalis* (Walker) (Crambidae), *Ectomyelois ceratoniae* (Zeller) (Pyralidae), *Ostrinia nubilalis* (Hubner) (Crambidae), and *Cydia pomonella* (L.) (Tortricidae). Although *Trichogramma* wasps are not used to control *T. absoluta* in Iran, the inundative release of them into tomato fields is being followed against the cotton bollworm, *Helicoverpa armigera* (Hubner) (Lepidoptera Noctuidae) in an area equal to 27000 ha (Attaran and Dadpour, 2011).

In this paper, the authors examined the efficiency of four indigenous *Trichogramma* populations collected from *H. armigera* eggs in tomato fields in Iran in controlling *T. absoluta*. The effectiveness of these populations was initially evaluated by comparing their life-table parameters on a factitious host, *Ephestia kuehniella* (Zeller) (Lepidoptera Pyralidae), because of this host is used for mass rearing commercially, and later by assessing the parasitism rates on *T. absoluta* eggs under laboratory and greenhouse conditions. The aim of this research was to assist farmers in Iran to obtain healthy, fresh, and quality tomatoes through evaluating the effectiveness of an eco-friendly control method, as an alternative to the application of broad-spectrum insecticides, in controlling a key economic pest, i.e. *T. absoluta*.

Materials and methods

Insects

Four populations of *Trichogramma* wasps were used for the experiments. Two populations of *T. brassicae*, with (W^+) and without (W^-) *Wolbachia* infection, one population of *Trichogramma evanescens* Westwood, and one population of *Trichogramma principium* Sugonyaev et Sorokina were selected. To stablish a colony of a parasitoid wasp is often recommended to use a relatively high number of the founder population. Considering that there was low parasitism rate of *T. absoluta* eggs by *Trichogramma* wasps in the fields, so the colony was stablished by the wasps collected from *H. armigera* eggs in tomato fields. Having used taxonomic keys based on their anatomical characters (Pintureau, 2008; Poorjavad, 2011) and molecular data from the sequencing of the ITS2 regions (Sumer *et al*., 2009; Poorjavad *et al*., 2012), the authors identified all species prior to running the experiments. The presence of *Wolbachia* was determined by PCR using *Wolbachia* specific primers (*wsp*) (Braig *et al*., 1998), the details of which were well delineated in Poorjavad *et al*. (2012). A thelytokous mode of reproduction was traced in *T. brassicae* sample with *Wolbachia* infection, indicating that all offspring were females.

The wasps were reared on the UV-irradiated eggs (less than 12 hours old) of an alternative host, *E. kuehniella*. The adult wasps were fed with 10% honey-water solution and kept under laboratory conditions (25 ± 1 °C, 16:8 L:D photoperiod, and 70 ± 10% RH).

The colony of *T. absoluta* was established from the larvae collected from the infested leaves of the greenhouse-grown tomatoes in Isfahan, Iran. After emergence, the adults were placed on the tomato plants (Dafnis cultivar, Syngenta seeds, Switzerland) in the cages (2 × 2 × 2 m) under greenhouse conditions. The adult moths were fed with honey placed on the inner wall of the cage. *T. absoluta* eggs (less than 1-day-old) required for performing the experiments were obtained from placing the male and female adult moths inside the oviposition cages (50 × 50 × 50 cm) containing tomato leaflets as a host for the egg-laying process. After 24 hours, these leaflets were picked up.

Life-table parameters of *Trichogramma* populations reared on *E. kuehniella*

In order to estimate the fertility life-table parameters of the *Trichogramma* populations, 35 less than 24-h-old mated females were selected from each population. In the *T. brassicae* W^+ population all individuals were female and that is to say, mating did not occur because of *Wolbachia* infection. The age of females was standardized by exposing a piece of cardboard with approximately 1500 eggs of *E. kuehniella* (less than 12 hours old, irradiated by ultraviolet rays) to the parasitoid wasps inside the rearing containers for 12 hours. The emerged females were individually held in glass vials (10 cm length × 1 cm diameter), each of which had about 30 eggs of *E. kuehniella* (based on the preliminary tests, 30 eggs exceeded the maximum fecundity per day), and fed with a strip of 10% honey-water solution per glass vial. Under the same conditions described above, the host eggs were replaced by fresh ones every day until the death of females, and the exposed eggs were kept in a separate glass vial until the F_1 adult emergence. Female longevity, the number of parasitized eggs per female (for 35 females of each population), emergence rate, sex ratio, pre-adult development time, and pre-adult mortality in F_1 progeny were all recorded by daily inspection.

Parasitism of *T. absoluta* eggs on tomato leaves

An experiment was set up to analyse the potential of *Trichogramma* species/strains for parasitizing *T. absoluta* eggs in the laboratory conditions following the procedure proposed by Chailleux *et al*. (2012). Briefly, *Trichogramma* females (less than 24-h old) of each population were individually placed in a plastic tube sealed with a mesh to allow ventilation (16 cm length × 8 cm diameter), with 30 *T. absoluta* eggs laid on a tomato leaflet held in water in a cylindrical holder (6 cm length × 2 cm diameter). They fed with a 10% honey-water solution streaked on the wall of the tubes. After 24 hours, the leaflets were replaced by fresh ones containing *T. absoluta* eggs (less than 24-h old), and experiment lasted for three days. The leaflets were kept in a climate chamber under the aforementioned conditions for five days; the number of the parasitized eggs on each leaflet was then counted. For each population, 30 replications were conducted.

Parasitism of *T. absoluta* eggs held in cages under greenhouse conditions

The experiment was performed in cages (70 × 145 × 80 cm) coated with an insect-proof mesh containing eight potted tomato plants having seven to ten leaves (according to Chailleux *et al*., 2012). The cages were placed in a glass greenhouse located at Isfahan University of Technology. To perform the experiment, a completely randomized design was used with four treatments (four *Trichogramma* populations) and three replications, each of which was kept in semi-controlled conditions (16 to 32 °C, mean ≈25 °C and 33 to 80%, mean 70% RH) under natural light from May 15 to June 15. Twenty-five *T. absoluta* adults (mixed males and females, two-day old) were released in the cages. The release of each *Trichogramma* population was simultaneously set by locating a small cardboard containing 400 parasitized eggs of *E. kuehniella* at the centre of the cages. The parasitoids emerged one day after the release. After eight days, the parasitized and unparasitized *T. absoluta* eggs were counted with a stereomicroscope. Furthermore, their position on the leaves was recorded (upper, middle, and lower leaves) to determine the effects of the host egg position on parasitism rate.

Data analysis

The fertility life-table parameters of the *Trichogramma* populations reared on *E. kuehniella*, such as age-specific survival rates (l_x), age-specific fecundity (m_x), age-stage-specific survival rate (s_{xj}), net reproductive rate (R_0), generation time (T), intrinsic rate of increase (r_m), gross reproductive rate (GRR), and finite capacity for increase (λ) were calculated using age-stage, two-sex life-table program (Chi, 2015). The replications for the main fertility life table parameters were made using the jackknife estimation method (Meyer *et al*., 1986). The analysis of variance (ANOVA) was used to assess differences among demographic parameters estimated through fertility life table (SPSS, 2010).

Differences among parasitism percentages of *T. absoluta* eggs on different days (first, second and third days of the female life span) for each *Trichogramma* population and among different populations in the laboratory experiment were assessed by ANOVA. The analysis was also used to evaluate differences among the mean parasitism percentage of *T. absoluta* eggs in different leaf positions on tomato plants (upper, middle and lower leaves) by each *Trichogramma* population and the mean parasitism percentage by different populations in the greenhouse experiment. To compare the means and normalize the data in percentages in all experiments, a Least Significant Difference (LSD) test at the 5% probability level and Arc sin $\sqrt{x}$ data transformation were used, respectively (SPSS, 2010).

Results

Life-table parameters of *Trichogramma* populations on *E. kuehniella*

Biological characteristics and life table parameters of four *Trichogramma* populations on *E. kuehniella* are shown in table 1. The shortest pre-adult development time was observed in *T. evanescens*. The lowest and highest pre-adult mortality rates were associated with *T. principium* and *T. brassicae* populations regardless of *Wolbachia* infection, respectively. The highest parasitism rate was found in *T. evanescens*. In *T. brassicae*, the *Wolbachia* infected population (W^+) had a significantly higher parasitism rate than the uninfected population (W^-). Due to the parthenogenesis induced by *Wolbachia* infection in the *T. brassicae* W^+ population, the highest sex ratio (female/total) was recorded in this population. There was a significant difference between female adult longevity of populations with the highest and the lowest *T. evanescens* and *T. principium* populations. These two populations also induce the highest r_m, λ and R_0. Based on these values, the *T. brassicae* W^- population showed the lowest life table parameters (table 1).

The age-specific survival rate (l_x) curves showed that female mortality started sooner in the *T. brassicae* W^- population than in the W^+ population, but the curve of the W^+ population evidenced a sharper decrease (figure 1). One hundred percent mortality was reached after 28 days in the *T. evanescens* population, while this happened in other populations after 19 to 23 days (figure 1). The pre-adult development time was estimated to be about 11 days for all populations (table 1). The highest m_x was generally observed in the first three days after female emergence (figure 1) and decreased gradually until the female died, except for the *T. principium* population, whose age-specific fecundity curve showed an increase with a medium peak on the 18th day (figure 1).

The age-stage-specific survival rate (s_{xj}) of the *Trichogramma* populations indicated that they can survive successfully on *E. kuehniella* (figure 2). The highest s_{xj} were 0.90, 0.84, 0.74 and 0.50 for *T. brassicae* W^+, *T. brassicae* W^-, *T. principium* and *T. evanescens* females, respectively.

Table 1. Mean ± SE intrinsic rate of increase (r_m), finite capacity for increase (λ), net reproductive rate (R_0), generation time (T), gross reproductive rate (GRR) and some other biological parameters of *Trichogramma* populations on *E. kuehniella* eggs.

	T. brassicae W^-	*T. brassicae* W^+	*T. principium*	*T. evanescens*	
r_m (day^{-1})	0.25 ± 0.009^c	0.27 ± 0.005^b	0.29 ± 0.008^a	0.29 ± 0.010^a	$F_{3,164} = 2.844$ $P = 0.039$
λ (day^{-1})	1.29 ± 0.012^b	1.32 ± 0.007^{ab}	1.33 ± 0.011^a	1.34 ± 0.014^a	$F_{3,164} = 2.792$ $P = 0.042$
R_0 (off spring)	29.75 ± 4.18^c	40.55 ± 2.9^b	56.03 ± 6.41^a	48.89 ± 7.25^a	$F_{3,164} = 3.019$ $P = 0.031$
T (days)	13.19 ± 0.13^a	13.31 ± 0.06^a	13.81 ± 0.11^a	13.25 ± 0.17^a	$F_{3,164} = 3.642$ $P = 0.014$
GRR (offspring)	44.76 ± 6.2^b	45.48 ± 1.96^b	83.59 ± 13.88^a	66.47 ± 9.85^{ab}	$F_{3,164} = 3.230$ $P = 0.024$
Parasitized eggs per female	34.76 ± 4.34^d	44.6 ± 2.12^c	72.83 ± 5.26^b	92.9 ± 7.18^a	$F_{3,119} = 27.405$ $P < 0.001$
Pre-adult development time (days)	11.03 ± 0.02^a	11.16 ± 0.04^a	11.35 ± 0.04^a	10.57 ± 0.05^b	$F_{3,118} = 4.639$ $P = 0.018$
Pre-adult mortality (%)	8.89 ± 1.12^a	9.94 ± 0.91^a	2.28 ± 0.57^c	4.96 ± 0.75^b	$F_{3,115} = 15.55$ $P < 0.001$
Adult emergence	0.92 ± 0.01^b	0.89 ± 0.009^c	0.97 ± 0.006^a	0.94 ± 0.007^a	$F_{3,114} = 9.243$ $P < 0.001$
Sex ratio (female/Total)	0.79 ± 0.01^b	1.00 ± 0.00^a	0.78 ± 0.04^c	0.56 ± 0.04^d	$F_{3,114} = 47.354$ $P < 0.001$
Female longevity (days)	$5.\ 6 \pm 0.52^c$	6.50 ± 0.20^b	4.83 ± 0.24^d	9.03 ± 0.68^a	$F_{3,119} = 15.561$ $P < 0.001$

Means in each line followed by different letters are significantly different ($P < 0.05$, LSD test).

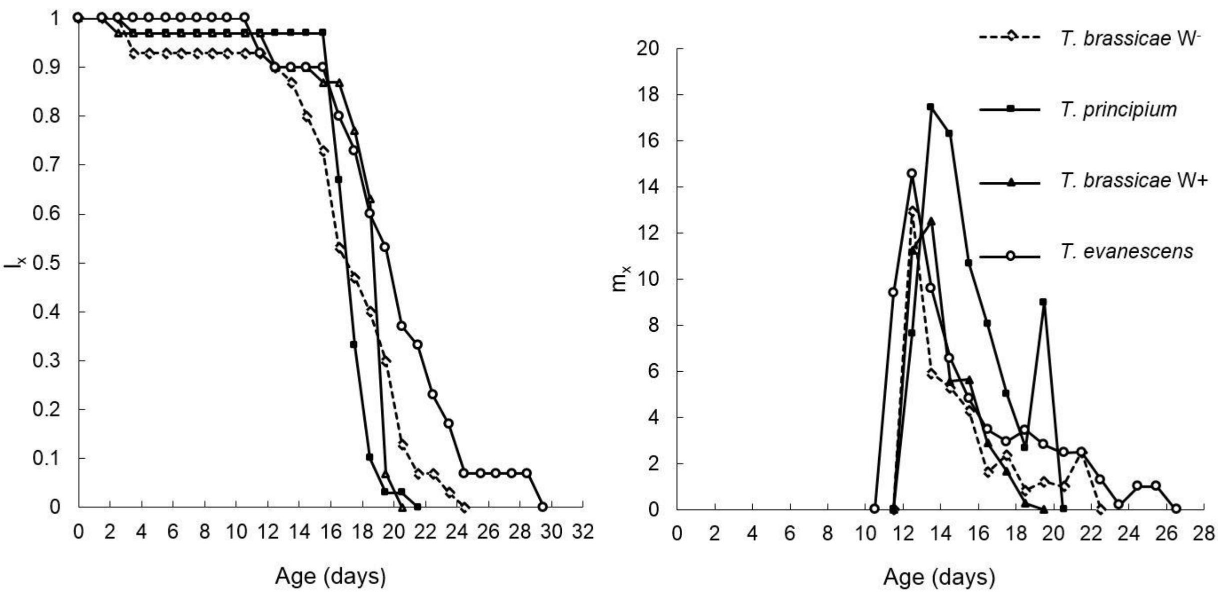

Figure 1. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of four *Trichogramma* populations reared from *E. kuehniella* eggs.

Parasitism of *T. absoluta* eggs by *Trichogramma* populations on tomato leaves

The parasitism rate of eggs on tomato leaves varied significantly depending on the population and age of female wasps. The highest parasitism percentage occurred by *T. evanescens* , and also the highest parasitism percentage was observed on the first day of the female life span in all populations (table 2).

Parasitism of *T. absoluta* eggs by *Trichogramma* populations in cages under greenhouse conditions

The ranking of *Trichogramma* populations based on parasitism percentage under laboratory conditions was not observed in cage experiments. The highest and lowest parasitism percentages were observed in *T. brassicae* (regardless of *Wolbachia* infection) and *T. principium* population, respectively. In all populations, except

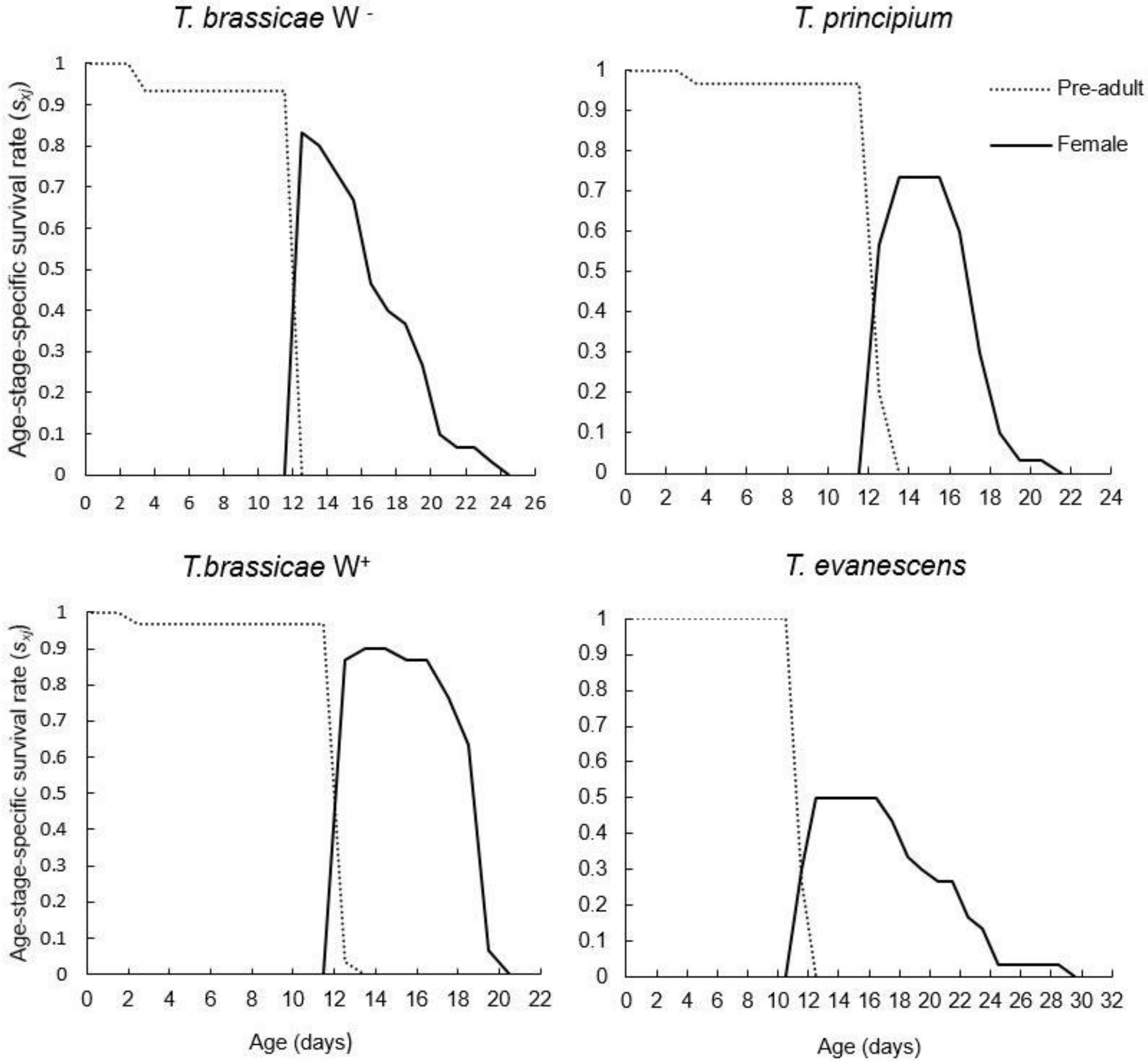

Figure 2. Age-stage-specific survival rate (s_{xj}) of four *Trichogramma* populations on *E. kuehniella* eggs.

Table 2. Mean ± SE egg parasitism percentage of *Tuta absoluta* by four *Trichogramma* populations in first three days of female life span on tomato leaves.

% parasitism	Species			
	T. brassicae W$^-$	*T. brassicae* W$^+$	*T. principium*	*T. evanescens*
First day	8.36 ± 1.17^a	6.83 ± 1.50^a	8.53 ± 2.00^a	13.86 ± 1.85^a
Second day	4.10 ± 0.750^b	5.33 ± 1.10^b	7.76 ± 1.80^b	8.86 ± 1.399^b
Third day	1.50 ± 0.394^c	2.43 ± 0.61^c	0.00 ± 0.00^c	4.10 ± 0.76^c
	$F_{2,348}$ = 33.50 P = 0.000	$F_{2,348}$ =17.71 P = 0.001	$F_{2,348}$ =9.56 P = 0.022	$F_{2,348}$ =11.49 P = 0.001
Total ($F_{3,348}$ = 7.57, P < 0.001)	13.96 ± 0.56^B	14.61 ± 0.67^B	16.29 ± 0.97^B	26.82 ± 0.90^A

Means followed by different lower-case letters in each column and different capital letters in the row are significantly different (P < 0.05, LSD test).

T. principium, parasitism percentage of *T. absoluta* eggs laid on the upper leaves of tomato plants was significantly higher than that of the eggs laid on the middle or lower leaves (table 3). Eggs laid on the upper and middle leaves were parasitized by *T. principium* significantly more than those laid on the lower leaves. Although the parasitism ability of these populations was significantly different, all of them showed low parasitism rates, less than 8% (table 3).

Discussion

Selecting the most suitable strain of *Trichogramma* based on laboratory, greenhouse and field experiments is a critical parameter affecting the success in biological control of *T. absoluta* using this parasitoid agent. Life table parameters of four *Trichogramma* species/populations reared on a factitious host (*E. kuehniella* eggs) under laboratory conditions yielded the highest values of growth

Table 3. Mean ± SE parasitism percentage of *T. absoluta* eggs by four *Trichogramma* populations in cages under greenhouse conditions.

% parasitism	Species			
	T. brassicae W^-	*T. brassicae* W^+	*T. principium*	*T. evanescens*
Upper leaves	9.65 ± 3.13^a	8.52 ± 2.08^a	3.49 ± 1.05^a	8.00 ± 2.31^a
Middle leaves	9.01 ± 2.40^a	4.88 ± 1.81^b	3.63 ± 1.50^a	4.23 ± 1.51^b
Lower leaves	4.81 ± 2.05^b	4.65 ± 1.97^b	2.38 ± 0.99^b	4.28 ± 1.29^b
	$F_{2,276} = 2.78$ $P = 0.038$	$F_{2,276} = 5.67$ $P = 0.021$	$F_{2,276} = 1.64$ $P = 0.037$	$F_{2,276} = 6.02$ $P = 0.030$
Mean ($F_{3,276} = 2.61$, $P = 0.042$)	7.82 ± 1.48^A	6.01 ± 1.13^A	3.17 ± 0.68^C	5.51 ± 1.02^B

Means followed by different lower case letters in each column and different capital letters in the row are significantly different ($P < 0.05$, LSD test).

and fertility parameters in *T. principium* and *T. evanescens* populations. *Wolbachia* infection had significant positive effects on parasitism percentage, female longevity, r_m and R_0 of *T. brassicae* populations. Subsequently, these four populations were further tested on *T. absoluta* eggs on a tomato leaflet during the first three days of the female wasp life span. The results showed that the most efficient *Trichogramma* wasps against *T. absoluta* was *T. evanescens* (about 27% parasitism rate), and parasitism percentage was significantly higher on the first day, compared to other days, in all populations. Furthermore, parasitism efficiency of these populations was tested on a larger scale, in cages under greenhouse conditions. The greenhouse results did not corroborate the laboratory data in that the highest parasitism efficiency was found in *T. brassicae* W^+ and W^- populations. Differences between laboratory and greenhouse results demonstrated that laboratory experiments are not sufficient for assessing the efficiency of natural enemies of *T. absoluta*. In addition to different environmental conditions in laboratory and filed-cage experiments, changes in searching ability of *Trichogramma* wasps on tomato leaves, which produce trichomes in large environments such as cages compared to confined areas such as tubes under laboratory conditions, can have a significant impact on the performance of the *Trichogramma* species parasitizing *T. absoluta*. Previous studies have demonstrated the susceptibility of *Trichogramma* wasps to plant trichomes (Kashyap *et al*., 1991; Romeis *et al*., 1999). Moreover, *Trichogramma* parasitism ability can be affected by the dispersal pattern of host eggs on a plant (Hassell, 1982). Naturally, *T. absolut*a eggs are laid individually by females on tomato leaves in a cage (Cocco *et al*., 2015), but laboratory experiments use an egg mass of *T. absoluta* on a leaflet in tubes.

The low efficiency of tested *Trichogramma* wasps for controlling *T. absoluta* shown by low parasitism rates (at the maximum level was 7.82%) can be attributed to several factors proposed by Chailleux *et al*. (2012). They tested European *Trichogramma* species/strains as a mean of controlling *T. absoluta* and concluded that the small size of *T. absoluta* eggs, compared to other hosts, as well as the unfavourable tomato plant characteristics may result in a low level of parasitism (Chailleux *et al*., 2012). In addition, studies on the efficiency of *Trichogramma* reared on factitious host species and then applied in a field to control other host species, have shown that host parasitism rates depend on the size of the factitious host eggs in that female wasps usually accept a host with same-size eggs or a host with eggs larger than their natal host eggs (Salt, 1940; El-Wakeil, 2007). *T. absoluta* eggs are three times smaller than *E. kuehniella* eggs (Chailleux *et al*., 2012), used as a host for rearing *Trichogramma* wasps in the present study.

Although our results showed low parasitism under greenhouse conditions, several species, especially *T. euproctidis*, *T. pretiosum* and *T. achaeae*, have been reported as effective biocontrol agents in tomato greenhouses with high parasitism levels (up to 90% parasitism) (Zappalà *et al*., 2013; El-Arnaouty *et al*., 2014;). Some researchers have considered multiple releases of *Trichogramma* wasps as a compensator for the low suitability of tomato, and *T. absoluta* eggs for wasp establishment and increasing wasp efficiency (Chailleux *et al*., 2012; Biondi *et al*., 2013; Chailleux *et al*., 2013; El-Arnaouty *et al*., 2014).

One of the effective factors of *Trichogramma* wasp efficiency in multiple releasing is their dispersal patterns within the host plant structure (Ables *et al*., 1980; Saavedra *et al*., 1997). Our cage experiment results revealed that all populations significantly preferred to parasitize host eggs laid on the upper leaves of tomato plants, except for *T. principium*, which parasitized eggs equally on both middle and upper leaves. This higher parasitism rate is in accordance with the oviposition behavior of *T. absoluta* females laying their eggs preferably on the upper part of host plants (Torres *et al*., 2001). Moreover, Faria *et al*. (2008) reported that levels of *T. absoluta* oviposition and parasitism by *T. pretiosum* were higher on the upper one-third of tomato plants and decreased towards the lower parts of the plants.

Our laboratory results showed that parasitism percentage and fertility life table parameters were different between species, and the host fitness of the species was affected by the *Wolbachia* infection state. Previous studies have reported biological variation between and within species of *Trichogramma* wasps (Ram *et al*., 1995; Scholler and Hassan, 2001; Kalyebi *et al*., 2005a; 2005b; Samara *et al*., 2008). Estimated fertility-life table values for *T. evanescens* obtained in the present study were similar to those reported in a study conducted by Poorjavad (2011) on four Iranian populations of these species collected from *O. nubilalis* eggs in a corn field. In the present study, the intrinsic increase rate, generation time and net reproductive rate estimated for *T. brassicae* species were in the ranges of 0.25-0.27 (day^{-1}), 13.1-13.3 (days), and 29.7-40.5 (offspring), respectively (table 1). Under same laboratory conditions, the obtained values for these variables were 0.28-0.32 (day^{-1}), 10.4-11.3 (days) and 24.6-41.1 (offspring), respectively, for eleven *T. brassicae* populations collected from *C. suppressalis* eggs in rice fields of northern Iran (Poorjavad *et al*., 2018). In *T. principium*, r_m, R_0, and T were 0.29 (day^{-1}), 56.0 (offspring) and 13.8 (days), respectively, while Poorjavad *et al*. (2011) reported higher values for these parameters, namely 0.25-0.27 (day^{-1}), 23.8-25.6 (offspring), and 11.9-12.6 (days), respectively, for three populations of *T. principium* collected from *E. ceratoniae* eggs in pomegranate orchards of central Iran. The observed differences between the results obtained by studies on Iranian populations of *T. brassicae* and *T. principium* are attributable to differences in their field-host, plant-host and climate adaptations.

Wolbachia infection showed positive effects on *T. brassicae* growth and parasitism ability of *E. kuehniella* eggs under laboratory conditions. However, this infection resulted in neutral and negative effects on *T. brassicae* wasps parasitizing *T. absoluta* eggs under laboratory and greenhouse conditions, respectively. These differences may be due to the negative effects of *Wolbachia* infection on wasps' foraging behaviour under greenhouse conditions. Effects of *Wolbachia* infection on the behaviour of *Trichogramma* wasps have rarely been studied. The results of a comparative study by Farrokhi *et al*. (2010) on the functional response of *Wolbachia* to infected and uninfected *T. brassicae* suggested that *Wolbachia* infected female wasps had a longer host-handling time than uninfected females. Almeida *et al*. (2010) also reported that the walking activity or walking speed of *Trichogramma atopovirilia* Oatman et Platner (Oatman and Platner, 1989) females was not affected by *Wolbachia* infection.

It can be concluded that *Trichogramma* species/strains released in tomato fields in Iran for several years against *H. armigera* are not effective biocontrol agents against *T. absoluta*. Effectiveness of other natural enemies of *T. absoluta* such as *M. caliginosus*, *N. tenuis*, and *P. nigrispinus*, which have naturally been observed in tomato fields of Iran (Baniameri and Cheraghian, 2012), and their combinations with insecticides should be considered in future studies to find an effective method with low environmental costs for controlling *T. absoluta* in Iran.

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