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BIOLOGICAL CONTROL

Dispersion and Persistence of *Trichogrammatoidea bactrae* (Nagaraja) over *Tuta absoluta* (Meyrick), in Tomato Greenhouses

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Abstract
Inundative biological control depends on the ability of natural enemies to disperse and persist in the environment. The objective was to evaluate the dispersion and persistence of *Trichogrammatoidea bactrae* (Nagaraja) on *Tuta absoluta* (Meyrick) eggs. Inundative releases of this parasitoid were performed in experimental tomato greenhouses. For vertical dispersion, leaves of the upper and middle third of plants were artificially infested with *T. absoluta* eggs; for horizontal dispersion, plants at increasing distances from a release point were infested. These eggs were renewed at days 2 and 4 to evaluate persistence. The amount of parasitized patches was registered. Logistic regression analysis was used. The position of the eggs in the plant did not affect the DE (discovery efficiency: proportion of parasitized patches). Time since release negatively affected the DE, while distance affected it only when plants were higher. These results could be used to adjust the release methodology of *T. bactrae*.

Introduction

Tomato (*Lycopersicon esculentum* Mill) is the most widely grown vegetable crop in greenhouses in Argentina (Rothman & Tonelli 2010). Several pests affect the tomato production causing serious economic losses. The tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is considered a key pest due to the severe damages caused by the larvae feeding on leaves, stems, and fruits (Estay & Bruna 2002, Desneux *et al* 2010). The use of insecticides to control *T. absoluta* is common but practiced alone this method of control is not sustainable and can be ineffective. Several factors contribute toward these failures, such as the larvae feeding behavior (penetrating in leaves, fruits, or stems), the selection of resistant populations to pesticides, and the negative effects over *T. absoluta* natural enemies (Siqueira *et al* 2000, Lietti *et al* 2005, Biondi *et al* 2012). Therefore, the development of more environmentally friendly control strategies, such as biological control, is strongly recommended.

Trichogrammatid wasps (Hymenoptera: Trichogrammatidae) are tiny egg parasitoids widely used to control lepidopteran pests worldwide by using both inoculative and inundative releases (Smith 1996, Parra & Zucchi 2004). Biological control of tomato leafminer with trichogrammatid parasitoids has been carried out through inundative releases of *Trichogramma pretiosum* Riley in Brazil (Villas-Bôas & França 1996, Pratissoli & Parra 2001, Medeiros *et al* 2005), *Trichogramma exigum* Pinto and Platner and *T. pretiosum* in Colombia (García-Roa & Jiménez 1996), *Trichogramma nerudai* Pintureau and Gerding and *Trichogrammatoidea bactrae* Nagaraja and *T. pretiosum* in Chile (Estay & Bruna 2002), and *Trichogramma achaeae* Nagaraja and Nagarkatti in Spain and France (Cabello *et al* 2009, Desneux *et al* 2010, Zappalà *et al* 2013). Furthermore, it has been observed that these parasitoids may be an important natural mortality factor of *T. absoluta* in organic tomato productions (Medeiros *et al* 2011). In Argentina, studies performed under laboratory conditions showed that *T. bactrae* is an efficient egg parasitoid of *T. absoluta* (Riquelme-Virgala & Botto 2010, 2011). Moreover, it was observed that this natural enemy could be compatible with the use of some insecticides commonly applied against *T. absoluta* (Riquelme-Virgala *et al* 2006). Although these features make *T. bactrae* a promissory biocontrol agent for *T. absoluta*, the performance of this parasitoid under greenhouse environment remains to be evaluated. In the field, the trichogrammatid wasp ability to locate and parasitize eggs could be influenced by the complexity of the habitat in which the female searches its host (Lawson *et al* 1997). When parasitoids are used in inundative programs, the aim is a quick effect of mass release rather than their establishment; the natural enemies must therefore move from the release points and spread throughout the infested area. The number of release points and the release frequency need to maximize parasitoid distribution in space and time, which is closely related to their ability to move away from a releasing point (dispersal capacity) and to maintain a high parasitic efficiency over time (persistence) (Parra & Zucchi 2004).

The objective of this study was to evaluate the dispersal capacity of *T. bactrae* and to estimate the persistence of its parasitic activity over *T. absoluta* in tomato greenhouses.

Material and Methods

The insects used in this study were obtained from the laboratory colonies maintained in the Insectario de Investigaciones para la Lucha Biológica, INTA Castelar. *Trichogrammatoidea bactrae* was reared on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), according to the modified protocol of Hassan (1997), and *T. absoluta* was reared on fresh tomato plants in wooden cages.

Since the parasitoid was introduced in the greenhouses in the pupal stage, control cards were used to check if the adult emergence and sex ratio met the standard quality criteria proposed by the IOBC (adult emergence > 80% and female proportion > 50%) (van Lenteren *et al* 1993, van Lenteren 2003). Each control consisted of a closed vial with a piece of cardboard with about 200 glued *T. bactrae* pupae, placed close to the releasing points.

Vertical dispersion

This study was carried out to evaluate the capacity of *T. bactrae* foraging for *T. absoluta* eggs within the tomato plant (moving up and down). The assay was conducted in three polyethylene experimental greenhouses of 40 m^2 located at INTA Castelar. Each greenhouse had eight rows with eight tomato plants cv. Daniela. One plant per row was randomly selected and artificially infested with *T. absoluta* fresh eggs (< 24 h old) (Fig 1). Six to eight (6–8) eggs were transferred with a fine paint brush along the main vein of two leaves, one positioned in the upper third of the plant nearby the terminal bud and the other in the middle third of the plant. Leaves of the upper and middle thirds were chosen because *T. absoluta* oviposit preferably leaves of these strata (Pratissoli *et al* 2003).

Opened plastic vials ($n = 12$) containing each a piece of cardboard with glued *T. bactrae* pupae ready to emerge were used as releasing devices. The vials were distributed two per row, in the six central rows. One vial per row was always positioned adjacent to an infested plant (Fig 1). The releasing devices were hanged in the middle third plant part. The released dose was 1067 *T. bactrae* pupae per device; the total number of pupae used per greenhouse was 12,800 (Riquelme-Virgala & Botto 2011). The first release of *T. bactrae* was made in the morning following the plant infestation with *T. absoluta* eggs. After 2 weeks, a new infestation and a second parasitoid release following identical procedures were performed.

Three days after the releases, infested leaflets were collected and placed in glass tubes in a Conviron E7 climatic chamber (25 ± 1°C, 60 ± 10% RH, and 14L:10D photoperiod). Eggs were observed daily in order to record parasitism symptoms. These were recognized by the dark coloration of the chorion on parasitized eggs (Hutchinson *et al* 1990). The infested plant height at the time of each release was measured.

Horizontal dispersion and persistence

This trial was conducted in two experimental greenhouses of 200 m^2 planted with tomatoes cv. Daniela. The horizontal dispersion was considered as the capacity of parasitoids to forage on tomato plants moving away from a release point set in the center of each greenhouse. Tomato plants located at increasing distances from the release point (2, 4, 8, 12, and 16 plants at 0.35, 0.70, 1.50, 2.25, and 3.00 m, respectively) were infested each with five fresh eggs of *T. absoluta* placed on one leaf of the upper third of the plant (Fig 2). In this way, the density of infested plants was consistently fixed at about one plant per meter of perimeter. A total of 12,800 *T. bactrae* pupae were released in the center of each greenhouse, with the same device previously described. The experiment was replicated twice with an interval time between releases of 2 weeks. The infested plant height was measured at each release.

To assess the persistence of the parasitoid activity during the horizontal dispersion study, *T. absoluta* eggs were renewed from the plant on days 2 and 4 after each release and the last batch of eggs was left in the field for 3 days. After each renewal, the infested leaves were placed in glass tubes

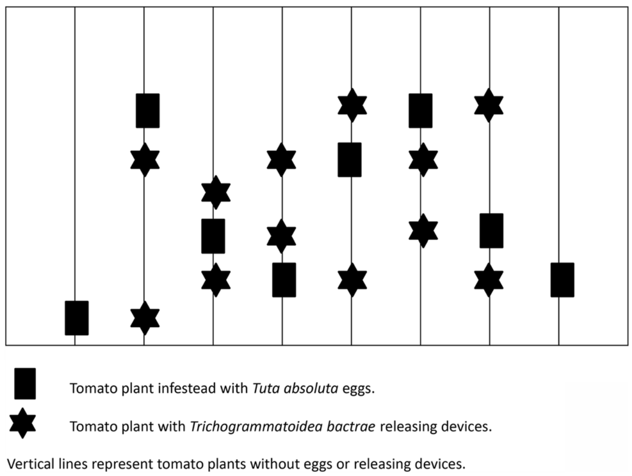

Fig 1 Experimental design of the vertical dispersion study. Each greenhouse had eight rows with eight tomato plants.

and kept in a climatic chamber under the same conditions as for the previous assay. Eggs were observed daily in order to record parasitism symptoms or moth emergence. At the beginning of the persistence assay, 4 traps with 50 sentinel *S. cerealella* eggs were placed in the perimeter of the greenhouse to observe whether *T. bactrae* spread out beyond the boundaries of the study area.

The maximum and minimum temperatures inside greenhouses were registered daily by a digital thermometer.

Statistical analysis

The dispersion capacity of *T. bactrae* in both vertical and horizontal dispersion was estimated by the discovery efficiency (DE) as defined by Bin & Vinson (1990): DE = PP / TP, where PP is the number of patches with at least one egg parasitized and TP is the total number of patches. The DE can be considered as an index that measures search capability, because it includes both the habitat discovery and the host encounter by the parasitoid (Bezemer & Mills 2000). The DE was analyzed by a logistic regression with the position of the egg within the tomato plant (top and middle) as the independent variable for the vertical dispersion study. In the horizontal dispersion and persistence trials, the independent variables were the distance (0.35, 0.70, 1.5, 2.2, and 3 m) from the release point and time (0–2, 2–4, and 4–7 days) after the release, respectively. In both studies, the greenhouse was considered as a block. The significance of the model parameters was estimated using the Wald statistic and the model fit by likelihood-ratio tests. The level of significance of the parameters considered was 0.10. Finally, the odds of each variable were calculated in the final model (Agresti 1996). GZM module (generalized linear models) of the STATISTICA software was used (STAT-SOFT 2000).

Results

Vertical dispersion

The height of the tomato plants at the first and second releases was 87.2 ± 1.39 and 119.0 ± 2.79 cm, respectively. The DE was not significantly affected by the height of the eggs within the plant ($Wald_{1(first\ release)} = 0.42$, $p = 0.53$; $Wald_{1(second\ release)} = 0.18$, $p = 0.67$) neither during the first nor the second release (Table 1).

Horizontal dispersion and persistence

The plant height at the time of the first and second release assays was 67.5 ± 1.29 and 92.9 ± 1.06 cm, respectively. During the first release, the DE of *T. bactrae* was affected by the distance foraged by the parasitoid from the release point ($Wald_{1(distance)} = 4.32$, $p = 0.04$) (Fig 3A). The DE decreased significantly for *T. bactrae* considering the elapsed time from the release moment ($Wald_{1(time)} = 56.83$, $p < 0.001$) (Fig 3A). The odds for the distance and for the time (Table 2) suggest that the chance to find a patch with parasitism is reduced by 33% for every meter away from the release point and 51% for each day after the releases take place.

During the second release assay, both the distance from the release point and the time after release had significant effects on DE ($Wald_{1(distance)} = 3.30$, $p = 0.07$, $Wald_{1(time)} = 27.76$, $p < 0.001$). According to the odds, the probability that a patch presents parasitism decreases by 28% for every meter away from the release point and by 37% for each day after the releasing time (Table 2) (Fig 3B).

Discussion

Vertical dispersion studies showed that the parasitoid forage within the plant was not affected by the strata (middle or upper third). DE values ranged between 90 and 70% egg patches found during the first and second release, respectively. Pratissoli *et al* (2005) found no differences between rates of parasitism of *T. absoluta* eggs by *T. pretiosum* at the three strata, top, middle, and bottom of tomato plants. Some authors agree that the search activity of a female parasitoid is strongly related to the oviposition sites preferred by their lepidopteran host, due primarily to the chemical signals that the moth leaves while laying eggs (Arantes-Faria *et al* 2008), while in other studies, this relationship was not evident (Wang *et al* 1997). *Tuta absoluta* females mainly oviposit on the leaves of the upper and middle tomato plant strata (Torres *et al* 2001, Pratissoli *et al* 2003, Riquelme-Virgala & Botto 2011). Although in this experiment the parasitoid behavior would have not been influenced by the marks left by female moths because the egg

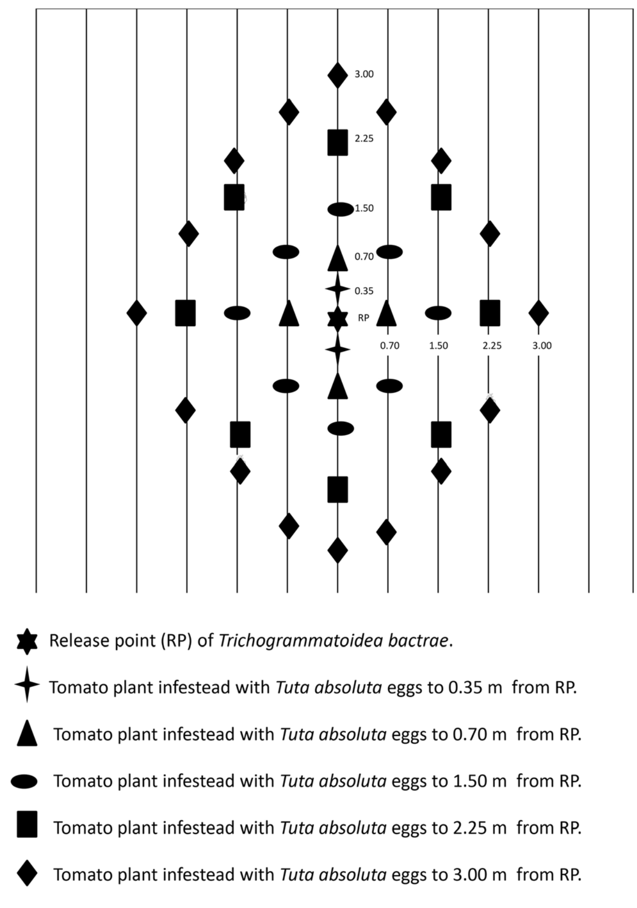

Fig 2 Experimental design of the horizontal dispersion and persistence study. Each greenhouse had 11 rows 20 m long with tomato plants. In the schematic diagram, only the tomato plants infested with *Tuta absoluta* eggs are shown.

deposition was artificial, the high levels of egg parasitism found in the upper and middle strata of the plant show that *T. bactrae* can forage and parasitize eggs at sites preferred for oviposition by *T. absoluta*.

In the horizontal dispersion experiment, when the height of the plants was still low (first release), the female parasitoids reached the maximum distance studied within the first 2 days after release and the DE ranged between 67 and 46% on average at 0.35 and 3.0 m from the release point, respectively. When the plants were taller (second release), the horizontal dispersion of *T. bactrae* also decreased with the distance, showing a DE that averaged between 58% at 0.35 m and 29% at 3.0 m. Sarhan *et al* (2015) studied the dispersal ability of *T. bactrae* and three *Trichogramma* spp. and showed that the percentages of parasitism decreased as distance from releasing point increased. Pratissoli *et al* (2005) found that *T. pretiosum* spreads by 7.5 m 1 day after the release on open field tomatoes, while Wang & Shipp (2004) observed a significantly lower dispersal capacity for the same species (from 0.4 to 0.9 m per day) in greenhouse tomato crop. These authors attributed this behavior to the lower effect of wind on flight capacity in protected crops. In general, the literature agrees that trichogrammatids can only fly short distances helped by wind and continuity of foliage (Mahrughan *et al* 2015) and in the direction of the light (Brower 1990). Moreover, there is a decrease in the parasitism at greater distances from the release point in the range between 4 and 50 m (Smith 1996). In this study, the DE decreases with the distance might be a consequence of the reduced effect of the wind inside the greenhouse. According to this literature about other *Trichogramma* spp., *T. bactrae* females could have reached longer distances than the maximum assessed (3 m) in this study which means that the dispersal potential of *T. bactrae* could have been underestimated. However, it is important to point out that the female DE observed in the sentinel traps placed in the perimeter of the greenhouse was on average 10% (data not shown) which suggests that dispersion beyond the experimental plot was low.

Other authors also observed a negative correlation between parasitism and distance in other trichogrammatid crop systems evaluated (Kanour & Burbutis 1984, Wang *et al* 1997, Ayvaz *et al* 2008, de Freitas Bueno *et al* 2011, Hegazi *et al* 2012, Mahrughan *et al* 2015, Sharma & Aggarwal 2015). This behavior can be attributed to the fact that, when the distance increases, there is higher number of plants and consequently a greater potential area to search. Therefore, there is smaller number of parasites per area and accordingly fewer patches found (Kanour & Burbutis 1984). The fact that in this experiment, the distance affected searching efficiency in both releases indicates that even small plants (first release) represent a complexity in the environment in terms of more potentially available searching sites. Ayvaz *et al* (2008) and de Freitas Bueno *et al* (2011) suggested that not only the leaf area but also the architecture of the crop plant (the variation among plant parts, such as seed heads, flowers and nectaries, and leaves with heterogeneous surfaces) could affect the ability of dispersion of *Trichogramma*. The species *Lycopersicon esculentum* lacks glandular trichomes that could interfere with the performance of trichogrammatids. However, some authors have suggested that the density of trichomes, even the non-glandular trichomes, may affect the ability of parasitism (Kauffman & Kennedy 1989, Arantes-Faria *et al* 2008). Therefore, the system complexity in the crop, besides the plant height, influences parasitoid behavior through the leaf area and the physical barriers that the females should overcome in their search.

Regarding the persistence of female activity within the greenhouse, the results obtained showed that females' DE is negatively correlated with time which is an expected output considering females' survivorship and fertility from the releasing time onwards. It is known that for *T. bactrae*, the maximum

Table 1 Discovery efficiency (DE) of *Trichogrammatoidea bactrae* (% of parasitized patches) in different tomato plant strata (vertical dispersion).

Plant stratum	Discovery efficiency (%)*	
	First release	Second release
Upper third	90.28 ± 5.01	73.61 ± 6.05
Middle third	95.83 ± 4.17	77.98 ± 4.87

*Means (± SE) within columns are not significantly different (logistic regression analysis; $\alpha = 0.10$).

Table 2 Effect of distance and time on discovery efficiency (DE) of *Trichogrammatoidea bactrae* on greenhouse grown tomatoes. *LR* logistic regression.

Release	Variable	LR coefficient*	Odds*
First	Time	− 0.72 (− 0.88; − 0.56)	0.49 (0.42; 0.57)
	Distance	− 0.40 (− 0.71; − 0.08)	0.67 (0.49; 0.92)
Second	Time	− 0.46 (− 0.61; − 0.33)	0.63 (0.54; 0.73)
	Distance	− 0.32 (− 0.61; − 0.03)	0.72 (0.54; 0.97)

*Coefficient (confidence interval of 95%).

fertility occurs within the first 4 days of its lifespan (Hutchinson *et al* 1990, Naranjo 1993, Riquelme-Virgala & Botto 2010).

Up to 4 days after the release, the DE ranged between 50 and 76% on average for the two releases carried out, but DE dropped dramatically after this period. This is consistent with the results observed by Coelho *et al* (2016) who found that the percentage of *Ephestia kuehniella*: Zeller egg patches parasited by *T. pretiosum* in maize decreased significantly with the time from the release (the parasitoids had the capacity to parasitize and persist at least for 3 days under field conditions). They estimated that the parasitoid activity in the field was reduced due to adverse environmental conditions. In our work, the maximum temperatures were 36 and 38°C for the first and second release, respectively. Naranjo (1993) and Riquelme-Virgala & Botto (2011) showed that high temperatures affect some biological parameters of this species so the temperatures developed in the assays could have reduced the survival of females.

In order to achieve an adequate female parasitoid activity during some days, Lawson *et al* (1997) recommended introducing into the crop a mixture of parasitized eggs of different ages. However, this procedure does not seem advisable for our system since Riquelme-Virgala & Botto (2011) observed high mortality when early preimaginal stages of *T. bactrae* were exposed to extreme temperatures similar to those registered in a greenhouse during tomato growing. On the other hand, in order to improve the efficiency of the parasitoids over the space, Hegazi *et al* (2012), Mahrughan *et al* (2015), and Sharma & Aggarwall (2015) suggest multiple releasing points to achieve an effective dispersal in the crop area and enough population of parasitoids in the field.

According to the results presented herein, to achieve a DE higher than 60%, the frequency of *T. bactrae* releases should be 4 days and the amount of release points should depend on the plant size. In the first release, with small plants, release points should cover an area of about 30 m^2 (3 m radius). As plants grow, the number of release points should be adjusted to cover a smaller area. Wang & Shipp (2004) recommended one release point per square meter of greenhouse tomato crop to ensure acceptable levels of parasitism (65%) of *Keiferia lycopersicella* (Walsingham) eggs by *T. pretiosum*.

This study provides information about the potential use of *T. bactrae* to control *T. absoluta* in greenhouse tomatoes. However, further assays with natural pest infestations along the entire crop cycle will be needed to evaluate the role of the moth semiochemicals and to estimate the effect of the releases on both the pest population density and on the damage caused by the pest on the crop.

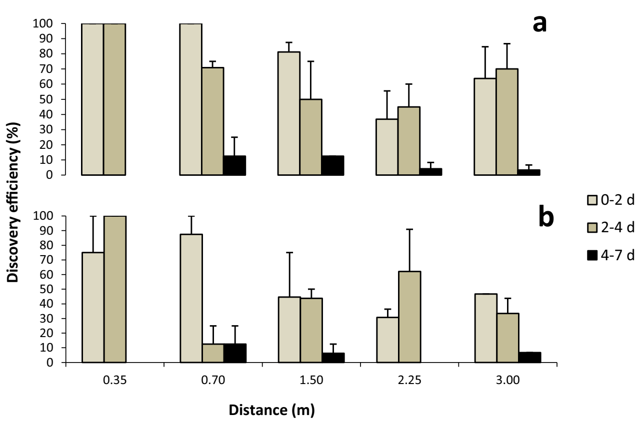

Fig 3 Effect of distance (horizontal dispersion) and time (persistence) on the discovery efficiency (DE) of *Trichogrammatoidea bactrae* (mean + SE). **A** First release. **B** Second release. T1, 0–2 days; T2, 2–4 days; and T3, 4–7 days represent days after release.

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