

Original Article

Do fall armyworm's Metaflumizone resistente populations affect the activity of *Trichogramma pretiosum*?

Populações da lagarta-do-cartucho resistentes à Metaflumizone afetam a atividade de *Trichogramma pretiosum*?

M. G. Barbosa^a , S. A. Souza^{b*} , T. P. P. André^c , A. D. S. Pontes^c , C. S. Teixeira^c , F. F. Pereira^d  and P. L. Pastori^c 

^aIN Soluções Biológicas LTDA, Fortaleza, CE, Brasil

^bUniversidade de São Paulo – UNESP, Faculdade de Ciências Agrônomicas, Departamento de Proteção de Plantas, Botucatu, SP, Brasil

^cUniversidade Federal do Ceará – UFC, Departamento de Fitotecnia, Laboratório de Entomologia Aplicada, Fortaleza, CE, Brasil

^dUniversidade Federal da Grande Dourados – UFGD, Faculdade de Ciências Biológicas e Ambientais, Dourados, MS, Brasil

Abstract

The possible interference of resistant pest's populations to insecticides in natural enemies in the action has not been clarified yet. Thus, this study aimed to evaluate *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) performance on *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) eggs with resistance frequency to the Metaflumizone over six generations of product exposure. Egg cards (2.0 x 7.0 cm) containing eggs from two populations of *S. frugiperda*, (resistant to Metaflumizone and the other susceptible), were exposed to *T. pretiosum* females for 24 hours in free-choice and no-choice testing in three generations (G₁, G₄, and G₆). A completely randomized experimental design was used with 25 replications, each consisting of an egg card (experimental unit) containing 20 eggs. The parameters evaluated were: parasitism (%), emergence (%), sex ratio, number of emerged parasitoids per egg and males/females longevity. ANOVA and Tukey test (P ≤ 0.05) were applied on the results. Results showed a reduction in parasitism [41.0% (G₁) and 28.4% (G₄)], egg emergence (17.5%) and parasitoids/egg [16.2 (G₄) and 17.2 (G₆)] in eggs originating from the population with resistance frequency. Females emerging from G₆ populations eggs without exposure to Metaflumizone had greater longevity (3.5 days more) than the resistant population. The sex ratio and male longevity were not affected. The results indicate a reduction in *T. pretiosum* activity if *S. frugiperda* populations have some frequency of resistance to Metaflumizone.

Keywords: biological control, fitness cost, insect resistance, parasitism, *Spodoptera frugiperda*.

Resumo

A possível interferência de populações de pragas resistentes na ação de inimigos naturais ainda não foi esclarecida. Assim, este trabalho teve como objetivo avaliar o desempenho de *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) em ovos de *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) com frequência de resistência à Metaflumizone ao longo de seis gerações de exposição ao produto. Cartelas (2,0 x 7,0 cm) com ovos de duas populações de *S. frugiperda*, (resistente à Metaflumizone e outra suscetível), foram expostas às fêmeas de *T. pretiosum* por 24 horas em condições de livre escolha e sem chance de escolha por três gerações (G₁, G₄ e G₆). O delineamento experimental foi inteiramente casualizado com 25 repetições, sendo cada repetição composta por uma cartela (unidade experimental) contendo 20 ovos. Os parâmetros avaliados foram: parasitismo (%), emergência (%), razão sexual, número de parasitoides emergidos por ovo e longevidade de machos e fêmeas. ANOVA e teste de Tukey (P ≤ 0,05) foram aplicados aos dados coletados. Os resultados mostraram redução do parasitismo [41,0% (G₁) e 28,4% (G₄)], emergência de ovos (17,5%) e parasitoides/ovo [16,2 (G₄) e 17,2 (G₆)] em ovos oriundos da população com frequência de resistência. As fêmeas emergidas de ovos da população G₆ sem exposição à Metaflumizone, tiveram maior longevidade (3,5 dias a mais) do que a população exposta ao inseticida. A razão sexual e a longevidade de machos não foram afetadas. Os resultados indicam uma redução na atividade de *T. pretiosum* se as populações de *S. frugiperda* apresentarem alguma frequência de resistência à Metaflumizone.

Palavras-chave: controle biológico, custo adaptativo, resistência de insetos, parasitismo, *Spodoptera frugiperda*.

*e-mail: suyanne-araujo@hotmail.com

Received: November 4, 2020 – Accepted: June 7, 2021



This is an Open Access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

1. Introduction

In spite of the diversity of control techniques, insecticides also constitute the basis of management practices to reduce damage caused by *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). However, adoption of a control strategy with solely on systematic applications of insecticides without rotation of active ingredients is bound to fail (Furlong et al., 2004; IRAC, 2021), leading to an increase in the percentage of damage due to the selection of resistant populations. Considering this situation, the adoption of some strategies that retard or reduce the development of resistance, associated with changes in the conception and behavior of growers, is of utmost importance.

Among the management practices inserted in a context of Integrated Pest Management (IPM), the natural enemies as the basis of practices for effective control of pest arthropods has been widely recognized (Furlong, 2015). In the case of *S. frugiperda*, control has been carried out through release of parasitoids of the genus *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) (Beserra et al., 2005; Dequech et al., 2013; Figueiredo et al., 2015; Balestrin and Bordin, 2016) that are used in programs of applied biological control since these agents parasitize the egg phase of the pest and impede the emergence of caterpillars and thus does not occur their attack. In Brazil, the natural occurrence of *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) parasitizing eggs of *S. frugiperda* (Beserra et al., 2002; Dequech et al., 2013; Balestrin and Bordin, 2016) offers good perspectives for its application because, in addition to its ability to act on the target pest, this parasitoid is easily rearing in the laboratory conditions.

Nevertheless, for this natural enemy to be effectively used, its activity, behavior, and efficiency must be understood (Barbosa et al., 2019) in its host. It is known that females of these parasitoids have strategies that facilitate identification of a quality host through surface contact of antennae (Bento and Nardi, 2012). Thus, the sequence of the activities of search and recognition behavior assist the female in identifying specific chemical or physical signs of the host; this helps in the decision of accepting the host or not for oviposition or even identifying if the host is nutritionally adequate or is sufficient for complete development of its offspring (Roriz et al., 2006; Brotodjojo and Walter, 2006).

In a biological control program, the capacity of the parasitoid to parasitize or develop in the host is a crucial step, because the existence of some characteristic that avoids oviposition or inhibits development of the parasitoid can cause failure in parasitism and, consequently, in control of the pest (Pereira et al., 2013). It is not known if physiological and metabolic changes involved in the process of evolution of resistance (Dingha et al., 2004; Guedes et al., 2006) affect specific characteristics of the host that interfere in the recognition and establishment processes of parasitoids. Thus, possible interferences of populations with frequency of resistance to insecticides on the action of natural enemies have not yet been duly clarified. Although *T. pretiosum* is highly used in biological

control programs throughout the world, information is still scarce in regard to its activity and efficiency, as well as how the biological characteristics of its offspring are affected when they find eggs of hosts that have a certain resistance to some insecticide. Such studies should be carried out to develop knowledge regarding the association of *T. pretiosum* in control of pests that have resistance to insecticides, and regarding recommendation of *T. pretiosum* in these cases.

Thus, the aim of this study was to evaluate the performance of *T. pretiosum* on eggs of populations of *S. frugiperda* with frequency of resistance to the insecticide Metaflumizone and exposure to the product over six generations.

2. Material and Methods

The experiment was conducted in the "Laboratório de Entomologia Aplicada - LEA" of the "Universidade Federal do Ceará (UFC)", Fortaleza, Ceará State, Brazil. The "guaraciaba" line of *T. pretiosum* used was collected when naturally parasitizing eggs of *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae) on tomato (*Solanum lycopersicum* L.) fruit (Oliveira et al., 2020). The population of *S. frugiperda* with frequency of resistant individuals was collected in commercial areas in the municipality of Quixeré, Ceará (Latitude 5°44'0"S, Longitude 7°59'7"W, and mean Altitude of 25.0 m AMSL), with mean maximum temperature of 35.0°C and mean minimum of 22.0°C. The system used to rearing *T. pretiosum* followed the method described by Parra (1997).

The experiment was conducted with eggs from two populations of *S. frugiperda* (one resistant population maintained under selection pressure for resistance to metaflumizone and the other without exposure to the product, considered the susceptible population), over six generations. The characterization of the resistance frequency of the populations used is described in Barbosa et al. (2020). The Metaflumizone, semicarbazone chemical group, is sodium channel inhibitor (SCI) insecticides by binding selectively to slow-inactivated (non-conducting) sodium channel states (Takagi et al., 2007; Song et al., 2011). No-choice (G_1 , G_4 , and G_6) and free-choice (only in G_6) trials were carried out. Both populations were kept in the laboratory in glass tubes (2.5 cm x 8.5 cm), containing an artificial diet (Greene et al., 1976).

To conduct the experiment, eggs from each population were placed on blue paperboard cards (8.0 x 2.5 cm) using gum arabic (30%) with the assistance of a moistened brush. In the no-choice test, each egg card (experimental unit) was composed of 20 eggs from one of the two populations. In the free-choice test, each egg card was composed of 10 eggs from both populations, for a total of 20 eggs per treatment. Before being offered to the parasitoids, the eggs were made inviable through exposure to a germicidal lamp for 30 minutes, preventing possible eclosion of non-parasitized caterpillars and loss of data since the caterpillars are cannibalistic.

The cards containing inviable eggs from one of the two populations in separation (no-choice cards) or containing inviable eggs from the two populations on the same

card (free-choice cards) were inserted in glass tubes (8.5 x 2.5 cm) containing a female parasitoid, where they remained exposed to parasitism for 24 hours. The tubes were closed with PVC plastic film to prevent the parasitoids from escaping. The female parasitoids were fed with a drop of pure honey placed on the wall of the tubes. After exposure, the cards were transferred to new glass tubes (8.5 x 2.5 cm) and they were placed under controlled conditions (25 ± 2°C, relative humidity of 70±10% and 12-hour photoperiod), remaining up to emergence of the following generation of the parasitoids.

The percentage of parasitism [(number of parasitized eggs / total number of eggs) x 100], percentage of emergence [(number of dark eggs with orifice / total number of parasitized eggs) x 100], sex ratio [number of emerged females / (number of females + males)], number of emerged parasitoids per egg (number of emerged parasitoids / total number of parasitized eggs), and the longevity (days) of males and females were the parameters evaluated in the no-choice test. For evaluation of this last parameter, 20 females and 10 males that had recently emerged were individualized in acrylic containers (3.5 x 1.5 cm) containing a drop of honey for food, and they were evaluated daily regarding time of life. In the free-choice test, performed in G₆, only the percentage of parasitism and of emergence were evaluated.

The experiments were conducted in a completely randomized experimental design, with 25 replications;

each replication consisted of an egg card containing 20 eggs. The data were submitted to the Shapiro-Wilk normality and Bartlett parametric variance homogeneity tests. ANOVA was used to analyze the data and the means were compared by the Tukey test (p ≤ 0.05) through the Statistical Analysis System (SAS) (SAS INSTITUTE, 2004).

3. Results

Parasitism of *S. frugiperda* eggs by *T. pretiosum* decreased in populations that were sequentially exposed to the insecticide Metaflumizone (G₁ and G₄), with reduction of approximately 41.0% and 28.4% (Table 1). In regard to emergence, 82.7% of the eggs of the population exposed to the insecticide, when parasitized, allowed emergence of the adults of the parasitoid but, even so, there was reduction of 17.5% compared to the control (Table 1).

Emergence of more than one parasitoid per egg was found in both host populations evaluated (minimum of 1.02 and maximum of 1.32 parasitoids / egg); however, there was a decrease of 16.2% and 17.2% when the populations were exposed to the insecticide in G₄ and G₆, respectively (Table 1).

Females of *T. pretiosum* that emerged from eggs coming from populations in G₆ maintained without exposure to the insecticide Metaflumizone lived longer; longevity was 3.5 days longer for these females than that of the

Table 1. Parasitism (%); emergence (%); sex ratio; number of adults emerged per egg; longevity (days) of *T. pretiosum* “guaraciaba” line, in eggs of two populations of *S. frugiperda* over six generations in a no-choice test.

Population	Generation (Mean ± standard error)		
	G ₁	G ₄	G ₆
	Parasitism		
Susceptible	86.23 ± 2.04 a	86.15 ± 2.10 a	82.96 ± 2.95 a
MET ¹	64.40 ± 4.38 b	75.52 ± 2.09 b	78.65 ± 3.88 a
	Emergence		
Susceptible	97.74 ± 0.84 a	100.00 ± 0.00 a	99.25 ± 0.35 a
MET	81.13 ± 4.71 b	89.66 ± 5.66 b	77.23 ± 6.71 b
	Sex ratio		
Susceptible	0.67 ± 0.04 a	0.75 ± 0.02 a	0.57 ± 0.05 a
MET	0.62 ± 0.05 a	0.73 ± 0.05 a	0.51 ± 0.06 a
	Parasitoids/egg		
Susceptible	1.41 ± 0.07 a	1.42 ± 0.04 a	1.22 ± 0.08 a
MET	1.28 ± 0.05 a	1.19 ± 0.03 b	1.01 ± 0.07 b
	Longevity of the female (days)		
Susceptible	6.68 ± 0.22 a	9.89 ± 0.35 a	13.42 ± 0.73 a
MET	6.23 ± 0.15 a	9.48 ± 0.53 a	9.89 ± 0.35 b
	Longevity of the male (days)		
Susceptible	5.76 ± 0.59 a	9.10 ± 0.48 a	10.26 ± 0.66 a
MET	5.50 ± 0.20 a	9.18 ± 0.68 a	9.09 ± 0.48 a

Mean values followed by the same lowercase letter in the column do not differ from each other by the Tukey test at the level of 5% 1MET = population with frequency of resistance to the insecticide metaflumizone.

population exposed to the product (Table 1). Regarding longevity of the males, only an effect of the generation factor was observed, with a mean of 5.6 in G₁ and 9.40 days in the G₄ and G₆ generations (Table 1).

The longevity of males and the sex ratio were not affected by the populations evaluated, and exhibited a variation from 5.50 to 10.26 and 0.51 to 0.75, respectively (Table 1).

In the free-choice test, there was a reduction in the percentage of parasitism of *S. frugiperda* and of emergence of *T. pretiosum* adults of 16.3% and 24.1%, respectively, in the trial with the *S. frugiperda* population resistant to the insecticide Metaflumizone (Table 2).

4. Discussion

Based on the results obtained and on knowledge regarding the behavior of *T. pretiosum* in regard to host selection, it can be inferred that female parasitoids rejected the “resistant” *S. frugiperda* host in the tests of free choice and no choice; and the eggs of this host, when parasitized, affected parameters related to the development of the offspring of *T. pretiosum*. The exploratory characteristic of the parasitoid species (Roriz et al., 2006; Brotodjojo and Walter, 2006) indicates that the females of *T. pretiosum*, distinguished differences in the host eggs and consequently rejected them in some moment by means of some external or internal signal present in the host egg coming from individuals that developed under the conditions of exposure to the insecticide. In initial contact with the host eggs, signals are recognized by the antennae, and for insertion of the ovipositor, the females need to perfectly evaluate the external and internal conditions of the host eggs (Desneux et al., 2012; Alsaedi et al., 2016; Damien et al., 2019). This evaluation determines acceptance or non-acceptance of the host for oviposition, according to its nutritional quality (Roriz et al., 2006), ensuring the success of the offspring of the parasitoid (Roriz et al., 2006; Brotodjojo and Walter, 2006).

Synergy trials conducted in populations of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) showed that resistance to Metaflumizone is associated with metabolic changes involving an increase in esterase (Su and Sun, 2014; Tian et al., 2014) and monooxygenase (Tian et al., 2014) activity. It is nothing new that these changes can result in an adaptive cost associated with resistance (Gould, 1998), where resources used by the physiological processes of the insect are allocated and used in a different manner, influencing metabolic processes and development in

resistant lines and in evolution (Dingha et al., 2004; Guedes et al., 2006). The adaptive cost has already been observed in *S. frugiperda* resistant to the insecticides and resistance plants (Santos-Amaya et al., 2017; Okuma et al., 2018), and also in *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) resistant to Metaflumizone (Shen et al., 2017). This indicates that, as resistance evolves, these metabolic changes can modify components in the chorion (egg membrane) or in its inner content, affecting the development of the parasitoid larvae and leading to reduction in emergence in the number of parasitoids / egg, and in the longevity of emerged females.

The number of parasitoids per egg that emerged from the population of *S. frugiperda* exposed to Metaflumizone was lower than the number of parasitoids per egg that emerged from the susceptible population. The surface contact and recognition of the host (Roriz et al., 2006; Brotodjojo and Walter, 2006) may have resulted in rejection of females in laying more than one egg in the host given the possibility of it not being able to ensure development of its offspring. The sign of a larger number of parasitoids / egg and of longer-living females of *T. pretiosum* in contact with the susceptible population shows that this parasitoid has greater probability of increasing its population in a shorter period of time than the *T. pretiosum* population in contact with *S. frugiperda* exposed to Metaflumizone.

Resistance to insecticides occurs through mutations that substitute alleles (Thomazoni, 2012), and selection pressure promotes genotypic variation from the initial population (Roush and McKenzie, 1987). Studies performed with *P. xylostella* suggest an effect on parasitism of *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae) and of *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) when the caterpillars exposed to parasitism come from host populations that have resistance to the insecticide teflubenzuron (Furlong and Wright, 1993). In contrast, possible effects were not found in *Camponotus flavicincta* (Ashmead) (Hymenoptera: Ichneumonidae) acceptance of *S. frugiperda* caterpillars susceptible and resistant to lambda-cyhalothrin (Thomazoni, 2012).

A noteworthy fact is that even with negative interference in parasitism of *T. pretiosum* caused by the eggs coming from the population of *S. frugiperda* that showed frequency of resistance, the parasitoid still maintained satisfactory performance, with a mean value greater than 70.0%. This shows the potential of this agent in reducing the damage caused by *S. frugiperda* even if the population has a certain degree of resistance to metaflumizone, thus emphasizing its use as a strategy that favors management of resistance to insecticides. It should also be emphasized that in the

Table 2. Parasitism (%) and emergence (%) of *T. pretiosum* “guaraciaba” line, in eggs of two populations of *S. frugiperda* in a free-choice test in G₆.

Population	Parameters (Mean ± standard error)	
	% Parasitism	% Emergence
Susceptible	93.75 ± 2.34 a	92.33 ± 2.24 a
MET ¹	84.70 ± 3.88 b	77.78 ± 2.94 b

Mean values followed by the same lowercase letter in the column do not differ from each other by the F test at the level of 5% probability. ¹MET= population with frequency of resistance to the insecticide metaflumizone.

field, there is a “coevolutionary” process that integrates parasitoids × hosts (Henter and Via, 1995), which cannot be evaluated in the laboratory under the same conditions as in the field, due to its complexity. Thus, the interference in the biological parameters examined was expressed in the most extreme condition. In a scenario where there are possibilities of development of physiological resistance on the part of the host, the parasitoids develop some manners of counter-attacking this resistance as time passes (Debolt, 1991). The reduction in parasitism in the population of *S. frugiperda* exposed to metaflumizone occurred in the first two generations and in artificially selected populations. It is known that through genetic drift, populations maintained in the laboratory can undergo changes associated with genetic control, resulting in effects of selection in existing genotypes and random loss of genotypes (Bartlett, 1985).

The results obtained in this study contribute useful information for planning possible management strategies for the purpose of retarding development of resistant populations of *S. frugiperda*. The interference observed in the performance of *T. pretiosum* highlights the importance of how erroneous use of insecticides can hurt the activity of natural enemies. However, *T. pretiosum* can still be successfully used in management programs within IPM because this parasitoid maintains its effectiveness even when in the presence of resistant populations in the field. The possibility of reversal of susceptibility when the use of insecticides is adopted in a correct manner (Barbosa et al., 2020) shows signs that joining diverse tactics in MRI can retard the evolution of frequency of resistance.

Acknowledgements

To “Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)”, “Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)” and the “Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP)” for the study scholarships.

References

- ALSAEDI, G., ASHOURI, A. and TALAEI-HASSANLOUI, R., 2016. Behavioral responses of the three *Trichogramma* species to different odor sources. *Journal of Entomology and Zoology Studies*, vol. 4, pp. 19-24.
- BALESTRIN, A.L. and BORDIN, S.S., 2016. Uso de *Trichogramma pretiosum* no controle de *Spodoptera frugiperda* em lavoura de milho. *Revista Eletrônica Científica da UERGS*, vol. 2, pp. 259-266. <http://dx.doi.org/10.21674/2448-0479.23.259-266>.
- BARBOSA, M.G., ANDRE, T.P.P., PONTES, A.D.S., SOUZA, S.A., OLIVEIRA, N.R.X. and PASTORI, P.L., 2020. Insecticide rotation and adaptive fitness cost underlying insecticide resistance management for *Spodoptera frugiperda* (Lepidoptera: noctuidae). *Neotropical Entomology*, vol. 49, no. 6, pp. 882-892. <http://dx.doi.org/10.1007/s13744-020-00800-y>. PMID:32632568.
- BARBOSA, R.H., PEREIRA, F.F., MOTOMIYA, A.V.A., KASSAB, S.O., ROSSONI, C., TORRES, J.B., MUSSURY, R.M. and PASTORI, P.L., 2019. *Tetrastichus howardi* density and dispersal toward augmentation biological control of sugarcane borer. *Neotropical Entomology*, vol. 48, no. 2, pp. 323-331. <http://dx.doi.org/10.1007/s13744-018-0646-z>. PMID:30456722.
- BARTLETT, A.C., 1985. Genetic changes during insect domestication. In: E.C. King and N.C. Leppla, ed. *Advances and challenges in insect rearing*. New Orleans: Agricultural Research Service, pp. 2-8.
- BENTO, J.M.S. and NARDI, C., 2012. Bioecology and nutrition versus chemical ecology: the multitrophic interactions mediated by chemical signals. In: A.R. Panizzi and J.R.P. Parra, ed. *Insect bioecology and nutrition for integrated pest management*. Boca Raton: CRC Press, pp. 163-175. <http://dx.doi.org/10.1201/b11713-9>.
- BESERRA, E.B., DIAS, C.T. and PARRA, J.R.P., 2005. Behavior of *Trichogramma atopovirilia* Oatman & Platner and *T. pretiosum* Riley (Hymenoptera: Trichogrammatidae) on *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) egg masses. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 65, no. 1, pp. 9-17. <http://dx.doi.org/10.1590/S1519-69842005000100003>. PMID:16025898.
- BESERRA, E.B., DIAS, C.T.S. and PARRA, J.R.P., 2002. Distribution and natural parasitism of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) eggs at different phenological stages of corn. *The Florida Entomologist*, vol. 85, no. 4, pp. 588-593. [http://dx.doi.org/10.1653/0015-4040\(2002\)085\[0588:DANPOS\]2.0.CO;2](http://dx.doi.org/10.1653/0015-4040(2002)085[0588:DANPOS]2.0.CO;2).
- BROTODJOJO, R.R.R. and WALTER, G.H., 2006. Oviposition and reproductive performance of a generalist parasitoid (*Trichogramma pretiosum*) exposed to host species that differ in their physical characteristics. *Biological Control*, vol. 39, no. 3, pp. 300-312. <http://dx.doi.org/10.1016/j.biocontrol.2006.08.011>.
- DAMIEN, M., BARASCOU, L., RIDEL, A., BAAREN, J.V. and LANN, C., 2019. Food or host: do physiological state and flower type affect foraging decisions of parasitoids? *Behavioral Ecology and Sociobiology*, vol. 73, no. 11, pp. 156. <http://dx.doi.org/10.1007/s00265-019-2758-9>.
- DEBOLT, J.W., 1991. Behavioral avoidance of encapsulation by *Leiophoron uniformis* (Hymenoptera: Braconidae), a parasitoid of *Lygus* spp. (Hemiptera: Miridae): Relationship between host age, encapsulating ability, and host acceptance. *Annals of the Entomological Society of America*, vol. 84, no. 4, pp. 444-446. <http://dx.doi.org/10.1093/aesa/84.4.444>.
- DEQUECH, S.T.B., CAMERA, C., STURZA, V.S., RIBEIRO, L.P., QUERINO, R.B. and PONCIO, S., 2013. Population fluctuation of *Spodoptera frugiperda* eggs and natural parasitism by *Trichogramma* in maize. *Acta Scientiarum. Agronomy*, vol. 35, pp. 295-300.
- DESNEUX, N., BLAHNIK, R., DELEBECQUE, C.J. and HEIMPEL, G.E., 2012. Host phylogeny and host specialisation in parasitoids. *Ecology Letters*, vol. 15, no. 5, pp. 453-460. <http://dx.doi.org/10.1111/j.1461-0248.2012.01754.x>. PMID:22404869.
- DINGHA, B.N., MOAR, W.J. and APPEL, A.G., 2004. Effects of *Bacillus thuringiensis* Cry1C toxin on the metabolic rate of Cry1C resistant and susceptible *Spodoptera exigua* (Lepidoptera: noctuidae). *Physiological Entomology*, vol. 29, no. 5, pp. 409-418. <http://dx.doi.org/10.1111/j.0307-6962.2004.00409.x>.
- FIGUEIREDO, M.L.C., CRUZ, I., SILVA, R.B. and FOSTER, J.E., 2015. Biological control with *Trichogramma pretiosum* increases organic maize productivity by 19.4%. *Agronomy for Sustainable Development*, vol. 35, no. 3, pp. 1175-1183. <http://dx.doi.org/10.1007/s13593-015-0312-3>.
- FURLONG, M.J. and WRIGHT, D.J., 1993. Effect of the Acylurea insect growth regulator teflubenzuron on the endo-larval stages of the Hymenopteran parasitoids *Cotesia plutellae* and *Diadegma semiclausum* in a susceptible and an Acylurea-resistant strain of *Plutella xylostella*. *Pesticide Science*, vol. 39, no. 4, pp. 305-312. <http://dx.doi.org/10.1002/ps.2780390409>.

- FURLONG, M.J., 2015. Knowing your enemies: integrating molecular and ecological methods to assess the impact of arthropod predators on crop pests. *Insect Science*, vol. 22, no. 1, pp. 6-19. <http://dx.doi.org/10.1111/1744-7917.12157>. PMID:25081301.
- FURLONG, M.J., SHI, Z.H., LIU, Y.Q., GUO, S.J., LU, Y.B., LIU, S.S. and ZALUCKI, M.P., 2004. Experimental analysis of the influence of pest management practice on the efficacy of an endemic arthropod natural enemy complex of the diamondback moth. *Journal of Economic Entomology*, vol. 97, no. 6, pp. 1814-1827. <http://dx.doi.org/10.1093/jee/97.6.1814>. PMID:15666732.
- GOULD, F., 1998. Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Annual Review of Entomology*, vol. 43, no. 1, pp. 701-726. <http://dx.doi.org/10.1146/annurev.ento.43.1.701>. PMID:15012402.
- GREENE, G.L., LEPPLA, N.C. and DICKERSON, W.A., 1976. Velvetbean caterpillar: a rearing procedure and artificial medium. *Journal of Economic Entomology*, vol. 69, no. 4, pp. 487-488. <http://dx.doi.org/10.1093/jee/69.4.487>.
- GUEDES, R.N.C., OLIVEIRA, E.E., GUEDES, N.M.P., RIBEIRO, B. and SERRÃO, J.E., 2006. Cost and mitigation of insecticide resistance in the maize weevil, *Sitophilus zeamais*. *Physiological Entomology*, vol. 31, no. 1, pp. 30-38. <http://dx.doi.org/10.1111/j.1365-3032.2005.00479.x>.
- HENTER, H.J. and VIA, S., 1995. The potential for coevolution in a host parasitoid system. I. Genetic variation within an aphid population in susceptibility to a parasitic wasp. *Evolution; International Journal of Organic Evolution*, vol. 49, no. 3, pp. 427-438. PMID:28565087.
- INSECTICIDE RESISTANCE ACTION COMMITTEE – IRAC, 2021 [viewed 14 January 2018]. *The diamondback moth, Plutella xylostella. Resistance management is the key to its control. 2016* [online]. IRAC. Retrieved from: <http://www.iraonline.org/documents/plutella-xylostella-irm-poster/?ext=pdf>
- OKUMA, D.M., BERNARDI, D., HORIKOSHI, R.J., BERNARDI, O., SILVA, A.P. and OMOTO, C., 2018. Inheritance and fitness costs of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) resistance to spinosad in Brazil. *Pest Management Science*, vol. 74, no. 6, pp. 1441-1448. <http://dx.doi.org/10.1002/ps.4829>. PMID:29239512.
- OLIVEIRA, R.C.M., PASTORI, P.L., COUTINHO, C.R., JUVENAL, S.O. and AGUIAR, C.V.S., 2020. Natural parasitism of *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) in *Neoleucinodes elegantalis* (Lepidoptera: Crambidae) eggs on tomato (Solanaceae) in the Northeast region, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 80, no. 2, pp. 474-475. <http://dx.doi.org/10.1590/1519-6984.206676>. PMID:31291404.
- PARRA, J.R.P. 1997. Técnicas de criação de *Anagasta kuehniella*, hospedeiro alternativo para a produção de *Trichogramma*. In: J.R.P. Parra and R.A. Zucchi, eds. *Trichogramma e o controle biológico aplicado*. Piracicaba: FEALQ, pp. 121-150.
- PEREIRA, F.F., ZANUNCIO, J.C., KASSAB, S.O., PASTORI, P.L., BARBOSA, R.H. and ROSSONI, C., 2013. Biological characteristics of *Palmistichus elaeisis* Delvare e Lasalle (Hymenoptera: Eulophidae) on refrigerated pupae of *Anticarsia gemmatalis* Hubner (Lepidoptera: Noctuidae). *Chilean Journal of Agricultural Research*, vol. 73, pp. 117-121.
- RORIZ, V., OLIVEIRA, L. and GARCIA, P., 2006. Host suitability and preference studies of *Trichogramma cordubensis* (Hymenoptera: trichogrammatidae). *Biological Control*, vol. 36, no. 3, pp. 331-336. <http://dx.doi.org/10.1016/j.biocontrol.2005.09.002>.
- ROUSH, R.T. and MCKENZIE, J.A., 1987. Ecological genetics of insecticide and acaricide resistance. *Annual Review of Entomology*, vol. 32, no. 1, pp. 361-380. <http://dx.doi.org/10.1146/annurev.en.32.010187.002045>. PMID:3545056.
- SANTOS-AMAYA, O.F., TAVARES, C.S., RODRIGUES, J.V.C., CAMPOS, S.O., GUEDES, R.N.C., ALVES, A.P. and PEREIRA, E.J.G., 2017. Fitness costs and stability of Cry1Fa resistance in Brazilian populations of *Spodoptera frugiperda*. *Pest Management Science*, vol. 73, no. 1, pp. 35-43. <http://dx.doi.org/10.1002/ps.4312>. PMID:27147125.
- SAS INSTITUTE , 2004. *SAS® 9.1 ETL studio: user's guide*. Cary: SAS Institute.
- SHEN, J., LI, D., ZHANG, S., ZHU, X., WAN, H. and LI, J., 2017. Fitness and inheritance of metaflumizone resistance in *Plutella xylostella*. *Pesticide Biochemistry and Physiology*, vol. 139, pp. 53-59. <http://dx.doi.org/10.1016/j.pestbp.2017.04.010>. PMID:28595922.
- SONG, W., SILVER, K.S., DU, Y.Z., LIU, Z.Q. and DONG, K., 2011. Analysis of the action of lidocaine on insect sodium channels. *Insect Biochemistry and Molecular Biology*, vol. 41, no. 1, pp. 36-41. <http://dx.doi.org/10.1016/j.ibmb.2010.09.010>. PMID:20888415.
- SU, J. and SUN, X., 2014. High level of metaflumizone resistance and multiple insecticide resistance in field populations of *Spodoptera exigua* (Lepidoptera: Noctuidae) in Guangdong Province, China. *Crop Protection*, vol. 61, pp. 58-63. <http://dx.doi.org/10.1016/j.cropro.2014.03.013>.
- TAKAGI, K., HAMAGUCHI, H., NISHIMATSU, T. and KONNO, T., 2007. Discovery of metaflumizone, a novel semicarbazone insecticide. *Veterinary Parasitology*, vol. 150, no. 3, pp. 177-181. <http://dx.doi.org/10.1016/j.vetpar.2007.08.031>. PMID:17980491.
- THOMAZONI, D., 2012. *Efeito da resistência de Spodoptera frugiperda (J.E. Smith, 1797) (Lepidoptera: Noctuidae) a lambda-cyhalothrin na interação com o milho geneticamente modificado (MON810) e na resposta imunológica ao parasitismo por Campoletis aff. flavicincta (Hymenoptera: Ichneumonidae)*. Piracicaba: Escola Superior de Agricultura "Luiz de Queiroz", 122 p. Tese de Doutorado em Ciências.
- TIAN, X., SUN, X. and SU, J., 2014. Biochemical mechanisms for metaflumizone resistance in beet armyworm, *Spodoptera exigua*. *Pesticide Biochemistry and Physiology*, vol. 113, pp. 8-14. <http://dx.doi.org/10.1016/j.pestbp.2014.06.010>. PMID:25052521.