

E-ISSN: 2320-7078 P-ISSN: 2349-6800 JEZS 2016; 4(4): 19-24 © 2016 JEZS Received: 05-05-2016 Accepted: 06-06-2016

Ghazwan Alsaedi

Department of Plant Protection, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran

Ahmad Ashouri

Department of Plant Protection, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran

Reza Talaei-Hassanloui

Department of Plant Protection, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran

Correspondence

Ahmad Ashouri Department of Plant Protection, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran

Journal of Entomology and Zoology Studies

Available online at www.entomoljournal.com



Behavioral responses of the three *Trichogramma* species to different odor sources

Ghazwan Alsaedi, Ahmad Ashouri and Reza Talaei-Hassanloui

Abstract

Tuta absoluta Meyrick (Lepidoptera: Gelechiidae), commonly known as the tomato borer, represents one of the tomato main pests since it had been explored. Eggs of the *T. absoluta* moth on tomato plants can be parasitized by variety species of *Trichogramma* as *T. brassicae*, *T. evanescens* and *T. embryophagum*. This study was conducted to test the behavioral responses of parasitoids to infested plants, herbivore induced plant odors from plants infested with *T. absoluta* and *Bacillus thuringiensis* (*Bt* treated plants) in an airflow Y-tube olfactometer. Odors emitted by tomato plant elicited a behavioral response from females of *Trichogramma* species. The results showed that parasitoid *T. embryophagum* females have been positively attracted to the healthy tomato plants (60%) comparing with clean air jar, *T. brassicae*, *T. evanescens* and *T. embryophagum* females have been positively attracted to the tomato plants infested with *T. absoluta* eggs/larvae (65%, 60% and 60%) comparing with non-infested plants female parasitoids were not attracted, and had a negative response, experiments preference ability to use *Trichogramma* spp. to control *T. absoluta* eggs. *Trichogramma* spp. females were consistently weaker toward *Bt* spray on tomato plants, that refer there are no effect from using *Bt* on control *T. absoluta* eggs.

Keywords: Trichogramma spp., Tomato, Tuta absoluta, Bacillus thuringiensis, olfactometric bioassays

1. Introduction

Plant chemicals may function as an indirect defence trait responsible for attracting natural enemies of herbivores and important chemical cues for parasitoids and predators to locate their host and direct defence may not only have a major effect on the herbivore's survival, but also on the survival of the natural enemies of the herbivore, leading to a possible conflict between the plant and the natural enemy that is attracted to the herbivore on that plant (Dicke et al 1990, Turlings et al 1990, Agrawal et al 2002, Gols et al 2008, Dicke and Baldwin 2010, Kessler and Heil 2011) ^[12, 40, 1, 20, 16, 26]. When volatiles are used to recruit natural enemies, they have been termed host-induced synomones, and they are regarded as an indirect chemical defence reaction by the plants (Dicke 1999, Dicke and van Loon 2000) ^[13, 15]. Deposition of insect eggs also can induce the production of volatiles or change leaf chemistry in a way that the plants attract and arrest certain egg parasitoids (Meiners and Hilker 1997, De Moraes et al 1998; Hilker et al 2002, Mumm et al 2003, Fatouros et al 2008) [29, 10, 23, 31, 18]. Chemical cues play a major role in the process of host selection by parasitoids, a process that has been discriminated into several steps such as habitat location, host location and host acceptance (Milonas et al 2009) ^[28]. The egg parasitoids are expected to frequently exploit chemical cues from other sources for host location as well. In the case of lepidopteran hosts, this includes, for example, pheromones and compounds released from scales of the wings of ovipositing females (Shu and Jones 1989, Colazza et al 1997) [38, 8]. Egg parasitoids belonging to the genus Trichogramma (Hymenoptera: Trichogrammatidae) are important natural enemies of a wide range of pests and are successfully used in biological control programmes worldwide (van Lenteren 2000)^[42]. Trichogramma wasps were attracted to volatiles of egg-induced plants, and this attraction depended on the *Trichogramma* strain used (Nina *et al* 2014) ^[32]. Since then, a number of studies have investigated the response of Trichogramma spp. to volatiles derived from fresh plant material and plant extracts using airflow olfactometers. In most studies, parasitoids were found to be responsive (Boo and Yang 1998) ^[6]. Female T. brassicae wasps were shown to spy on an anti-aphrodisiac pheromone innately, and mated P. brassicae females marked with this pheromone, and parasitize the freshly laid eggs of butterflies (Fatouros et al 2005a) [17]. This espionage-and-ride strategy was confirmed in T. evanescens after learning (Huigens et al 2009)^[24]. Furthermore B. thuringiensis and the parasite T. achaeae can provide

good control of *T. absoluta* in tomato greenhouses (Desneux *et al* 2010, Molla *et al* 2011) ^[11, 30]. *B. thuringiensis* and *T. achaeae* have been shown to be effective against *T. absoluta* and could be a supplement to the mirid predator *N. tenuis* (Calvo *et al* 2012a) ^[7]. We conducted a laboratory experiments In Y-tube olfactometer to investigate whether the parasitoids responded to the natural odors of tomato plants and *Bt*. We tested responses of three species of *Trichogramma* females to infested tomato plants of *T. absoluta* (Lepidoptera: Gelechiidae), and to plants infested spray with/without *Bt*.

2. Material and methods

2.1 Plants and Insects

Tomato plants (Solanum lycopersicum L.) were grown in a greenhouse (25±2°C, 60-70% RH, 16L: 8D). Seeds originated from the University of Tehran, Department of Plant Protection, Ecology and Behavior Lab (Karaj, Iran) during 2015. Five weeks old Plants were used in the experiments. The plants were grown in small pots (8 cm height, 9 cm diameter) in mixture of soil and perlite (1:1). Tomato plants were introduced into cages with approximately 30 T. absoluta females and removed 24 h later, after oviposition was used for the volatiles odors, tomato plants with eggs were kept at the same conditions in the growth chambers until used for volatile odors. All used insects were collected from University of Tehran. Mated females of T. absoluta were obtained by pairing a virgin male and a virgin female moth, one day after mating, T. absoluta females were used in the experiments. T. and Τ. brassicae Τ. evanescens embryophagum (Hymenoptera: Trichogrammatidae), were reared on eggs of the moth Ephestia kuehniella in the University of Tehran, in a climate chamber (25±2°C, 60-70% RH, L16:D8). Only mated, 2-5 days old, wasps were used in the experiments. None of the wasps used in the experiments have previous contact with any plant material or host residues.

Y-tube olfactometer and general bioassay Y-tube olfactometer (stem 14cm; arms 19cm at 130° angle; internal section 22×22mm) sandwiched between two glass sheaths. The odour sources were reversed after testing parasitoid females. The responses of 20 parasitoid females (12h mated) will be tested for the treatments one adult females of T. brassicae, T. Τ. embryophagum evanescens and was released simultaneously and their preference for one of the two odour sources was recorded. After 5 minutes, the wasp collected in each of the end arm was counted; insects then were positioned individually at the beginning of the central arm of the Y-tube and observed for 5 minutes. When the wasps crossed the threshold line (located in the middle of each arm) and stayed in the arm end for 20 sec, this was considered as "choice", and when a wasp did not make a choice within 5 minutes, it was recorded as a "no response" and excluded from the statistical analysis. In total, 140 wasps were tested with seven different experiments and each wasp was used only once, there were seven experiments: The first experiment were designed to investigate female wasps responses to healthy tomato plants comparing with clean air Jar in a Y-tube olfactometer, leaves tomato plants being used in this experiment were from 5 to 6 week age tomato seedling. That plant was in a healthy status and growing from plastic pot that including natural soil mixed with local peat moss. Twenty females of Trichogramma sp. had been bioassayed in these experiments. The second experiment was designed to investigate female wasp's responses to infested tomato plants with T. absoluta larvae/egg comparing with clean air Jar in a Y-tube olfactometer, tomato plants reared under the same

conditions described in the first experiment. The third was performed to investigate female wasps responses to healthy tomato plants comparing with infested tomato plants with T. absoluta larvae/egg tomato plants reared under the same conditions described in the first experiment. The fourth experiment was done to investigate female wasps responses to healthy plants spryed with B. thuringiensis (Bt) comparing with infested tomato plants infested with T. absoluta larvae/egg and sprayed with B. thuringiensis (Bt). Three suspension concentrations (10⁴, 10⁵, 10⁶ cells/ml) and water (control) sprayed on tomato plants reared under same conditions described for the first experiment. The fifth experiment was designed to indicate female wasps responses to infested tomato plants with T. absoluta larvae/egg comparing with infested tomato plants by T. absoluta larvae/egg and sprayed with B. thuringiensis (Bt). Three suspension concentrations (10⁴, 10⁵, 10⁶ cells/ml) and water (control) sprayed on tomato plants reared under the same conditions described for the first experiment. The sixth experiment was performed to evaluate female wasp's responses to B. thuringiensis (Bt) comparing with clean air Jar in a Y-tube olfactometer. Tomato plants reared under the same conditions described for the first experiment. The seventh experiment was planned to investigate female wasp's responses to T. absoluta egg comparing with clean air Jar in a Y-tube olfactometer. Tomato plants reared under the same conditions described for the first experiment.

2.2 Data analysis

Differences between behavioral responses of parasitoids under pairs of treatments were analyzed by chi-square tests. Individuals that did not make a choice were excluded from the statistical analysis. Statistical analysis was performed using the software IBM SPSS Statistics 21.

3. Results

The results showed the Parasitoids were able to detect the odor and were attracted toward the odor-source arm (Fig. 1, 2, 3), but intensity was different among the Parasitoid females species.

First experiment showed the *T. embryophagum* strong attractiveness toward the jar that contained a healthy tomato seedling (Fig. 3), 12 *T. embryophagum* females of 20 females (almost 60%) were attracted (X^2 =6.700, P=0.035) (Table1), while 5 females showed either no responding toward the clean air jar comparing, Also there was no attractiveness between

T. brassicae and *T. evanescens* toward the jar that contained a healthy tomato seedling (Fig. 1, 2) were 8 and 9 females of 20 females (almost 40% and 45%) respectively (X^2 =1.600, P=0.449; X^2 =1.900, P=0.387) (Table 1).

The results of the Parasitoid females *Trichogramma* spp. showed the greatest attraction movements toward *T. absoluta* eggs/larvae infested tomato seedlings, without and with *Bt* (experiment 2, 3, 4) comparing with the clean air, healthy tomato seedling and tomato seedling with *Bt* were similarly positive. The responding *T. brassicae*, *T. evanescens* and *T. embryophagum* females in these experiments were 13, 12 and 12 of 20 females (almost 65%, 60% and 60%) respectively for second experiment (X²=9.100, P=0.011; X²=6.700, P=0.035; X²=9.100, P=0.008; X²=6.400, P=0.041; X²=9.700, P=0.008) and for fourth experiment was12, 11 and 12 of 20 females (almost 60%, 55% and 60%) respectively(X²=6.400, P=0.041; X²=6.100, P=0.041; X²=6.100, P=0.047; X²=6.700, P=0.035) (Table 1). The

results of the fourth, fifth and sixth experiment showed the females *T. brassicae*, *T. evanescens* and *T. embryophagum* females' no attractiveness toward *T. absoluta* eggs/larvae infested tomato seedling with *Bt* comparing with the *T. absoluta* eggs/larvae infested tomato seedling (experiment 5) since they were 5, 9 and 9 of 20 female (almost 25%, 45%

and 45%) respectively (X²=1.300, P=0.522; X²=1.300, P=0.522; X²=1.300, P=0.522) (Table 1); Bt comparing with the clean air (experiment 6) since they were 6, 5 and 7 of 20 female (almost 30%, 25% and 35%) respectively (X²=2.800, P=0.247; X²=2.500, P=0.287; X²=0.700, P=0.705) (Table 1).

 Table 1: Responses of Trichogramma spp. females to the odors of Tuta absoluta egg and larvae infested tomato plants in a Y-tube olfactometer and number of non-responding individuals recorded for each odor pair.

Odor-source pairs	Trichogramma sp.	No. of responses to stimulus test	No. of responses to control stimulus	No. of Non responses	X ²	Р
Healthy Plant and Clean Air	T. brassicae	8	8	4	1.600	0.449
	T. evanescens	9	7	4	1.900	0.387
	T. embryophagum	12	5	3	6.700	0.035
Infested Plant and Clean Air	T. brassicae	13	4	3	9.100	0.011
	T. evanescens	12	5	3	6.700	0.035
	T. embryophagum	12	7	1	9.100	0.011
Infested Plant and Healthy Plant	T. brassicae	13	5	2	9.700	0.008
	T. evanescens	12	4	4	6.400	0.041
	T. embryophagum	13	5	2	9.700	0.008
Infested Plant+ Bt and Healthy Plant+ Bt	T. brassicae	12	4	4	6.400	0.041
	T. evanescens	11	7	2	6.100	0.047
	T. embryophagum	12	5	3	6.700	0.035
Infested Plant+ Bt and Infested Plant	T. brassicae	5	9	6	1.300	0.522
	T. evanescens	9	6	5	1.300	0.522
	T. embryophagum	9	6	5	1.300	0.522
Bt and Clean Air	T. brassicae	6	4	10	2.800	0.247
	T. evanescens	5	5	10	2.500	0.287
	T. embryophagum	7	8	5	0.700	0.705
Tuta eggs and Clean Air	T. brassicae	12	4	4	6.400	0.041
	T. evanescens	12	3	5	6.700	0.035
	T. embryophagum	14	2	4	12.400	0.002



Fig 1: shows responses of *T. brassicae* females to the odors of *T. absoluta* infested tomato seedlings with/without Bt in a Y-tube olfactometer and the non-responding of *T. brassicae* females.



Fig 2: shows responses of *T. evanescens* females to the odors of *T. absoluta* infested tomato seedlings with/without Bt in a Y-tube olfactometer and the non-responding of *T. evanescens* females.



Fig 3: shows responses of *T. embryophagum* females to the odors of *T. absoluta* infested tomato seedlings with/without Bt in a Y-tube olfactometer and the non-responding of *T. embryophagum* females.

Seventh experiment showed the higher significantly number of individual *T. brassicae*, *T. evanescens* and *T. embryophagum* females in attractiveness toward *T. absoluta* eggs comparing with clean air since they were 12, 12 and 14 of 20 female (almost 60%, 60% and 70%) respectively (X^2 =6.400, P=0.041; X^2 =6.700, P=0.035; X^2 =12.400, P=0.002) (Table 1).

5. Discussion

Our results reveal that Parasitoid females have been shown to respond to volatiles emanating from both undamaged plants (Li *et al* 1992, Reddy *et al* 2002, Romeis *et al* 2005) ^[27, 35, 36] and damaged plants (Turlings *et al* 1990, Dicke *et al* 1999) ^[40, 14], tomato plants are known to respond to herbivore and activate both direct and indirect defense mechanisms (Kant *et al* 2004, Angeles Lopez *et al* 2012) ^[25, 3]. Insect parasitoids and predators are known to utilize the different volatile profile of infested plants vs. non-infested plants to detect their hosts

and prey (Wei et al 2007)^[44]. These volatile compounds can be induced either by feeding (herbivore induced plant volatiles) or by egg laying (oviposition-induced plant volatiles) activities of insect herbivores and may play multiple roles as communication signals and defence agents, mediating interactions with other plants, microorganisms and animals (Kessler and Heil 2011, Pangesti et al 2013, Hilker and Fatouros 2015) ^[26, 33, 21], Elucidating the chemical ecology of natural enemies, herbivores and host plants is important in the development of effective and successful integrated pest management strategies where abundance and distribution of natural enemies could be manipulated by semi-chemicals (Hilker and Fatouros 2015) ^[21]. According to the theory proposed by Vet and Dicke (1992) ^[43], specialist parasitoids should respond innately to volatiles released by host-damaged plants, our results are in agreement with this for T. embryophagum females and exact opposite for T. brassicae, T. evanescens, Wei et al (2007) [44] found Insect parasitoids

and predators are known to utilize the different volatile profile of infested plants vs non-infested plants to detect their hosts and prey (Vet and Dicke 1992, Tumlinson et al 1993, Anastasaki et al 2015) ^[43, 39, 2] who that tomato plants bearing T. absoluta eggs are activated to produce herbivore-induced plant volatiles that may mediate indirect defense against herbivores. These compounds (plant volatiles) are reported to play a role in tomato resistance against other insects (Bleeker et al 2009) ^[5]. Volatiles emitted from herbivore infested tomato plants had quantitative and qualitative differences from undamaged plants. Even below-ground infestation by a microbe has been found to cause changes in the headspace volatile profile of tomato plants (Battaglia et al 2013)^[4]. The composition of the Herbivore-induced plant volatiles plays an important role in the attraction of the parasitoid, and some later induced volatiles like aromatic compounds and sesquiterpenes may distort and/or mask the attractiveness of the active volatiles (Penaflor et al 2011)^[34]. The results of our Bt experiments showed the responses of parasitoid Trichogramma spp. females were consistently weaker or there were no effect from using Bt on T. absoluta toward Bt because the larvae feed far less, which results in a strong reduction in volatile emissions (Schuler et al 1999) [37], and Because of the direct effect of the Bt also on the feeding rate of S. littoralis, Turlings et al (2005) [41] opted for a standardized artificial induction of the plants by scratching leaves and applying regurgitant. Our results reveal that Trichogramma spp. generalist egg parasitoids may use plant volatiles to locate plants with potential hosts and In agreement with Penaflor et al (2011) ^[34], oviposition by herbivorous insects can induce indirect plant defence responses whereby volatiles are emitted that attract egg parasitoids (Hilker and Meiners 2006) [22]. Plants that are able to produce herbivoreinduced plant volatiles in response to egg deposition have the advantage of defending themselves early on, before hatching larvae can damage the plant (Anastasaki et al 2015)^[2]. Insect oviposition induced volatiles in several plant species has been associated with some kind of physical damage during oviposition, adult feeding or an excretion that is used for eggs adherence (Colazza et al 2004, Fatouros et al 2012)^[9, 19]. The egg induced volatile emission effect in tomato, an economically important crop plant. It has been proved that generalist egg parasitoids such as Trichogramma species respond to oviposition-induced volatiles released by the plants after oviposition by an herbivore (Fatouros et al 2012, Anastasaki et al 2015, Hilker and Fatouros 2015)^[19, 2, 21].

6. Conclusion

This study showed that parasitoids *Trichogramma* species have very good preference to tomato plants and to the presence of *T. absoluta* as one of herbivores, since tomato volatiles induced by *T. absoluta* feeding are more attracting natural enemies of the eggs herbivore. That suggests, there will be good opportunities and new options for putting these parasitoids within the sort of valuable assets of any of the IPM strategies against *T. absoluta* for generations to come in order to reduce the use of chemicals and, consequently, improve food safety and environment quality.

7. Acknowledgements

The authors wish to thank the department of Plant Protection, University of Tehran, Karaj, Iran for providing the fund for this research work.

8. References

1. Agrawal A, Janssen A, Bruin J, Posthumus M, Sabelis M.

An ecological cost of plant defence: attractiveness of bitter cucumber plants to natural enemies of herbivores. Ecology Letters. 2002; 5:377-385.

- Anastasaki E, George B, Nikos E, Antonios N, Panagiotis G. Oviposition induced volatiles in tomato plants. Phytochemistry Letters. 2015; 13:262-266.
- 3. Angeles Lopez Y, Martinez-Gallardo N, Ramirez-Romero R, Lopez M, Sanchez-Hernandez C, Delano-Frier J. Cross-kingdom effects of plant–plant signaling via volatile organic compounds emitted by tomato (*Solanum lycopersicum*) plants infested by the greenhouse whitefly (*Trialeurodes vaporariorum*). Journal of Chemical Ecology. 2012; 38:1376-1386.
- 4. Battaglia D, Bossi S, Cascone P, Digilio M, Prieto J, Fanti P *et al.* Tomato below ground-above ground interactions: *Trichoderma longibrachiatum* affects the performance of *Macrosiphum euphorbiae* and its natural antagonists. Journal of Molecular Plant-Microbe Interactions. 2013; 26:1249-1256.
- 5. Bleeker P, Paul J, Kai A, Jose G, Monique W, Stefan S, *et al.* The role of specific tomato volatiles in tomato-whitefly interaction. 2009; DOI:10.1104/pp.109.142661.
- 6. Boo K and Yang J. Olfactory response of *Trichogramma chilonis* to *Capsicum annuum*. Journal of Asia-Pacific Entomology. 1998; 1:123-129.
- Calvo DGD, de Luxan-Delgado B, Rodriguez-Gonzalez S, Garcia-Macia M, Suarez FM, Solano JJ, et al. Interleukin 6, soluble tumor necrosis factor receptor I and red blood cell distribution width as biological markers of functional dependence in an elderly population: a translational approach. Cytokine. 2012; 58:193-198.
- Colazza S, Rosi M, Clemente A. Response of the egg parasitoid *Telenomus busseolae* to sex pheromone of *Sesamia nonagrioides*. Journal of Chemical Ecology. 1997; 23:2437-2444.
- 9. Colazza S, Mc Elfresh J, Millar J. Identification of volatile synomones, induced by *Nezara viridula* feeding and oviposition on bean spp., that attract the egg parasitoid *Trissolcus basalis*. Journal of Chemical Ecology. 2004; 30:945-964.
- De Moraes C, Lewis W, Pare P, Alborn H, Tumlinson J. Herbivore-infested plants selectively attract parasitoids. Journal of Nature. 1998; 393:570-573.
- 11. Desneux N, Wajnberg E, Wyckhuys KAG, Burgio G, Arpaia S, Narvaez Vasquez CA, *et al.* Biological invasion of European tomato crops by *Tuta absoluta*: ecology, history of invasion and prospects for biological control. Journal of Pest Science. 2010; 83:197-215.
- Dicke M, Sabelis MW, Takabayashi J, Bruin J, Posthumus MA. Plant strategies of manipulating predador prey interactions through allele chemicals: prospects for application in pest control. Journal of Chemical Ecology. 1990; 16:3091-3118.
- Dicke M. Evolution of induced indirect defense of plant. In The Ecology and Evolution of Inducible Defenses (ed. Tollrian R and Harvell CD). Princeton, New Jersey: Princeton University Press. 1999, 62-88.
- 14. Dicke M, Gols R, Ludeking D, Posthumus MA. Jasmonic acid and herbivory differentially induce carnivore attracting plant volatiles in lima bean plants. Journal of Chemical Ecology. 1999; 25:1907-1922.
- 15. Dicke M, van Loon JJA. Multi-trophic effects of herbivore induced plant volatiles in an evolutionary context. Journal of Entomologia Experimentalis et Applicata. 2000; 97:237-249.

- Dicke M, Baldwin IT. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trends in Plant Sciences. 2010; 15:167-175.
- Fatouros NE, Huigens ME, Van Loon JJA, Dicke M, Hilker M. Chemical communication butterßy antiaphrodisiac lures parasitic wasps. Journal of Nature (Lond.). 2005a; 433-704.
- Fatouros NE, Dicke M, Mumm R, Meiners T, Hilker M. Foraging behavior of egg parasitoids exploiting chemical information. Journal of Behavioral Ecology. 2008; 19:677-689.
- 19. Fatouros NE, Lucas-Barbosa D, Weldegergis BT, Pashalidou FG, van Loon JJA, Dicke M, *et al.* Plant volatiles induced by herbivore egg deposition affect insects of different trophic levels. Journal of Plos One. 2012; 7:43607.
- 20. Gols R, Wagenaar R, Bukovinszky T, van Dam NM, Dicke M, Bullock JM, *et al.* Genetic variation in defense chemistry in wild cabbages affects herbivores and their endo parasitoids. Journal of Ecology. 2008; 89:1616-1626.
- Hilker M, Fatouros NE. Plant responses to insect egg deposition. The Annual Review of Entomology. 2015; 60:493-515.
- 22. Hilker M, Meiners T. Early herbivore alert: insect eggs induce plant defense. Journal of Chemical Ecology. 2006; 32:1379-1397.
- 23. Hilker M, Kobs C, Varama M, Schrank K. Insect egg deposition induces Pinus to attract egg parasitoids. Journal of Experimental Biology. 2002; 205:455-461.
- Huigens ME, Pashalidou FG, Qian M, Bukovinszky T, Smid HM, Van Loon JJA, *et al.* Hitch-hiking parasitic wasp learns to exploit butterfly antiaphrodisiac. Proceedings of the National Academy of Sciences U.S.A. 2009; 106:820-825.
- Kant MR, Ament K, Sabelis MW, Haring MA, Schuurink RC. Differential timing of spider mite-induced direct and indirect defenses in tomato plants. Plant Physiology. 2004; 135:483-495.
- Kessler A, Heil M. The multiple faces of indirect defences and their agents of natural selection. Journal of Functional Ecology. 2011; 25:348-357.
- Li Y, Dickens JC, Steiner WWM. Antennal olfactory responsiveness of *Microplitis croceipes* (Hymenoptera: Braconidae) to cotton plant volatiles. Journal of Chemical Ecology. 1992; 18:1761-1773.
- Milonas PG, Martinou AF, Kontodimas DCH, Karamaouna F, Konstantopoulou MA. Attraction of Different *Trichogramma* Species to *Prays oleae* Sex Pheromone. Entomological Society of America. 2009; 102(6):1145-1150.
- 29. Meiners T, Hilker M. Host location in *Oomyzus* gallerucae (Hymenoptera: Eulophidae), an egg parasitoid of the leaf beetle *Xanthogaleruca luteola* (Coleoptera:Chrysomelidae). Oecologia. 1997; 112:87-93.
- Molla A, Cooper V, Pittayachawan S. The Green IT readiness (G-Readiness) of organizations: An exploratory analysis of a construct and instrument. Communications of the Association for Information Systems. 2011; 29(1):67-96.
- Mumm R, Kai S, Stefan S, Monika H. Chemical Analysis of Volatiles Emitted by *Pinus sylvestris* After Induction by Insect Oviposition. Journal of Chemical Ecology. 2003; 29(5):1235-1252.

- 32. Nina E, Fatouros A, Pineda ME, Huigens C, Broekgaarden MM, Shimwela IA, *et al.* Synergistic effects of direct and indirect defences on herbivore egg survival in awild crucifer. Journal of Proceedings of the Royal Society of London. 2014; B281:20141254.
- Pangesti N, Pineda A, Pieterse CMJ, Dicke M, Van Loon JJA. Two-way plant-mediated inter-actions between rootassociated microbes and insects: from ecology to mechanisms. Journal of Frontiers in Plant Science. 2013; 4:414.
- 34. Penaflor MFGV, Erb M, Miranda LA, Werneburg AG, Bento JMS. Herbivore-Induced Plant Volatiles Can Serve as Host Location Cues for a Generalist and a Specialist Egg Parasitoid. Journal of Chemical Ecology. 2011; 37:1304-1313.
- 35. Reddy GVP, Holopainen JK, Guerrero A. Olfactory responses of *Plutella xylostella* natural enemies to host pheromone, larval frass, and green leaf cabbage volatiles. Journal of Chemical Ecology. 2002; 28:131-143.
- Romeis J, Dirk B, Felix LW, Thomas GSh. Habitat and plant specificity of Trichogramma egg parasitoids underlying mechanisms and implications. Basic and Applied Ecology. 2005; 6:215-236.
- Schuler TH, Potting RPJ, Denholm I, Poppy GM. Parasitoid behaviour and Bt plants. Nature. 1999; 400: 825-826.
- Shu S, Jones RL. Kinetic effects of kairomone in moth scales of the European corn borer on *Trichogramma nubilale* Ertleand Davis (Hymenoptera: Trichogrammatidae). The Journal of Insect Behavior. 1989; 2:123-131.
- Tumlinson JH, Turlings TCJ, Lewis WJ. Semiochemically mediated foraging behavior in beneficial parasitic insects. Archives of Insect Biochemistry and Physiology. 1993; 22:385-391.
- 40. Turlings TCJ, Tumlinson JH, Lewis WJ. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Journal of Science. 1990; 250:1251-1253.
- 41. Turlings TCJ, Philippe MJ, Matthias H, Thomas D. Evaluating the induced-odour emission of a *Bt* maize and its attractiveness to parasitic wasps. Transgenic Research. 2005; 14:807-816.
- 42. Van Lenteren JC. Success in biological control of arthropods by augmentation of natural enemies. In Gurr G. and Wratten S. (Eds.), Biological control: measures of success. Hingham: Kluwer Academic Publishers. 2000, 77-103.
- 43. Vet LEM, Dicke M. Ecology of info chemical use by natural enemies in a tritrophic context. The Annual Review of Entomology. 1992; 37:141-172.
- 44. Wei J, Wang L, Zhu J, Zhang S, Nandi OI, Kang L. Plants attract parasitic wasps to defend themselves against insect pests by releasing hexenol. Journal of Plos One. 2007; 2:e852.