



# Tomato plant responses to feeding behavior of three zoophytophagous predators (Hemiptera: Miridae)



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## HIGHLIGHTS

- Zoophytophagous predators as Miridae induce plant responses in tomatoes.
- Phytophagy of *Nesidiocoris tenuis* repels *Bemisia tabaci* and *Tuta absoluta*.
- Phytophagy of *Macrolophus pygmaeus* and *Dicyphus maroccanus* does not repel *B. tabaci*.
- Phytophagy of *M. pygmaeus* and *D. maroccanus* results in attraction to *T. absoluta*.
- Phytophagy of the three mirid predators induces the attraction of *Encarsia formosa*.

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## ABSTRACT

Plant responses induced by zoophytophagous plant bugs (Miridae) have not been thoroughly studied. Here, we show that three different zoophytophagous predators (*Nesidiocoris tenuis*, *Macrolophus pygmaeus* and *Dicyphus maroccanus*) have different capacities for the induction of responses in tomato plants, resulting in varying degrees of attractiveness of the plants to pests and natural enemies. Tomato plants punctured by *N. tenuis* were less attractive to the whitefly *Bemisia tabaci* and to the lepidopteran *Tuta absoluta*. In contrast, tomato plants punctured by *M. pygmaeus* and *D. maroccanus* were not able to repel *B. tabaci* and, more interestingly, became more attractive to *T. absoluta*. The ability of *N. tenuis* to make tomato plants less attractive to *B. tabaci* was attributed to the activation of the abscisic acid (ABA) signaling pathway, which was only up-regulated in plants punctured by *N. tenuis*. However, the phytohormones involved in the behavioral responses of *T. absoluta* could not be identified; therefore, further studies are required. Additionally, all three zoophytophagous mirid predators activated jasmonic acid (JA) signaling pathways, which resulted in the parasitoid *Encarsia formosa* being attracted to tomato plants. Here, the implications of these results on the efficacy of these three predators as biocontrol agents are discussed.

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## 1. Introduction

Recent successes in the biological control of protected crops in Southern Europe have occurred due to the development of control strategies that use generalist predators (Calvo et al., 2009a, 2011, 2012a). Generalist predators that feed on more than one trophic level are called omnivores (Coll and Guershon, 2002). A special case of omnivory is zoophytophagy, which is defined as predators feeding on prey and plants during the same developmental stage

(Castañé et al., 2011). Phytophagy has multiple benefits, including facilitating the establishment of these predators in the crop and preserving them when prey is scarce (Perdikis et al., 1999; Sanchez et al., 2004; Urbaneja et al., 2005). This is the case for some zoophytophagous mirid predators (Hemiptera: Miridae), such as *Macrolophus pygmaeus* Rambur, which has been commercially released for many years for several protected crops (Arnó et al., 2000; Enkegaard et al., 2001; Gabarra et al., 2006; Messelink et al., 2014; Perdikis and Lykouressis, 2000) and *Nesidiocoris tenuis* Reuter, which has been extremely effective at controlling key tomato pests in Southern Europe in recent years (Calvo et al., 2012b; Urbaneja et al., 2012). The aforementioned

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benefits of mirids and the great recent success of tomato biocontrol programs using mirids (Calvo et al., 2012c) have prompted studies focused on finding new candidate mirid species for tomato biocontrol programs (Abbas et al., 2014; Bueno et al., 2013; Ingegno et al., 2013) and studies focused on exploring the use of mirids in other vegetable crops (Messelink et al., 2015; Pérez-Hedo and Urbaneja, 2015).

Additionally, a recent study by Pérez-Hedo et al. (2015) demonstrated that mirids can activate the same defense mechanisms as strict herbivores (Halitschke et al., 2011; Kessler and Baldwin, 2004). It is well documented that plants respond to herbivore attacks through several signaling pathways, resulting in the production of herbivore-induced plant volatiles (HIPVs) (Dicke, 2009). These HIPVs can modify the behavior of both the phytophagous pests and their natural enemies (Pare and Tumlinson, 1997). By feeding on plants, *N. tenuis* activates abscisic acid (ABA) and jasmonate acid (JA) pathways in tomato plants, which makes them less attractive to *B. tabaci* and more attractive to the whitefly parasitoid *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae), respectively. In addition, HIPVs from *N. tenuis*-damaged plants can induce plant defenses in neighboring, undamaged plants via JA pathways, resulting in the attraction of parasitoids. Nevertheless, the effects of the feeding activity of *N. tenuis* on other phytophagous pests and natural enemies are still unknown. In this respect, it is interesting to address the effect of these HIPVs on the key tomato pest *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). Similarly, other mirid species are expected to be capable of inducing defense responses in tomato plants. Therefore, this study compares the previously described tomato plant responses to *N. tenuis* (Pérez-Hedo et al., 2015) with the tomato plant responses to two other predatory mirids, *M. pygmaeus* and *Dicyphus maroccanus* Wagner (Hemiptera: Miridae), the second of which is a mirid predator that spontaneously appeared in tomato crops in the middle east of Spain (Abbas et al., 2014).

*M. pygmaeus* and *D. maroccanus* are believed to extract the content of mesophyll cells, whereas *N. tenuis* feeds on vascular tissue by extracting plant sap (Castañé et al., 2011; Wheeler, 2001); thus, different plant defense responses triggered by the herbivory of these three mirids are expected to occur in tomato plants. In this work, we studied whether puncturing of tomato plants by these three mirid predators influences the host-plant selection of two major tomato pests, the whitefly *B. tabaci* and the lepidopteran *T. absoluta*, and the parasitoid *E. formosa*, which was commercially released for whitefly control in tomato worldwide (van Lenteren, 2012). For this study, we evaluated the olfactory responses of the two herbivore pests and the parasitoid exposed to mirid-punctured plants and intact plants, for comparison, in a Y-tube olfactometer. Based on previous results obtained by Pérez-Hedo et al. (2015), which demonstrated that *N. tenuis* activated the ABA and JA signaling pathways in punctured tomato plants, we used gene expression analysis to assess whether *M. pygmaeus* and *D. maroccanus* were also able to activate both the ABA and JA signaling pathways.

## 2. Materials and methods

### 2.1. Plants and insects

The responses of *B. tabaci*, *T. absoluta* and *E. formosa* to *Solanum lycopersicum* (cv. Optima) after different experimental treatments to the plants are described below. The plants were germinated in soil, and 2 weeks after germination, the seedlings were individually transferred to pots and maintained at  $25 \pm 2$  °C with high relative humidity (>60%) and a 16:8 h L:D photoperiod. Six-week-old plants with seven to eight fully expanded leaves were used for the experiments.

*B. tabaci*, *E. formosa*, *N. tenuis* and *M. pygmaeus* individuals were obtained directly from mass rearings of Koppert Biological Systems, S.L. (Águilas, Murcia, Spain), whereas *D. maroccanus* and *T. absoluta* individuals were obtained from colonies maintained at IVIA (Abbas et al., 2014). The three mirid rearing systems were based on tomato plants. Newly emerged adult females of the six species of insects (1–5 days old) were used in all trials.

### 2.2. Attraction to volatiles

The behavioral responses of *B. tabaci*, *T. absoluta* and *E. formosa* females to plant volatiles were investigated in a Y-tube olfactometer (Analytical Research Systems, Gainesville, FL) consisting in a Y-shaped glass tube (2.4 cm in diameter with a base of 13.5 cm in length) connected via plastic tubes to two identical 5 L glass jars, each of which contained a tested odor source and was connected to an air pump that produced a unidirectional airflow. The environmental conditions in the Y-tube experiments were  $23 \pm 2$  °C and  $60 \pm 10\%$  RH (Pérez-Hedo and Urbaneja, 2015).

Each female was observed until she had walked at least 3 cm up one of the side arms or until 15 min had elapsed. Females that had not walked up one of the side arms after 15 min were considered to be 'non-responders' and were excluded from the subsequent data analysis. Each individual was tested only once. After testing five individuals, odor sources were interchanged to avoid any influence of asymmetry in the setup of the apparatus.

The following combinations were tested: (i) intact plants that were undisturbed isolated from arthropods until use and (ii) Miridae-punctured plants obtained by introducing 100 *N. tenuis*, *M. pygmaeus* or *D. maroccanus* individuals into a plastic cage of  $60 \times 60 \times 60$  cm (BugDorm-2; MegaView Science Co., Ltd.; Taichung, Taiwan) and then enclosing four intact tomato plants in the cage for 24 h. All mirid individuals were removed from the punctured plants before the experiment.

### 2.3. Quantification of plant gene expression

The transcriptional response of the *ASR1* (abscisic acid stress ripening protein) and *PIN2* (proteinase inhibitor II) genes (i.e., genes encoding JA-regulated defense proteins), which are ABA and JA responsive, respectively, were studied (Lopez-Raez et al., 2010). The apical tomato plant samples were immediately ground in liquid nitrogen. Portions of the ground samples were used for RNA extraction. Total RNA (1.5 µg) was extracted using a Plant RNA Kit (Omega Bio-Tek Inc., Doraville, GA, USA) and was treated with RNase-free DNase (Promega Corporation, Madison, Wisconsin, USA) to eliminate genomic DNA contamination. The RT reaction and the PCR SYBR reaction were performed as described by Pérez-Hedo et al. (2015) and using the same primers as Pérez-Hedo et al. (2015). Quantitative PCR was performed using the Smart Cycler II (Cepheid, Sunnyvale, CA, USA) sequence detector with standard PCR conditions. Expression of EF1 was used for normalization as a standard control gene.

### 2.4. Data analyses

$\chi^2$ -Tests were used to test the hypothesis that the distribution of side-arm choices between pairs of odors deviated from the null model of odor sources being chosen with equal frequency. The results of the transcriptional responses for the *ASR1* and *PIN2* genes were subjected to one way analysis of variance, and the Tukey test was used for mean separation at  $P < 0.05$ . The results are expressed as the means  $\pm$  SE.

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