Olfactory response of the ladybird beetle *Stethorus gilvifrons* to two preys and herbivore-induced plant volatiles

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Abstract The spider mites *Tetranychus urticae* Koch and *Panonychus ulmi* (Koch) (Tetranychidae) cause severe economic losses to vegetable farms and deciduous fruit orchards in Turkey. One of their predators, the ladybird beetle *Stethorus gilvifrons* (Muls.) (Col., Coccinellidae), aggregates on mite-infested patches of plants. The present study assessed whether there is a role for herbivore-induced plant volatiles (HIPVs) and/or odors emitted directly from these two mite species in the aggregative response of ladybird beetles. The olfactory responses of the predator females to volatiles from *T. urticae*- and/or *P. ulmi*-infested sweet pepper (four cultivars, viz. 'Demre', 'Yalova Carliston', 'Kandil Dolma' and 'Yag Biberi'), kidney bean (cv. 'Barbunya') and apple (M9 rootstock) were investigated using a two-choice olfactometer. Our results showed that HIPVs emitted from both *T. urticae*- and *P. ulmi*-infested plants significantly attracted *S. gilvifrons* adults for all plants except the sweet pepper cv. Yag Biberi. In addition, it was found that volatiles from apple plants infested by *T. urticae* and, especially, *P. ulmi* are more attractive for *S. gilvifrons* females than those emitted by other infested plants. The results also suggest that the odors of *T. urticae* adults and their products might influence the attraction of *S. gilvifrons* females.

Keywords *Tetranychus urticae · Panonychus ulmi ·* HIPVs · Y-tube olfactometer

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Introduction

A wide variety of spider mite species can be found in many cropping systems worldwide. However, two species, the two-spotted spider mite *Tetranychus urticae* Koch and the European red spider mite *Panonychus ulmi* Koch (Acari: Tetranychidae), are of commercial importance. *T. urticae* is a generalist herbivore and a serious pest in many crops throughout the world. *P. ulmi* causes significant losses in apple and other deciduous fruit orchards in parts of Europe, the eastern USA, and many other regions (Helle and Sabelis 1985). A major problem in the control of the mites is their ability to develop resistance to pesticides (Nauen et al. 2001). Their high reproductive potential and numerous annual generations, combined with

continued and repeated use of a variety of broad spectrum insecticides in commercial fields, has disrupted the control of spider mite populations by natural enemies and led to resurgences in mite outbreaks and development of pesticide resistance (Auger et al. 2003; Kim et al. 2004; Kumral et al. 2008; Nauen et al. 2001). Thus, alternatives to the use of insecticides are needed, and biological control provides one of the best options.

Biological control with predatory mites and insects is often an important part of integrated mite management, which has produced outstanding success worldwide (Solomon et al. 2000). One predator of spider mites is the ladybird beetle, *Stethorus gilvifrons* (Muls.) (Col., Coccinellidae), which consumes immature and adult mites, including *P. ulmi*, *T. urticae*, *T. cinnabarinus* (Boisd.)*, T. turkestani* (Ugarov and Nikolskii), *T. atlanticus* McG., and *Amphitetranychus viennensis* (Zacher) (Chazeau 1985; Helle and Sabelis 1985; Hodek 1973), on cotton, citrus, strawberry, apple, fig, and vegetables in the Middle East and in southern Europe (El-Adawy et al. 2001; Kaylani 1967; Oncuer 1991; Uygun 1981). *Stethorus gilvifrons* can effectively control and sometimes even eliminate spider mite populations (Ahmed et al. 2006; Aksit et al. 2007; Gencer et al. 2002).

Research on biological control of arthropod pests has gradually broadened from the study of interactions between herbivores and their natural enemies to tritrophic interactions among plants, herbivores, and natural enemies. Indirect interactions between a plant and its natural enemies have been increasingly recognized as important, since plants generally possess inducible indirect defences (Janssen et al. 1998). One such defence is the attraction of predators by the release of herbivore-induced volatiles (infochemicals), which qualitatively and/or quantitatively differ from the volatiles of mechanically damaged leaves. Those volatile infochemicals that are induced in plants by herbivory and that attract predators are called synomones (Sabelis and Van de Baan 1983). This specific group of volatiles also has been termed herbivore-induced plant volatiles, or HIPVs (Sabelis et al. 1999; Van den Boom et al. 2002).

Recent research has demonstrated that predators can recognize HIPVs induced both by prey and non-prey herbivores (Boer et al. 2008). Also, there is strong evidence that olfaction is implicated in responses of phytoseiid and heteropteran predators to spider mite-infested plants (e.g. bean and sweet pepper) and that these predators respond to the following HIPVs: jasmonic acid, linalool, (E)-β-ocimene, (E,E)-α-farnesene, methyl salicylate, and several monoterpenes (Llusia and Penuelas 2001; Moayeri et al. 2006a, b, 2007; Sabelis and Van de Baan 1983; Sabelis et al. 1999; Shimoda et al. 2005).

Stethorus species are thought to search randomly for mite prey in the absence of mite webbing (Helle and Sabelis 1985). Although the ability of *Stethorus* adults to find prey at low population levels has been observed and attributed to olfactory attractiveness, the experimental support for this inference has been questioned (Helle and Sabelis 1985). Furthermore, the response of three *Stethorus* species (viz. *S. japonicus* Kamiya, *S. punctillum* Weise, *S. punctum picipes* Casey) to HIPVs was demonstrated in the field or in Y-tube olfactometers (James 2005; James and Price 2004; Takahashi et al. 2001).

Although olfaction responses by other coccinellid species and some *Stethorus* spp. to herbivore-attacked plants have been reported recently (Lentz et al. 2004; Sengonca and Kranz 2001; Takahashi et al. 2001), such information is lacking for *S. gilvifrons*. In addition, the production of herbivore-induced volatiles differs among plant species and cultivars (Takabayashi et al. 1994; Takabayashi and Dicke 1996). Therefore, this work investigated the attraction of *S. gilvifrons* to *T. urticae*-induced plant volatiles released by several plant species from different families, as well as the attraction of *S. gilvifrons* to *P. ulmi*-induced volatiles released by apple. Many researchers have reported that predators were attracted not only to HIPVs but also to odors emitted directly by adult mites and their products, such as webs (Gols et al. 2003; Moayeri et al. 2006a). Therefore, this work also investigated the responses of *S. gilvifrons* to odors from the spider mites *T. urticae* and *P. ulmi* to determine whether odors emitted directly by the spider mite (and/or their products) are responsible for the predatory beetle's response.

Materials and methods

Plant material The test plants used in the olfactometer experiments are listed in Table 1. These plants were grown in a climate-controlled room with a 16 h light (500 μmol m^{-2} s^{-1} PAR; at 27±1°C, and 60±5% r.h.) /

Table 1 Plants used in olfactometer tests

Family	Species	Common name	Cultivar	Age (weeks)	Plant phenology[x]
Solanaceae	*Capsicum annuum* L.	Sweet pepper	Demre	8[z]	Seedlings with six leaves
Solanaceae	*C. annuum*	Sweet pepper	Yalova Carliston	8[z]	Seedlings with six leaves
Solanaceae	*C. annuum*	Sweet pepper	Kandil Dolma	8[z]	Seedlings with six leaves
Solanaceae	*C. annuum*	Sweet pepper	Yag Biberi	8[z]	Seedlings with six leaves
Fabaceae	*Phaseolus vulgaris* L.	Kidney bean	Barbunya	2[z]	Seedlings with developed primary leaves
Rosaceae	*Malus domestica* Borkh.	Apple (M9-rootstock)	-	4[y]	Young twig with 6±2 leaves

[z] Age calculated from the time the seed was sown

[y] The age in weeks of young twigs of 4-year-old seedlings.

[x] Indicates the vegetation that was used in the olfactometer

8 h dark (18±1°C and 60±5% r.h.) cycle supplemented with white lamps. Plants were irrigated every third day with tap water and fertilized at 15-day intervals with a commercial water-soluble fertilizer containing macro- and micronutrients (Rocket 20-20-20 NPK; Merkez Anadolu Kimya Sanayi, Antalya, Turkey). The ages and vegetation stages of the plants used for the experiments are listed in Table 1.

Rearing of mites and ladybird beetles The spider mites *T. urticae* and *P. ulmi* were reared on kidney bean plants (*Phaseolus vulgaris* L. (Fabaceae)) and apple seedlings (*Malus domestica* L. (Rosaceae)), respectively, in different climate-controlled rooms under the conditions mentioned above. The predatory beetles, *S. gilvifrons*, were originally obtained from an apple orchard in Barakfaki village (Kestel district, Turkey, 40.217 N, 29.272 E). The predator beetle was reared on kidney beans infested with *T. urticae*.

Response of S. gilvifrons to spider mite-induced plant odors Seven tests were carried out to determine the response of *S. gilvifrons* to two spider mite species-induced plant odors:

> 1–6: uninfested control plants *vs* plants previously infested with *T. urticae*
> 7: uninfested control plants *vs* plants previously infested with *P. ulmi*

Three days prior to the experiment, uniform plants with six fully expanded mature leaves having about equal leaf areas were selected (Table 1). After the plants had been artificially infested with 25 female spider mites per leaf (i.e., 150 mites per plant), the infested plants and uninfested plants were transferred to the climate-controlled room. In addition, the newly emerged female beetles were allowed a 2-day adaptation period, during which they were given a combination of spider mite species and plant species (or cultivar) using the procedure previously described (Dicke et al. 1990; Maeda et al. 2000). Then, the adults were kept in a small box without prey and plants for 24 h prior to the test. Two hours prior to the test, the aboveground parts of the infested and uninfested plants were cut off and placed inside different glass jars. To avoid wilting, the plants were wrapped in wet cotton wool and covered with Parafilm. All olfactometer experiments for each plant species (or cultivar) were carried out on three different days. Each beetle adult was used only once.

Response of S. gilvifrons to odors emitted directly from prey Three tests were carried out to determine the response of *S. gilvifrons* to odors emitted directly by two spider mite species:

> 1 and 2: clean air *vs* odors emitted directly by *T. urticae* or *P. ulmi* adults along with their products
> 3: odors emitted directly by *T. urticae* adults along with their products and clean air *vs* those of *P. ulmi*.

For collected volatiles emitted directly from the spider mites and their products (eggs, exuviae and silks), 300 adult spider mites were placed in a Pyrex tube connected to the Y-tube 2 h before the test. The spider mite colonies used in this test (viz. *T. urticae, P. ulmi* and *T. urticae+ P. ulmi*) were given to the female beetles in a Pyrex glass box for 2 days.

Subsequently, the adults were kept in a small box without prey for 24 h prior to the test. Each test was repeated on three different days with new sources of odors obtained from spider mites.

Olfactometer setup The response of the predatory beetles to odor sources was studied in two-choice tests with a closed system Y-tube olfactometer, using a slight modification of the method of Sabelis and Van de Baan (1983) and Takabayashi and Dicke (1992). The olfactometer setup consisted of a Y-shaped Pyrex tube (2.5 cm in diameter) with an entry arm (20 cm in length) and two side arms (each 20 cm in length and at an angle of 75° apart). In olfactometer experiments with spider mite-induced plants, two 1 l glass jars that contained the odor sources were connected to the Y-tube. In olfactometer experiments with odors emitted directly from prey, two Pyrex tubes (2.5 cm in diameter) with an entry arm (20 cm in length) were connected to the Y-tube as odor containers. The containers had an air inlet and outlet (0.8 cm in diameter) in opposite walls. The airflow was established from each container through the olfactometer arms *via* an air pump, with the airflow adjusted with a flowmeter to 1.5 l min^{-1}, and humidified with deionized water. The air passed through activated charcoal before reaching the cylinders and the airflow was measured in the entry arm. The glass Y-tube was positioned 30° vertically because insects perform better in this setup. Before the start of the experiment, the arms of the olfactometer were flushed with air going through the odor sources for ~10 min. A single female beetle to be tested was introduced into the tube and observed until it had walked at least 7 cm up one of the arms or until 5 min had elapsed. Females that did not choose a side arm within 5 min were recorded as no choice and excluded from the statistical analysis. After each test, the Y-tube was cleaned with alcohol (70%) and left to dry for 5 min (Moayeri et al. 2006a, b; Takabayashi and Dicke 1992).

Statistics The Pearson chi-square test was performed on the total number of predators attracted towards one of the odor sources per test plant and prey (Van den Boom et al. 2002). The null hypothesis was that predators had 50:50 distributions across the two odor sources for each replicate. The predators that did not make a choice were excluded from the statistical analysis. Moreover, a one-way analysis of variance was also performed on the percentages of *S. gilvifrons* responses to HIPVs. The data were normalized by arcsine transformation before ANOVA (JMP 2001).
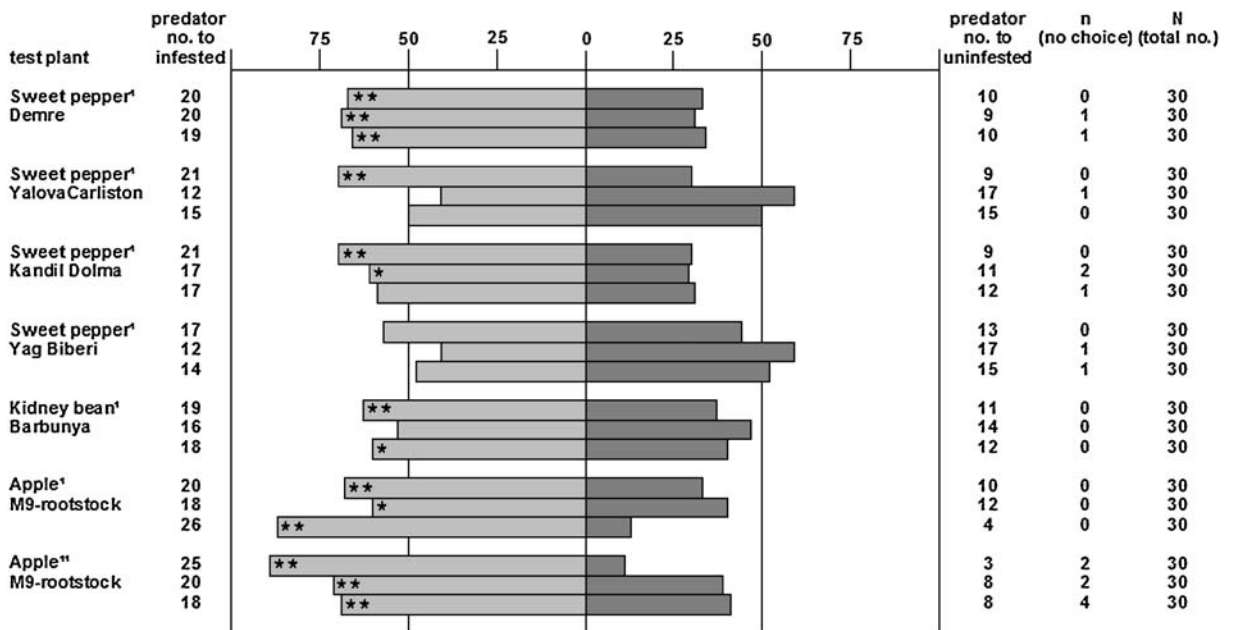
Fig. 1 Olfactory response of *Stethorus gilvifrons* to various test plants infested with *Tetranychus urticae* ([1]) or *Panonychus ulmi* ([11]), *vs* clean test plants, in a Y-tube olfactometer. *$P<0.05$; **$P<0.01$ (for chi-square test)
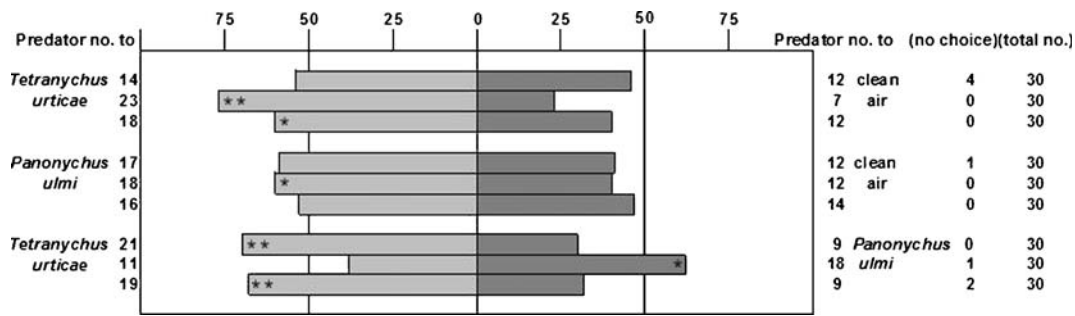
Fig. 2 Olfactory response of *Stethorus gilvifrons* to odor from adults of *Tetranychus urticae* or *Panonychus ulmi* (and their products such as webbing) *vs* clean air, and odor from adults of *T. urticae* (and their products) *vs P. ulmi,* in a Y-tube olfactometer. *P<0.05; **P<0.01 (for chi-square test)

Results

The response of *S. gilvifrons* to *T. urticae*-induced plant odors is shown in Fig. 1. It showed the strongest attraction to the infested apple rootstock, with 87% of the predatory beetles moving towards the plant leaves infested with *T. urticae* ($\chi2$=53.8; *P*<0.01). Additionally, the response of *S. gilvifrons* to the three infested sweet pepper cultivars infested with *T. urticae* (Demre, Yalova Carliston, Kandil Dolma) was significantly different compared with clean leaves of the same plants in each three, one and two of the three replicates of the tests, respectively (Demre: $\chi2$= 11.1, 14.4, 9.6, *P*<0.01; Yalova Carliston: $\chi2$=15.9, *P*<0.05; Kandil Dolma: $\chi2$=15.9, 4.6, *P*<0.05). In contrast, *T. urticae* infestation of cv. Yag Biberi sweet pepper did not affect the behavior of the beetles, because there were no significant differences in any of the replicates. In addition, a significant attraction of *S. gilvifrons* to the *T. urticae*-infested leaves of kidney bean (cv. Barbunya) was observed in two replicates ($\chi2$=7.1, *P*<0.01; $\chi2$ =3.9, *P*<0.05). However, no significant preference was detected among odors emitted by the plant species and/or cultivars induced by *T. urticae* (*F*=2.26, df=12, *P*=0.11). Figure 1 shows the response of *S. gilvifrons* to *T. urticae*- or *P. ulmi*-induced apple odors. The predators were significantly attracted toward odors emitted by apple rootstock leaves infested with both *P. ulmi* ($\chi2$=61.7, 18.4, 14.8; *P*<0.01) and *T. urticae* ($\chi2$=11.1, 3.9, 53.8; *P*<0.01, *P*<0.05, *P*<0.01, respectively) in all replicates. In addition, there was no significant difference between the odors induced in apple leaves infested with *T. urticae* and *P. ulmi* (*F*=0.29, df =4, *P*=0.62).

The olfactory response of *S. gilvifrons* to odors emitted directly by the two spider mite species is shown in Fig. 2. In one of these odor-mediated preference tests, significantly more *S. gilvifrons* moved towards *T. urticae* adults and their products than towards clean air in two replicates ($\chi2$=28.4; 3.9 *P*<0.01 and *P*<0.05, respectively). In contrast, in one replicate the beetles appeared to prefer odors emitted directly from the *P. ulmi* adults or their products ($\chi2$= 3.9; *P*<0.05). Similarly to the tests with the volatiles induced by *T. urticae*, the odors emitted directly by *T. urticae* adults and their associated products attracted significantly more predators than those of *P. ulmi* in two replicates ($\chi2$=15.9; 12.8; *P*<0.01). The opposite was observed in one replicate ($\chi2$=5.8; *P*< 0.05). There was no significant difference among prey preference tests (*F*=0.22, df =6, *P*=0.81).

Discussion

This study showed that the herbivore-induced plant volatiles (HIPVs) emitted from plants infested by both *T. urticae* and *P. ulmi* attracted *S. gilvifrons* adults in sweet pepper, kidney bean and apple. Previous studies had demonstrated that predator insects and mites are attracted to the odors of plants infested by their prey, spider mites, in preference to the odor of uninfested plants (Collier et al. 2001; Drukker et al. 1995; Drukker et al. 2000; Llusia and Penuelas 2001; Moayeri et al. 2006a,b; 2007; Sabelis and Van de Baan 1983; Sabelis et al. 1984a, b; Sabelis et al. 1999; Scutareanu et al. 1997; Shimoda et al. 2005; Van den Boom et al. 2002). As far as we know, this is the first report of a response of *S. gilvifrons* to plant volatiles induced by spider mites. Only three studies of the olfaction responses of *Stethorus* spp. to HIPVs were published previously. Takahashi et al. (2001) demon-

strated that the volatiles of lima bean plants infested with *T. urticae* attracted *S. japonicus*. Lentz et al. (2004) showed the potential use of olfactory cues emanating from the plant–herbivore complex in *S. punctillum* searching for prey habitat, and suggested that spider mite-induced synomones might be of major importance for the long-distance orientation of the lady beetles. James (2005) found that *S. punctum picipes* was attracted to sticky traps baited with certain HIPVs such as methyl salicylate, *cis*-3-hexen-1-ol and benzaldehyde, under natural conditions.

The present study demonstrated that apple volatiles induced by *T. urticae* and *P. ulmi* are quite effective for attracting *S. gilvifrons* females. Our results are similar to those of Llusia and Penuelas (2001), who suggested that apple odors induced by *P. ulmi* might be used as cues to find prey by the predatory mite *Amblyseius californicus* McGregor (Acarina: Phytoseiidae). In addition, these researchers emphasized that total HIPV emission rates and total volatile leaf concentrations were higher in apple trees infested by *P. ulmi*. The tests on apple by another research group demonstrated that the phytoseiid mite *Neoseiulus californicus* (McGregor) (Acarina: Phytoseiidae) was significantly attracted to allelochemicals associated with leaves previously infested by both *P. ulmi* and *T. urticae* (Collier et al. 2001).

Our results suggest that odors emitted by three of the four sweet pepper cultivars—Demre, Yalova Carliston and Kandil Dolma, when infested with *T. urticae*, attract adults of *S. gilvifrons*. A similar result was reported by Moayeri et al. (2006a) in relation to *Macrolophus caliginosus* Wagner. These authors showed that the predatory mirid bug was attracted to volatiles from *T. urticae*- infested pepper. Van den Boom et al. (2004) found that spider mite-infested sweet pepper (cv. Lambada) emitted three HIPVs in large amounts, namely, the terpenes (E)-β-elemene, germacrene A and (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. The researchers concluded that the indirect defence of sweet pepper against herbivores was strong. Our results indicate that the odors of kidney bean plants infested with *T. urticae* attract *S. gilvifrons*, which is in accordance with Takahashi et al. (2001), who reported that HIPVs of *T. urticae*-infested lima bean plants attracted *S. japonicus*.

The present study constitutes also the first attempt to determine the response of *S. gilvifrons* to plant volatiles induced by *T. urticae* in different sweet pepper cultivars through olfactory mediation. It is possible that the differences between cultivars might be due to their chemical compositions. In further studies, chemical analyses should be conducted to clarify the differences among volatiles (especially HIPVs) from leaves of different sweet pepper cultivars infested with spider mites.

Our results indicate that *S. gilvifrons* responds to odors emitted directly by adults of spider mites and their products (viz. eggs, exuviae and webs). Similarly, Moayeri et al. (2006a) demonstrated that the response of *M. caliginosus* was mediated through odors emitted directly by mite-associated products. Moreover, Gols et al. (2003) showed that the predatory phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot was strongly attracted to *T. urticae*-associated products. Collier et al. (2001) found that the phytoseiid mite *N. californicus* responds to a mixture of odors from associated products (viz. feces, eggs, exuviae and webs) of *P. ulmi* and *T. urticae*. However, in our study, *S. gilvifrons* showed a stronger preference for direct odors of *T. urticae* adults and their associated by-products, compared with those of *P. ulmi*. This result might be related to the fact that *P. ulmi* produces fewer webs than *T. urticae* (Van de Vrie 1985). Further studies (e.g. chemical analysis of odors emitted by the mite) are needed to identify the chemical cues involved in the olfactory response of *S. gilvifrons* to *T. urticae* (Moayeri et al. 2006a).

References

Ahmed, S. A., El-Adawy, A. M., Ahmed, Y. M., El-Sebae, A. A., & Ibrahim, M. M. (2006). Release of the coccinelld predator *Stethorus gilvifrons* (Mulsant) and bio-rational pesticides to suppress the population of *Tetranychus urticae* Koch on cantaloupe plants in Egypt. *Egyptian Journal of Biological Pest Control, 16,* 19–24.

Aksit, T., Cakmak, I., & Ozer, G. (2007). Effect of temperature and photoperiod on development and fecundity of an acarophagous ladybird beetle, *Stethorus gilvifrons*. *Phytoparasitica, 35,* 357–366.

Auger, P., Bonafos, R., Guichou, S., & Kreiter, S. (2003). Resistance to fenazaquin and tebufenpyrad in *Panonychus ulmi* Koch (Acari: Tetranychidae) populations from South

of France apple orchards. *Crop Protection, 22*, 1039–1044.

Boer, J. G., Hordijk, C. A., Posthumus, M. A., & Dicke, M. (2008). Prey and non-prey arthropods sharing a host plant: effects on induced volatile emission and predator attraction. *Journal of Chemical Ecology, 34*, 281–290.

Chazeau, J. (1985). Predaceous insects. In W. Helle & M. W. Sabelis (Eds.), *Spider mites, their biology, natural enemies and control, vol.1B*, pp. 211–246. Amsterdam, the Netherlands: Elsevier.

Collier, K. F. S., Albuquerque, G. S., Eiras, A. E., Blackmer, J. L., Araujo, M. C., & Monteiro, L. B. (2001). Olfactory stimuli involved in prey location by *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) on apple and alternate host plants. *Neotropical Entomology, 30*, 631–639.

Dicke, M., Van der Maas, K. J., Takabayashi, J., & Vet, L. E. M. (1990). Learning affects response to volatile allelochemicals by predatory mites. *Proceedings of Experimental and Applied Entomology, 1*, 31–36.

Drukker, B., Scutareanu, P., & Sabelis, M. W. (1995). Do anthocorid predators respond to synomones from *Psylla*-infested pear trees in field conditions? *Entomologia Experimentalis et Applicata, 77*, 193–203.

Drukker, B., Bruin, J., & Sabelis, M. W. (2000). Anthocorid predators learn to associate herbivore-induced plant volatiles with presence or absence of prey. *Physiological Entomology, 25*, 260–265.

El-Adawy, A. M., Abdel-Gawad, N. M., & El-Sharkawy, T. A. (2001). Castor bean, *Ricinus communis*, a promising source of mite's predators. *Egyptian Journal of Agricultural Research, 79*, 149–160.

Gencer, N. S., Coskuncu, K. S., & Kumral, N. A. (2002). Bursa İlinde Bursa Siyahı incirlerinde bulunan zararlı akar türleri ve doğal düşmanları üzerinde araştırmalar. [Studies on fig mites and their natural enemies on Bursa Siyahi fig in Bursa province.]. *Journal of Turkish Entomology, 26*, 229–239.

Gols, R., Roosjen, M., Dijkman, H., & Dicke, M. (2003). Induction of direct and indirect plant responses by jasmonic acid, low spider mite densities, or a combination of jasmonic acid treatment and spider mite infestation. *Journal of Chemical Ecology, 29*, 2651–2666.

Helle, W., & Sabelis, M. W. (1985). *Spider mites. Their biology, natural enemies and control, vol. IB*. Amsterdam, The Netherlands: Elsevier.

Hodek, I. (1973). *Biology of Coccinellidae*. The Czech Republic: Academia, Publishing House of the Czechoslovak Academy of Sciences.

James, D. G. (2005). Further field evaluation of synthetic herbivore-induced plant volatiles as attractants for beneficial insects. *Journal of Chemical Ecology, 31*, 481–495.

James, D. G., & Price, T. S. (2004). Field-testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. *Journal of Chemical Ecology, 30*, 1613–1628.

Janssen, A., Pallini, A., Venzon, M., & Sabelis, M. W. (1998). Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. *Experimental and Applied Acarology, 22*, 497–521.

JMP. (2001). *JMP statistical software, version 5*. Cary, NC, USA: SAS Institute.

Kaylani, S. (1967). Biology and life history of *Stethorus gilvifrons* Mulsant (Coccinellidae: Coleoptera) in Lebanon. *Magon Institut de Recherches Agronomiques Publication (Serie Scientifique), 11*, 1–24.

Kim, Y. J., Lee, S. H., Lee, S. W., & Ahn, Y. J. (2004). Fenpyroximate resistance in *Tetranychus urticae* (Acari: Tetranychidae): cross-resistance and biochemical resistance mechanisms. *Pest Management Science, 60*, 1001–1006.

Kumral, N. A., Susurluk, H., Gencer, N. S., & Gurkan, M. O. (2008). Resistance to chlorpyrifos and lambda-cyhalothrin along with detoxifying enzyme activities in field-collected female populations of European red mite. *Phytoparasitica, 37*, 7–15.

Lentz, C., Petersen, G., Molck, G., & Wyss, U. (2004). Olfactory orientation of the spider mite predator *Stethorus punctillum*. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie, 14*(1–6), 191–194.

Llusia, J., & Penuelas, J. (2001). Emission of volatile organic compounds by apple trees under spider mite attack and attraction of predatory mites. *Experimental and Applied Acarology, 25*, 65–77.

Maeda, T., Takabayashi, J., Yano, S., & Takafuji, A. (2000). The effects of rearing conditions on the olfactory response of predatory mites, *Phytoseiulus persimilis* and *Amblyseius womersleyi* (Acari: Phytoseiidae). *Applied Entomology and Zoology, 35*, 345–351.

Moayeri, H. R. S., Ashouri, A., Brodsgaard, H. F., & Enkegaard, A. (2006a). Odour-mediated responses of a predatory mirid bug and its prey, the two-spotted spider mite. *Experimental and Applied Acarology, 40*, 27–36.

Moayeri, H. R. S., Ashouri, A., Brodsgaard, H. F., & Enkegaard, A. (2006b). Odour-mediated preference and prey preference of *Macrolophus caliginosus* between spider mites and green peach aphids. *Journal of Applied Entomology, 130*, 504–508.

Moayeri, H. R. S., Ashouri, A., Poll, L., & Enkegaard, A. (2007). Olfactory response of a predatory mirid to herbivore induced plant volatiles: multiple herbivory vs. single herbivory. *Journal of Applied Entomology, 131*, 326–332.

Nauen, R., Stumpf, N., Elbert, A., Zebitz, C. P. W., & Kraus, W. (2001). Acaricide toxicity and resistance in larvae of different strains of *Tetranychus urticae* and *Panonychus ulmi* (Acari: Tetranychidae). *Pest Management Science, 57*, 253–261.

Oncuer, C. (1991). *A catalogue of the parasites and predators of insect pests of Turkey*. Izmir, Turkey: Ege University, Agricultural Faculty Press.

Sabelis, M. W., & Van de Baan, H. E. (1983). Location of distant spider-mite colonies by phytoseiid predators: Demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi* (Acari: Phytoseiidae, Tetranychidae). *Entomologia Experimentalis et Applicata, 33*, 303–314.

Sabelis, M. W., Afman, B. P., & Slim, P. J. (1984a). Location of distant spider-mite colonies by *Phytoseiulus persimilis*: Localisation and extraction of a kairomone. In D. A. Griffiths & C. E. Bowman (Eds.), *Acarology VI, vol. 1*, pp. 431–440. New York, NY: Wiley.

Sabelis, M. W., Vermaat, J. E., & Groeneveld, A. (1984b). Arrestment responses of the predatory mite, *Phytoseiulus*

persimilis, to steep odor gradients of a kairomone. *Physiological Entomology, 9*, 437–446.

Sabelis, M. W., Van Baalen, M., Bakker, F. M., Bruin, J., Drukker, B., Egas, M., et al. (1999). Evolution of direct and indirect plant defence against herbivorous arthropods. In H. Olff, V. K. Brown & R. H. Drent (Eds.), *Herbivores: between plants and predators*, pp. 109–166. Oxford, UK: Blackwell Science.

Scutareanu, P., Drukker, B., Bruin, J., & Sabelis, M. W. (1997). Volatiles from *Psylla*-infested pear trees and their possible involvement in attraction of anthocorid predators. *Journal of Chemical Ecology, 23*, 2241–2260.

Sengonca, C., & Kranz, J. (2001). A modified, four-armed olfactometer for determining olfactory reactions of beneficial arthropods. *Journal of Pesticide Science, 74*, 127–132.

Shimoda, T., Ozawa, R., Sano, K., Yano, E., & Takabayashi, J. (2005). The involvement of volatile infochemicals from spider mites and from food-plants in prey location of the generalist predatory mite *Neoseiulus californicus*. *Journal of Chemical Ecology, 31*, 2019–2032.

Solomon, M. G., Cross, J. V., Fitzgerald, J. D., Campbell, C. A. M., Jolly, R. L., Olszak, R. W., et al. (2000). Biocontrol of pests of apples and pears in Northern and Central Europe-3. Predators. *Biocontrol Science and Technology, 10*, 91–128.

Takabayashi, J., & Dicke, M. (1992). Response of predatory mites with different rearing histories to volatiles of uninfested plants. *Entomologia Experimentalis et Applicata, 64*, 187–193.

Takabayashi, J., & Dicke, M. (1996). Plant–carnivore mutualism through herbivore-induced carnivore attractants. *Trends in Plant Science, 1*(4), 109–113.

Takabayashi, J., Dicke, M., & Posthumus, M. A. (1994). Volatile herbivore-induced terpenoids in plant–mite interactions: variation caused by biotic and abiotic factors. *Journal of Chemical Ecology, 20*, 1329–1354.

Takahashi, H., Takafuji, A., Takabayashi, J., Yano, S., & Shimoda, T. (2001). Seasonal occurrence of specialist and generalist insect predators of spider mites and their response to volatiles from spider-mite-infested plants in Japanese pear orchards. *Experimental and Applied Acarology, 25*, 393–402.

Uygun, N. (1981). *Taksonomische Untersuchungen über die Coccinellidenfauna (Coleoptera) der Turkei*. Adana, Turkey: Cukurova University Agriculture Faculty Press.

Van de Vrie, M. (1985). Apple. In W. Helle & M. W. Sabelis (Eds.), *Spider mites: Their biology, natural enemies and control. vol 1B*, pp. 311–325. Amsterdam, the Netherlands: Elsevier.

Van den Boom, C. E. M., Van Beek, T. A., & Dicke, M. (2002). Attraction of *Phytoseiulus persimilis* (Acari: Phytoseiidae) towards volatiles from various *Tetranychus urticae*-infested plant species. *Bulletin of Entomological Research, 92*, 539–546.

Van den Boom, C. E. M., Van Beek, T. A., Posthumus, M. A., De Groot, A., & Dicke, M. (2004). Qualitative and quantitative variation among volatile profiles induced by *Tetranychus urticae* feeding on plants from various families. *Journal of Chemical Ecology, 30*, 69–89.