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Tritrophic relationships among tomato cultivars, the rust mite, *Aculops lycopersici* (Massee) (Eriophyidae), and its predators

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ABSTRACT

Trichome-mediated defence in wild and cultivated tomato cultivars has been extensively studied against some mite species for several decades. Previous studies have shown that this mechanism negatively affects phytophagous mites and their predators. To better explain the tritrophic relationship of tomatoes, the interactions between population densities of the tomato rust mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae), and its predators on the tomato cultivars, namely, Dora, Etna, Grande, H2274, Jana and M1103, and the trichome densities of these cultivars were investigated in both a climatic room and an organic tomato field from 2014-2015. Under both controlled and field conditions, the *A. lycopersici* population density was significantly higher in the stake tomato cultivars, Jana and Etna, than in other tomato cultivars. When the tomato rust mite's population density was the highest during mid-August and mid-September in the tomato field, the population density of the predator species, *Tydeus kochi* Oudemans (Tydeidae), showed a similar population pattern and significant positive correlation with the *A. lycopersici* density. However, density of this predator mite was significantly lower than that of *A. lycopersici* over the entire season. Remarkably, the glandular trichome type VI density was significantly higher in the stake cultivars than other cultivars. In contrast, significantly fewer glandular trichomes were found in the indeterminate tomato cultivars, Grande and H2274, which had fewer tomato rust mites and larger tydeid mite predator densities. These results support the hypothesis that trichomes provide excellent shelter for tomato rust mites and are obstacles for its predator mites. However, the population density of the insect predator, *Macrolophus* sp., was not affected by the trichome density or tomato cultivar, but its population density was not significantly correlated with that of the *A. lycopersici* population.

Introduction

The tomato rust mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae), is a significant pest of cultivated tomato cultivars and feeds on some wild tomato species and other solanaceous species, such as eggplant and nightshade (Mason and Huber 2001; Shipp *et al.,* 2001; Haque and Kawai 2002; Kim *et al.,* 2002; Goldsmith 2004; Ozman-Sullivan and Ocal 2005; Kumral and Cobanoglu 2015a,b). In tomatoes, this mite first causes leaf necrosis, which is similar to a lack of micro-elements in the leaves. High mite populations lead to water stress with smaller, distorted and dusty brown-coloured leaves. When mites feed on the generative organs, inflorescence and young fruit become shrivelled with dropped flowers and russeted fruit, and if uncontrolled, the plants will die (Royalty and Perring 1988; Kumral *et al.,* 2014). In addition,

heavy mite infestations lead to crop losses of more than 65% in tomato production (Celar and Valič 2003).

To control these pests in the outdoor tomato fields of Turkey, the standard method is to spray synthetic acaricides based on a calendar date (Anonymous, 2015). Because mites are small, they are difficult to see with a simple magnifier. Chemical treatments are often unsuccessful at controlling these pests as they inaccurately estimate the control time. This method often results in poor mite control and ecological problems, such as destroying non-target organisms and natural enemies of the pests (Yu 2008, Khalighi *et al.*, 2016). Additionally, when the mite population density becomes high, the tomato plant is in its phenological fruit-ripening period. To avoid chemical residue on crops, most growers refrain from using chemicals during this period. Although some biological agents feed on *A. lycopersici*, they are usually insufficient because the leaves and saps of some plant cultivars are extensively covered with glandular and non-glandular trichomes (Brodeur *et al.*, 1997; Fischer and Mourrut-Salesse 2005; Van Houten *et al.*, 2013a).

The most important factors in the host plant's favour are type, density and the trichomes' toxic chemical composition (Van de Boom *et al.,* 2003; Kang *et al.,* 2010). Trichomes are reported to help protect against insects and spider mite attacks (Chatzivasileiadis and Sabelis 1998; Gonçalves *et al.,* 1998; Pocoví *et al.,* 1998; Aragão *et al.,* 2002; Antonious and Snyder 2006; Maluf *et al.,* 2007, 2010; Schie *et al.,* 2007; Alba *et al.,* 2009; McDowell *et al.,* 2011). Glandular and non-glandular trichomes also restrict some predator species from moving on the plant leaf surfaces as well as being toxic and limiting predator development (Kennedy 2003; Buitenhuis *et al.,* 2015). In addition, trichomes can shelter some small pests, protecting them from their natural enemies (Van Houten *et al.,* 2013b).

Such tritrophic interactions may affect *A. lycopersici* population dynamics in different tomato cultivars. Different cultivars may also reduce the mite's fitness on the host plant or activate its natural enemies. Consequently, to keep the mite levels below the economic threshold, tomato cultivars that are unsuitable for *A. lycopersici*, but suitable for its predators, are required. This study determined the population development of *A. lycopersici* on six tomato hybrid cultivars, namely, Dora, Etna, Grande, H2274, Jana and M1103, under controlled and natural field conditions and evaluated tritrophic interactions among plant trichomes and population densities of *A. lycopersici* and its predators under field conditions.

Materials and methods

Mite origin and mass rearing

Aculops lycopersici were collected from tomato plants on Gorukle Campus (Bursa, Turkey). The species was identified by Eddie A. Ueckermann (Agriculture Research Council, Plant Protection Research Institute, Pretoria, South Africa) based on morphological characteristics viewed under both light and scanning electron microscopes (Kumral *et al.,* 2014). The mite population was mass-reared on potted tomato plants grown in a climate-controlled room. Synchronous mite populations were obtained by rearing at least two generations on each tomato cultivars.

Growth of tomato plants

Three stake tomato cultivars, Dora, Etna, and Jana (May-Agro Company, Bursa, Turkey), and three indeterminate hybrid tomato cultivars, Grande, H2274 and M1103, (Agromar Company, Bursa, Turkey) were grown in 2.5-L pots filled with Klasmann TS 1 type peat (Deilmann, Geeste, Germany) in a climate-controlled room on a 16 h light: 8 h dark cycle (27 ± 1°C, 65 ± 5%). Seedlings were irrigated every third day with tap water and fertilized weekly with water-soluble fertilizer containing macro and micronutrients: 3% total nitrogen (N), 7% phosphorus (P_2O_5), 4.5% potassium (K_2O), 0.1% sulphur (SO_4.S), 0.25% iron (Fe), 0.01% copper (Cu),

0.1% zinc (Zn), 0.1% manganese (Mn), 0.01% boron (B), and 0.001% molybdenum (Mo) (University of Uludag, Department of Soil Science and Nutrition, Bursa, Turkey). For the population development studies under natural conditions, twenty-five-day-old plants were transferred to a field for sowing. Before sowing, the field was fertilized with only organic manure containing nitrogen. The plants were irrigated at two-day intervals by a drip irrigation system. Tomato seedlings were sprayed with insecticide (40 g/l azdirachtin, Nimiks 4.5, Agrikem Certus, USA) and fungicide (65.82 g/l copper sulphate pentahydrate, Mastercop®M, Bravo Ingeneri Industrial S.A. de C.V., Mexico) during and after the sowing period. For the population development studies under controlled conditions, plants in full bloom with five fully expanded, combined mature leaves of approximately equal area, were used.

Mite population development under controlled conditions

To determine population development under controlled conditions, full bloom tomato plants were artificially infested with 25 female mites from the synchronous *A. lycopersici* population with a soft-bristle paintbrush in 2014. Twenty-one days after infestation, mobile mites were counted on all leaf surfaces and stalks under a stereomicroscope (Leica EZ4, Germany). Each tomato cultivar included three replicates with 3 plants per replicate.

Mite population development in the field

To assess population development under natural conditions, the field experiment was conducted in a 0.1 ha tomato field at the Uludag University Agricultural Faculty in Bursa in 2015. Experimental plots containing 10 plants per plot were constructed based on a Latin square design (Figure 1) with six replicate plots per cultivar. Three leaves were collected at three different heights (top, middle and bottom) from 3 plants per plot. Fifty-four leaves from each cultivar were collected weekly from early June to late October. *A. lycopersici* mobile stages and their predator mites and insects on the tomato leaves and stalks were counted under a stereomicroscope. Predator mites were preserved in alcohol (70%), then cleaned, stained and mounted in Hoyer's medium (Hoy 2011). Mounted mite species were identified under an optical microscope per the methods of Baker (1970), Ueckermann & Grout (2007), Faraji *et al.* (2011). The mite specimens were deposited in Acarology Laboratory of Bursa Uludag

Figure 1 Tomato cultivarplot positions based on a Latin square design (D: Dora; E: Etna; G: Grande; H: H2274; J: Jana; M: M1103).

Table 1 Mean number of mobile stages of *Aculops lycopersici* on Dora, Etna, Grande, H2274, Jana and M1103 tomato cultivars under controlled conditions.

Cultivars	Mean number of mite per plant ± SE		
	Adaxial	Abaxial	All surfaces
Dora	215.33±71.42b*	279.45±111.59b	494.78±183.01b
Etna	437.89±128.13ab	217.11±49.52b	655.00±177.65b
Grande	130.67±24.69b	107.11±20.28b	237.78±44.97b
H2274	35.67±9.83b	32.22±7.49b	67.89±17.32b
Jana	899.78±225.83a	765.89±162.47a	1665.67±383.30a
M1103	197.33±53.89b	171.67±46.97b	369.00±100.86b

* Means followed by the same letter in a column are not significantly different (Tukey, $P < 0.01$).

University. Based on species identification, weekly mean mite abundance was calculated for each cultivar, and abundance was the number of mites per leaf on each sampling date.

Types and densities of tomato trichome

Five leaves were collected from five different levels per tomato when the plants reached the fruit set period under natural conditions. Six 1-mm^2 areas on each leaf were examined for trichome density on both the abaxial and adaxial leaf surfaces using a template with different positions for the 1-mm^2 areas. Sampled leaves were the same age and position and not selected randomly. Each tomato cultivar included three replicates with 3 plants per replicate. Non-glandular (types II and V) and glandular (type VI) trichomes were identified per the methods of Channarayappa et al. (1992) and McDowell et al. (2011). Trichome density was represented as 1 mm^2.

Statistical analyses

The weekly mean mite population densities were compared among weeks with a repeated measures analysis of variance, followed by Tukey's multiple comparison test using SAS statistical software (SAS, 2007). One-way analysis of variance (textitANOVA) was performed on the data from the trichome density and mite population development in controlled conditions, and significant differences among the mean mite numbers and trichome density for the six cultivars were calculated using the Least significant Difference test at $P < 0.05$. Multivariate analyses were performed on the mean density of *A. lycopersici* versus predator mites, insect densities, and densities of the different glandular and non-glandular trichomes of the six tomato cultivars versus *A. lycopersici* and its predator densities under natural conditions in 2015 using the JMP 7 statistical package (SAS, 2007).

Results

Aculops lycopersici population development

The mean numbers of *A. lycopersici* mobile stages differed significantly among the six tomato cultivars under controlled conditions (Table 1, $F_{5,48}$=9.21, P<0.01). Similarly, the mean mite numbers differed significantly among both the abaxial and adaxial surfaces of the six tomato cultivars ($F_{5,48}$=7.77, P<0.01, $F_{5,48}$=9.31, P<0.01), and the mean mite number for Jana was significantly higher than the other cultivars. Although the H2274 cultivar had fewer mites, the difference was not significant compared with the other tomato cultivars.

The *A. lycopersici* density among the six tomato cultivars varied remarkably throughout the entire growing season under natural conditions (Table 2, $F_{5,409}$=2.93, P=0.0013). *Aculops*

Table 2 Mean total number of mobile stages of *Aculops lycopersici* throughout the entire growing season on Dora, Etna, Grande, H2274, Jana and M1103 tomato cultivars under natural conditions in 2015.

Cultivars	Mean number of mite per plant ± SE		
	Adaxial	Abaxial	All surfaces
Dora	9.71±1.37b*	25.24±3.39ab	34.94±4.71b
Etna	12.59±2.09ab	34.61±4.40ab	47.20±6.37ab
Grande	6.28±0.95b	15.99±2.49b	22.27±3.38b
H2274	7.17±1.47b	24.76±4.13ab	31.93±5.53b
Jana	14.58±1.98ab	31.96±4.26ab	46.55±5.97ab
M1103	23.84±7.30a	34.74±7.21a	58.57±13.94a

* Means followed by the same letter in a column are not significantly different (Tukey, $P < 0.01$)

lycopersici on M1103 had a significantly higher population density, followed by the Etna and Jana cultivars, respectively. Similar to the controlled condition results, mean mite numbers were significantly lower on the Grande and H2274 cultivars than the others. Mean mite numbers significantly differed on both the lower and upper surfaces of these tomato cultivars (Table 2, $F_{5,409}=2.50$, $P=0.03$, $F_{5,409}=3.59$, $P=0.0034$). The population trends and densities of *A. lycopersici* on the six tomato cultivars under natural conditions for 2015 are shown in Figure 2A. The mite density increased in early August and peaked in late August. The highest *A. lycopersici* density was significant on 24 August for Jana and H2274 and on 31 August for the M1103, Dora, Grande and Etna cultivars ($P<0.01$). The population density gradually decreased from mid-September to mid-October.

Population development of predator mites

In the present study, 5 predator species belong to Phytoseiidae were obtained from the six tomato cultivars under natural conditions. These species were *Neoseiulus barkeri* Hughes*, Euseius finlandicus* (Oudemans)*, Typhlodromus (Anthoseius) recki* Wainstein*, Typhlodromus (Typhlodromus) athiasae* Porath and Swirski and *Phytoseius finitimus* Ribaga (Acari: Phytoseiidae). In addition, two species were detected from Tydeidae and Iolinidae, *Tydeus kochi* Oudemans and *Pronematus ubiquitus* (McGregor), which have varied feeding habits including predatory.

Tydeus kochi density varied significantly among the six tomato cultivars throughout the entire growing season under natural conditions (Table 3, $F_{5,409}=2.28$, $P=0.046$). The highest significant density of *T. kochi* was found on the H2274 and Grande cultivars. In contrast to the *A. lycopersici* results, mean mite numbers were significantly lower on the Jana and Dora cultivars than the other cultivars (Table 3). *T. kochi* population trends and densities on the six tomato cultivars under natural conditions for 2015 are shown in Figure 2B. Similar to the *A. lycopersici* trend*, T. kochi* was first observed in late July to early August and peaked significantly twice on 31 August and 20 September ($P<0.01$). The *T. kochi* population trend was positively correlated with that of *A. lycopersici* on all tomato cultivars (Table 4, $r= 0.22$ to 0.59, $P<0.01$ or <0.05). In addition, although the *P. ubiquitus* densities varied significantly among the six tomato cultivars, they were not significantly correlated with the *A. lycopersici* population trend (Table 3 and 4, Figure 2C, $F_{5,409}=2.79$, $P=0.017$, $r=-0.11$ to 0.12, $P>0.05$). However, although phytoseiid were observed between early August and early September, these population trends were not correlated with those of *A. lycopersici*, and the difference in their population density among the six tomato cultivars was not significant (Tables 3 and 4, Figure 2D, $P>0.05$, $r= -0.15$ to 0.05, $P>0.05$).
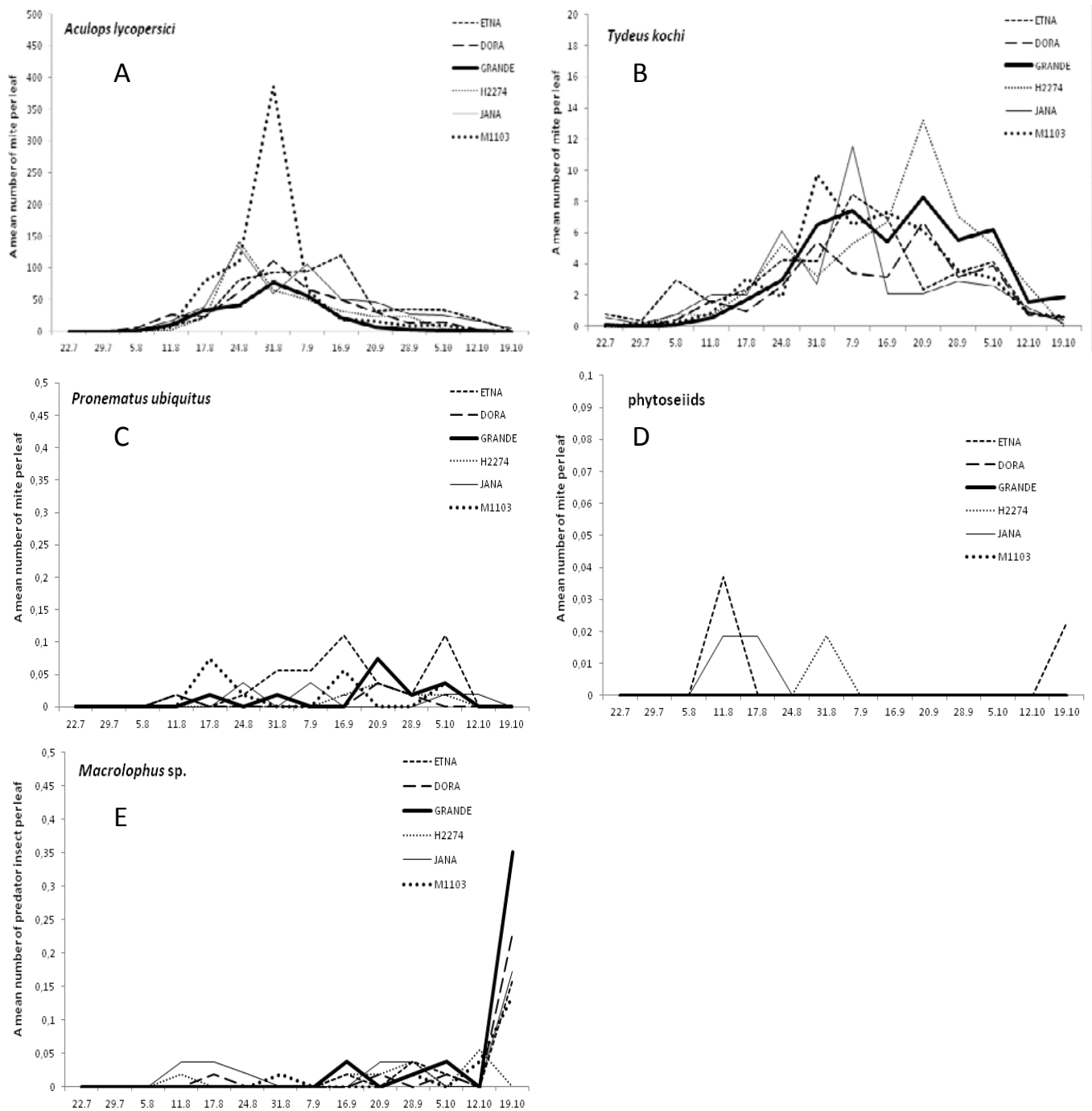
Figure 2 Mean weekly mobile stage densities of: A –*Aculops lycopersici*; B – *Tydeus kochi*; C – *Pronematus ubiquitus*; D – phytoseiid species; E – *Macrolophus* sp.; throughout the entire growing season on Dora, Etna, Grande, H2274, Jana and M1103 tomato cultivars under natural conditions in 2015.

Table 3 Mean total number of mobile stages of *Tydeus kochi*, *Pronematus ubiquitus*, phytoseiid species and *Macrolophus* sp. throughout the entire growing season on Dora, Etna, Grande, H2274, Jana and M1103 tomato cultivars under natural conditions in 2015.

Predator species	*Tydeus kochi*			*Pronematus ubiquitus*		
Cultivars	Adaxial [NS]	Abaxial*	Both surface*	Adaxial [NS]	Abaxial [NS]	Both surface*
Dora	0.83±0.09	1.99±0.21bc	2.82±0.29c	0.003±0.002	0.003±0.002	0.006±0.003b
Etna	1.34±0.17	2.17±0.23abc	3.51±0.38b	0.011±0.005	0.026±0.011	0.037±0.012a
Grande	1.04±0.11	3.15±0.31ab	4.20±0.40a	0.005±0.004	0.009±0.005	0.015±0.007ab
H2274	1.32±0.17	3.19±0.36a	4.51±0.49a	0.00±0.00	0.008±0.004	0.008±0.004b
Jana	1.28±0.21	1.88±0.28c	3.15±0.47c	0.003±0.002	0.007±0.003	0.009±0.005ab
M1103	1.07±0.13	2.58±0.33abc	3.64±0.43b	0.002±0.002	0.014±0.006	0.015±0.006ab

Predator species	Phytoseiid species			*Macrolophus sp.*		
Cultivars	Adaxial [NS]	Abaxial [NS]	Both surface[NS]	Adaxial [NS]	Abaxial[NS]	Both surface[NS]
Dora	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.008	0.010±0.006	0.026±0.011
Etna	0.00±0.00	0.06±0.05	0.06±0.05	0.005±0.003	0.015±0.007	0.021±0.008
Grande	0.00±0.00	0.00±0.00	0.00±0.00	0.017±0.009	0.016±0.008	0.033±0.013
H2274	0.00±0.00	0.02±0.01	0.02±0.01	0.003±0.002	0.009±0.004	0.012±0.004
Jana	0.00±0.00	0.04±0.03	0.04±0.03	0.010±0.005	0.017±0.005	0.027±0.007
M1103	0.00±0.00	0.00±0.00	0.00±0.00	0.013±0.007	0.005±0.002	0.017±0.007

* Means followed by the same letter in a column are not significantly different (Tukey, $P < 0.01$).

[NS] Means are not significantly different.

Predator insect population development

In this study, the mite predatory species, *Macrolophus* sp. (Heteroptera: Miridae) was observed on all tomato cultivars under natural conditions (Table 3 and Figure 2E), but the cultivar did not significantly affect the population density of the predatory insect ($F_{5,409}$=0.69, P=0.63). The *Macrolophus* sp. density was slightly higher on the Grande, Etna and M1103 cultivars. Similar to *A. lycopersici,* the predator insect was first observed in early August (Figure 2E). In contrast, the highest significant population densities were seen on 16 September and 5 and 19 October (P<0.01); however, these were not positively correlated with the *A. lycopersici* population density (Table 4*, r=-0.24* to -0.02).

Trichome density and its effect on pest and predator densities

Non-glandular (types II and V) and glandular trichome (type VI) densities on the tomato leaves under natural conditions differed significantly (Table 5, type II $F_{5,24}$=8.91, P<0.01, type V $F_{5,24}$=57.55, P<0.01, type VI $F_{5,24}$=19.13, P<0.01). While trichome density was higher on the abaxial surface for all cultivars, their densities on both surfaces differed significantly among the six tomato cultivars (type II $F_{5,24}$=9.99, P<0.01, $F_{5,24}$=5.97, P<0.01, type V $F_{5,24}$=26.99, P<0.01, $F_{5,24}$=63.57, P<0.01, type VI $F_{5,24}$=7.53, P<0.01, $F_{5,24}$=32.07, P<0.01). The trichome densities of non-glandular type II, and especially type V, on both surfaces were highest on Jana, followed by H2274 and Dora. The lowest trichome densities were detected on Grande (Table 5). Similarly, glandular type VI trichomes were high for Jana and low for Grande (Table 5).

Multivariate analysis results for the glandular and non-glandular trichome densities of the six tomato cultivars versus *A. lycopersici* and its predator densities under natural conditions are shown in Table 6. Although the *A. lycopersici* density showed a significant positive correlation

Table 4 Multivariate analysis of *Aculops lycopersici* versus its predator densities under natural conditions in 2015

Cultivars		*Tydeus kochi*	*Pronematus ubiquitus*	phytoseiid species	*Macrolophus sp*
Dora	r	0.3617	-0.099	0	-0.024
	P	0.0023*	0.41	-	0.05*
Etna	r	0.51	0.13	-0.15	-0.24
	P	<0.01*	0.29	0.24	0.05*
Grande	r	0.22	-0.11	0	-0.24
	P	0.05*	0.4	-	0.05*
H2274	r	0.11	-0.04	0.05	-0.09
	P	0.38	0.74	0.64	0.47
Jana	r	0.59	0.12	-0.05	-0.22
	P	<0.01*	0.31	0.67	0.07
M1103	r	0.45	0.1	0	-0.07
	P	<0.01*	0.39	-	0.56

with type V non-glandular and type VI glandular trichome densities, type II non-glandular and type VI glandular trichome densities were negatively correlated with the predator, *T. kochi*. Similar negative correlations were found for both *P. ubiquitus* and *Macrolophus* sp. vs. type V.

Discussion

The present study showed that differences in tomato plant cultivars can significantly affect *A. lycopersici* population densities in both controlled and natural conditions. The mite population density was significantly higher in the Jana cultivar followed by the Etna and M1103 cultivars. However, Grande and H2274 had lower mite population densities. These findings are consistent with other studies that reported differences among tomato cultivars/accessions or wild tomato species infested with *A. lycopersici* (Kamau *et al.,* 1992; Leite *et al.,* 2000; Kitamura and Kawai 2006; Wang *et al.,* 2008).

Under natural conditions, the *A. lycopersici* density reached its highest yearly population from mid-August to mid-September, when the mean temperature and relative humidity were 25.6°C and 60.9%, respectively. Consistent with our results, the optimum conditions for *A. lycopersici* have shown to be 26-29°C and 53-75% relative humidity (Baradan-Anakari and Daneshvar 1992; Kim *et al.,* 2002; Haque and Kawai 2002; Kawai and Haque 2004; Xu *et al.,* 2006). In accordance with our findings, it is reported that the mites first emerge in early August when the mean temperature reaches 26.1-28.3°C and the tomato phenology is in the beginning of the fruit ripening period in north and western Turkey (Hıncal *et al.* 2002; Yanar *et al.,* 2008). These researchers noted that the mite population and damage gradually increased in mid-August and peaked in early September.

Our results showed significant differences in both glandular and non-glandular trichome densities among the six tomato cultivars. In this study, only non-glandular type II and V and glandular type VI trichomes were observed on all six tomato cultivars, because we did not use a wild cultivar (McDowell *et al.,* 2011). Remarkably, the greatest significant numbers of glandular and non-glandular trichomes were found on the Jana cultivar, followed by Etna, which both had higher mite population densities. Similar to the population density results

Table 5 Mean total non-glandular and glandular trichome densities on Dora, Etna, Grande, H2274, Jana and M1103 tomato cultivars under natural conditions in 2015.

Cultivars	Adaxial			Abaxial			Both surface		
	Mean (±SE) number of nonglandular type II trichome/ leaf area	Mean (±SE) number of nonglandular type V trichome/ leaf area	Mean (±SE) number of glandular type VI trichome/ leaf area	Mean (±SE) number of nonglandular type II trichome/ leaf area	Mean (±SE) number of nonglandular type V trichome/ leaf area	Mean (±SE) number of glandular type VI trichome/ leaf area	Mean (±SE) number of nonglandular type II trichome/ leaf area	Mean (±SE) number of nonglandular type V trichome/ leaf area	Mean (±SE) number of glandular type VI trichome/ leaf area
Dora	0.40±0.40c*	530.20±45.64ab	31.00±3.30ab	2.00±0.32ab	1101.40±59.41a	24.00±2.47b	2.40±0.68b	1631.60±96.97ab	55.00±5.55bc
Etna	7.20±1.72a	417.00±15.52b	30.80±1.53ab	3.20±0.80a	903.20±31.69b	40.00±2.45a	10.40±2.38a	1320.20±45.92c	70.80±3.68ab
Grande	0.60±0.40c	225.40±19.68c	21.40±1.12b	1.80±0.20ab	314.60±46.78c	11.20±0.74c	2.40±0.51b	540.00±59.64d	32.60±1.81d
H2274	2.80±0.37bc	663.60±30.18a	21.60±2.29b	0.80±0.20b	1137.40±33.29a	34.60±2.62a	3.60±0.51b	1801.00±33.72ab	56.20±4.27bc
Jana	5.60±1.03ab	670.60±33.56a	39.00±2.93a	3.40±0.51a	1233.60±30.32a	42.80±1.88a	9.00±1.38a	1904.20±56.46a	81.80±3.41a
M1103	2.20±0.20bc	443.00±39.49b	28.20±2.58	1.00±0.32b	1117.20±44.91a	25.40±1.72b	3.20±0.20b	1560.20±77.63bc	53.60±3.28c

* Means followed by the same letter in a column are not significantly different (Tukey, $P < 0.01$).

for *A. lycopersici,* both trichome densities were much smaller in the Grande cultivar than the other cultivars. In addition, high type V and type VI trichome densities positively affected the population density of *A. lycopersici.* This effect likely occurred because the mite is smaller than the trichomes (Van Houten *et al.,* 2013b), confirming our hypothesis that trichomes provide excellent shelter for pest mites.

Seven species of predatory mites (*N. barkeri, E. finlandicus, T. (A.) recki, T. (T.) athiasae, P. finitimus, P. ubiquitus* and *T. kochi*) obtained in the current study were found to be associated with *A. lycoperesici* in previous studies (Bayan 1998, Can and Çobanoğlu 2010; Momen and Abdel-Khalek 2008; Çobanoğlu and Kumral 2014; Kumral and Çobanoğlu 2015a,b). Among these species, few phytoseiids were found among all tomato cultivars, but there were no significant differences between the six tomato cultivars with different trichome densities in this study. As mentioned in previous studies, glandular and non-glandular trichomes may affect phytoseiid populations (Fischer and Mourrut-Salesse 2005; Sato *et al.,* 2011; Van Houten *et al.,* 2013a;b). Thus, among glandular trichomes, type VI, is an important defence for tomato plants that entrap arthropods and phytoseiids (Kennedy 2003). The non-glandular trichome density can also limit phytoseiid prey-searching behaviours (Van Houten *et al.,* 2013b). Although it was reported by Van Houten *et al.* (2013b) that the phytoseiid mite, *Amblydromalus limonicus* Garman and McGregor suppressed *A. lycopersici* due to glandular trichome destruction by *T. urticae* in the early period our results confirmed that the trichomes influenced phytoseiid density under natural conditions (in the presence of *T. urticae*).

In our study, the *T. kochi* density showed a similar pattern to that of *A. lycopersici*, and the mite was associated with *A. lycopersici* populations. Consistent with our results, some tydeid species as an unspecialized group, e.g., *T. kochi, Tydeus californicus* (Banks), *Tydeus caudatus* Dugès, *Tydeus caryae* Kanjani & Ueckermann, appeared to associate with eriophyid members (Rasmy 1971; Khanjani and Mirab-balou 2005; Lorenzon *et al.,* 2009; Çobanoğlu and Kumral 2014). Similarly, Rasmy (1971) reported that *T. kochi* was a biological control agent of the citrus brown mite, *Eutetranychus orientalis* (Klein) (Acari: Eriophyidae), in citrus orchards in Egypt.

Remarkably, this study found that *T. kochi* and *A. lycopersici* densities were smaller and greater, respectively, regarding which cultivars had higher trichome densities. Thus, high type II and type VI trichome densities negatively affected the population density of *T. kochi.* These findings support the hypothesis that trichome-mediated defences in tomato plants implicated negative tritrophic effects mediated by direct (entrap and kill predators, increasing predation time) and indirect effects (limit development, modify food/prey quality) on natural enemies

Table 6 Multivariate analysis of different glandular and non-glandular trichome densities of the six tomato cultivars versus *Aculops lycopersici* and its predator densities under natural conditions in 2015.

		Aculops lycopersici	*Tydeus kochi*	*Pronematus ubiquitus*	phytoseiid species	*Macrolophus sp*
Type II	*r*	0.2	-0.46	0.29	0.78	0.19
	P	0.3	0.011*	0.11	>0.01*	0.31
Type V	*r*	0.46	-0.33	-0.37	0.37	-0.51
	P	0.009*	0.07	0.04*	0.04*	0.004*
Type VI	*r*	0.39	-0.58	-0.01	0.73	-0.02
	P	0.033*	0.001*	0.95	>0.01*	0.89

* Correlations are significantly different.

with trichomes (Farrar and Kennedy 1987; Drukker *et al*. 1997, Van de Boom *et al.* 2003; Kennedy 2003; Simmons and Gurr 2005; Koller *et al*., 2007, Buitenhuis *et al.* 2015). In addition to tydeid mites, the Iolinidae mite, *Pronematus ubiquitus*, obtained in the current study, has different feeding habits including predation, phytophagy, fungivory and scavenging. Both tydeid and iolinid populations can persist when eriophyid levels are low because their diets include non-prey foods such as pollen and fungi (Hessein and Perring 1986; Lorenzon *et al.,* 2009). Because of these feeding habits, the mites have never reduced eriophyid densities below the economic threshold as phytoseiids (Gerson *et al.,* 2003). The predator insect, *Macrolophus* sp., shows a delayed density-dependent numerical response to *A. lycopersici* density from early September to early October. In contrast to predator mites, the insect density was unaffected by varietal differences, probably due to the larger insect size. However, the non-glandular trichome type V density negatively affected the *Macrolophus* sp. density. This result was consistent with Nannini and Carboni (2003) who found that *Macrolophus caliginosus* Wagner (Heteroptera: Miridae) reduced the *A. lycopersici* density. Regarding tritrophic interactions, Economou *et al.,* (2006) indicated that, except for the time spent grooming, *Macrolophus pygmaeus* Rambur and *Orius niger* Wolff nymphs' probing and moving activities were unaffected by extensive trichome density on the tomato cultivars.

In conclusion, both bitrophic and tritrophic interactions tested under natural conditions showed that the Grande cultivar was a less suitable host for *A. lycopersici.* Before making a selection from hundreds of tomato cultivars for growing, the cultivar should be examined to assess whether it is unfavourable to *A. lycopersici* while also being suitable to their predators, such as phytoseiids, tydeids and iolinids. The present study may provide evidence for developing new tomato russet mite-resistant tomato lines.

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