

Varying abundance and dispersal of the two-spotted spider mite (*Tetranychus urticae* Koch, 1836, Acari: Prostigmata: Tetranychidae) on *Mi*-tomato plants differing in allelic combination

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Abstract: It is well known that the presence of the *Mi-1.2* gene determines the resistance of tomato plants (*Solanum lycopersicum* L.) to 3 root-knot nematode species and some insect herbivores of the order Hemiptera. In this study, the density and dispersal of two-spotted spider mites (*Tetranychus urticae*) on tomato plants of 4 cultivars were evaluated under greenhouse conditions, to find out whether tomatoes differing in allelic combination of the *Mi-1.2* gene exhibit similar or different resistance to the mite pest. The results show, for the first time, that the same initial number of mites develops into populations that vary in abundance and distribution depending on tomato allelic composition of the *Mi-1.2* gene. The results indicate that the mite-pest develops more slowly on tomato plants of cultivar ‘Motelle’, carrying 2 dominant alleles for the *Mi-1.2* gene, than on heterozygous ‘Altess F1’ tomatoes and both cultivars carrying only recessive alleles of this gene: ‘Moneymaker’ and ‘Plaisence F1’. This suggests that the *Mi-1.2* gene may be involved in tomato resistance against spider mites when this dominant gene is expressed homozygously, but this needs to be verified by further research.

Keywords: spatio-temporal spread, distribution, *Solanum lycopersicum* L., spider mites, *Tetranychus urticae*, *Mi-1.2* gene

INTRODUCTION

During cultivation, tomato (*Solanum lycopersicum* L., 1753) plants are exposed to various stress factors, both biotic (pathogens, pests) and abiotic (drought, salinity, extremes in temperature, UV light radiation, etc.), which limit plant growth and yield. The majority of commercially available tomato cultivars have been equipped with traits of resistance to some pathogens, but only few tomato cultivars carry the *Mi-1.2* gene, which was introduced with traditional breeding methods (SMITH 1944). The presence of the *Mi-1.2* gene product significantly reduces the development of 3 species of root-knot nematodes (*Meloidogyne incognita* Kofoid et White, 1919; *M.*

arenaria Neal, 1889; and *M. javanica* Treub, 1885) (MILLIGAN et al. 1998) and thus limits the losses in tomato plant yield (TALAVERA et al. 2009). Studies in recent years have shown that the *Mi-1.2* gene also determines the resistance of tomato plants to some insect herbivores of the order Hemiptera, such as the potato aphid (*Macrosiphum euphorbiae* Thomas, 1877) (KALOSHIAN et al. 1995; ROSSI et al. 1998; GOGGIN et al. 2001), the sweet potato whitefly (*Bemisia tabaci* Genn., 1889) (NOMBELA et al. 2003), and the tomato psyllid (*Bactericera cockerelli* Sulc) (CASTEEL et al. 2006).

Mite herbivores, very much like aphids or whiteflies (insects of the order Hemiptera), are equipped with piercing-sucking mouthparts, but mites differ from the hemipterans in their mode of feeding and leaf tissue damage. Aphids and whiteflies feed on phloem sap, whereas mites feed on mesophyll cell content. The two-spotted spider mite (*Tetranychus urticae* Koch, 1836, Acari: Prostigmata: Tetranychidae) is an economically important mite-pest for a number of crop plants and may heavily infest tomato plants (NIHOUL et al. 1991; KIELKIEWICZ 1996, 2003). So far, there are no data available on *Mi*-tomato-mite interactions, except an assessment of population parameters of *T. urticae* on detached tomato leaves carrying dominant or recessive alleles of the *Mi-1.2* gene, showing comparable mite reproductive potential (GODZINA et al. 2010a). The assessment of spatio-temporal mite dynamics on intact plants seems to be a more reliable indicator of *Mi*-tomato susceptibility and/or resistance to this arthropod pest. Therefore, in this study, mite density and dispersal on tomato plants of 4 cultivars were evaluated under greenhouse conditions to find out whether tomatoes differing in allelic combination of the *Mi-1.2* gene exhibit similar or different resistance to the mite pest.

MATERIALS AND METHODS

Four tomato cultivars carrying different or the same form of the *Mi-1.2* gene were chosen: 2 cultivars from the INRA gene bank (France), i.e. 'Motelle' (dominant homozygote for the *Mi-1.2* gene) and 'Moneymaker' (recessive homozygote); and 2 commercially available cultivars, i.e. 'Altess F1' (heterozygote) and 'Plaisence F1' (recessive homozygote) (DeRuiter, Switzerland). Plants of all cultivars were grown in a greenhouse in a peat substrate from 21 March to 3 July 2009. In the present study, 9-week-old plants were used, as it is known from literature that the *Mi-1.2* mediates tomato resistance to insect pests but does not reveal itself until plants reach the age of 6 weeks (GOGGIN et al. 2004). The mean number of leaves per plant was 15 in cultivars 'Motelle' and 'Moneymaker' and 13 in 'Altess F1' and 'Plaisence F1'. Plants of all cultivars were divided into 2 groups: the control (not mite-infested, $n = 16$) and the mite-infested group ($n = 16$).

Plants were artificially infested with young females of *T. urticae* from a colony established on the commercial tomato cultivar 'Robin F1' (PNOS, Ożarów Mazowiecki, Poland) in the greenhouse. On the first compound leaf under the first cluster, 25 young females were placed (i.e. 5 females on each of 5 leaflets). Using a magnifying glass, all mobile stages of *T. urticae* were counted on each leaf of each plant once a week for 6 weeks. The density of the mite-pest was expressed as the number of mobile stages per leaf and per plant.

Differences in the density of mobile stages between cultivars were compared using one-way analysis of variance (ANOVA) followed by the Tukey honestly significant difference (HSD) test (Statgraphics® Plus for Windows 4.1). When the data were not normally distributed, the non-parametric test of Kruskal-Wallis was used instead. In each analysis, significance was assumed at $P = 0.05$.

RESULTS

The dynamics of *T. urticae* population development in all cultivars (Fig. 1) shows that the equal initial number of *T. urticae* on leaves of all cultivars multiplied similarly (on average 4-fold) until the 3rd week of observations (4 June 2009). From the beginning of the 4th week, mite density started to differ among the cultivars examined ('Moneymaker', 'Motelle', 'Altes F1' and 'Plaisance F1') (Fig. 1; Fig. 4; Table 1). After 6 weeks, the largest number of mites occurred on plants of commercial cultivars ('Altes F1' and 'Plaisance F1'), while the number of individuals on plants of cultivars 'Motelle' and 'Moneymaker' was significantly lower (Kruskal-Wallis test: $H = 17.61$; $P = 0.0005$) (Fig. 1; Fig. 4).

The mobile stages of *T. urticae* started moving up the plant noticeably at the beginning of the 4th week and continued their upward movement as the population density increased (Table 1; Fig. 2a-b; Fig. 3a-b). The distribution of the mobile stages on

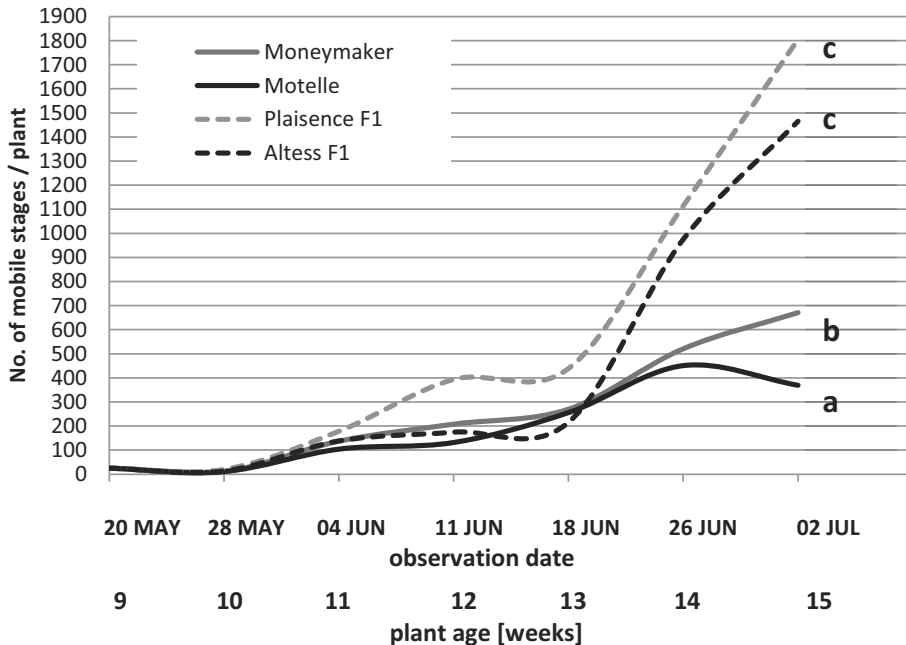


Fig. 1. Comparison of *T. urticae* population development on 4 tomato cultivars with different allelic combinations of the *Mi-1.2* gene. Different letters indicate significant differences (02 Jul 2009) (Kruskal-Wallis test: $H = 17.61$; $P = 0.0005$)

Table 1. Average number of *Tetranychus urticae* mobile stages per leaf in 4 tomato cultivars at 4, 5 and 6 weeks post infestation. Different letters in columns indicate significant differences at $P < 0.05$ (F and P values for Tukey HSD test; H value for Kruskal-Wallis test)

Tomato cultivar	Average number of <i>Tetranychus urticae</i> mobile stages on consecutive leaves													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	4 weeks post infestation													
'Motte'	43.0	18.8a	31.8	17.0	41.0	10.2	25.6	6.2	22.6	8.0	2.8	4.8	11.6	0.8
'Money-maker'	76.2	24.4a	37.0	83.2	11.8	23.4	6.0	2.2	1.0	0.0	2.6	0.8	1.0	
'Altess F1'	2.7	25.7a	48.7	19.0	21.0	21.7	7.3	6.7	6.0	1.7	10.7	20.3	6.7	3.7
'Plaisance F1'	123.3	72.0b	76.3	65.7	43.0	28.0	10.0	14.3	5.7	0.3				
P	0.0057													
$F_{3,12}$	ns													
H	ns													
	5 weeks post infestation													
'Motte'	28.8	19.2a	50.8a	35.2a	79a	37.2a	42.4	16.6	47.6	27.8	7.0	10.6	25b	3.2
'Money-maker'	16.4	64.0ab	71.4ab	136b	68a	47.4ab	35.2	15.4	12.4	16.0	12.6	15.0	3a	3.4
'Altess F1'	0.0	129.7bc	141.7bc	170b	155.3ab	109.7bc	64.7	62.7	28.7	41.7	35.3	25.3	7.3ab	3.0
'Plaisance F1'	19.3	156.3c	164.7c	240b	188.3b	125.7c	78.7	51.0	26.7	42.7	15.0	5.3	0.3a	
P	0.0235													
$F_{3,12}$	0.0068													
H	0.0473													
	6 weeks post infestation													
'Motte'	0.6	21.0a	27.0a	28.0a	24.0a	14.0a	30.0a	15.0a	29.0a	19.0a	37.0ab	34.0	25.0	30.0
'Money-maker'	1.8	16.0a	44.0a	89.0ab	73.0a	74.0b	73.0ab	71.0b	30.0a	32.0a	31.0a	32.0	25.0	17.0
'Altess F1'	0.0	168.3b	171.7b	163.3b	165.7b	156.7c	140.0bc	96.3b	87.3b	90.0b	86.7b	56.7	39.7	43.0
'Plaisance F1'	0.0	153.3b	198.3b	293.3c	223.3b	200.0c	170.0c	115.0b	85.3b	110.0b	76.3ab	61.7	48.0	35.0
P	0.013													
$F_{3,12}$	0.0083													
H	0.0322													
	8 weeks post infestation													
'Motte'	10.7703	11.7423	13.7909	13.1615	13.4315	13.0782	9.5552	10.6313	26.29	8.4094	ns	ns	ns	ns
$F_{3,12}$	8.782													
H	0.0383													

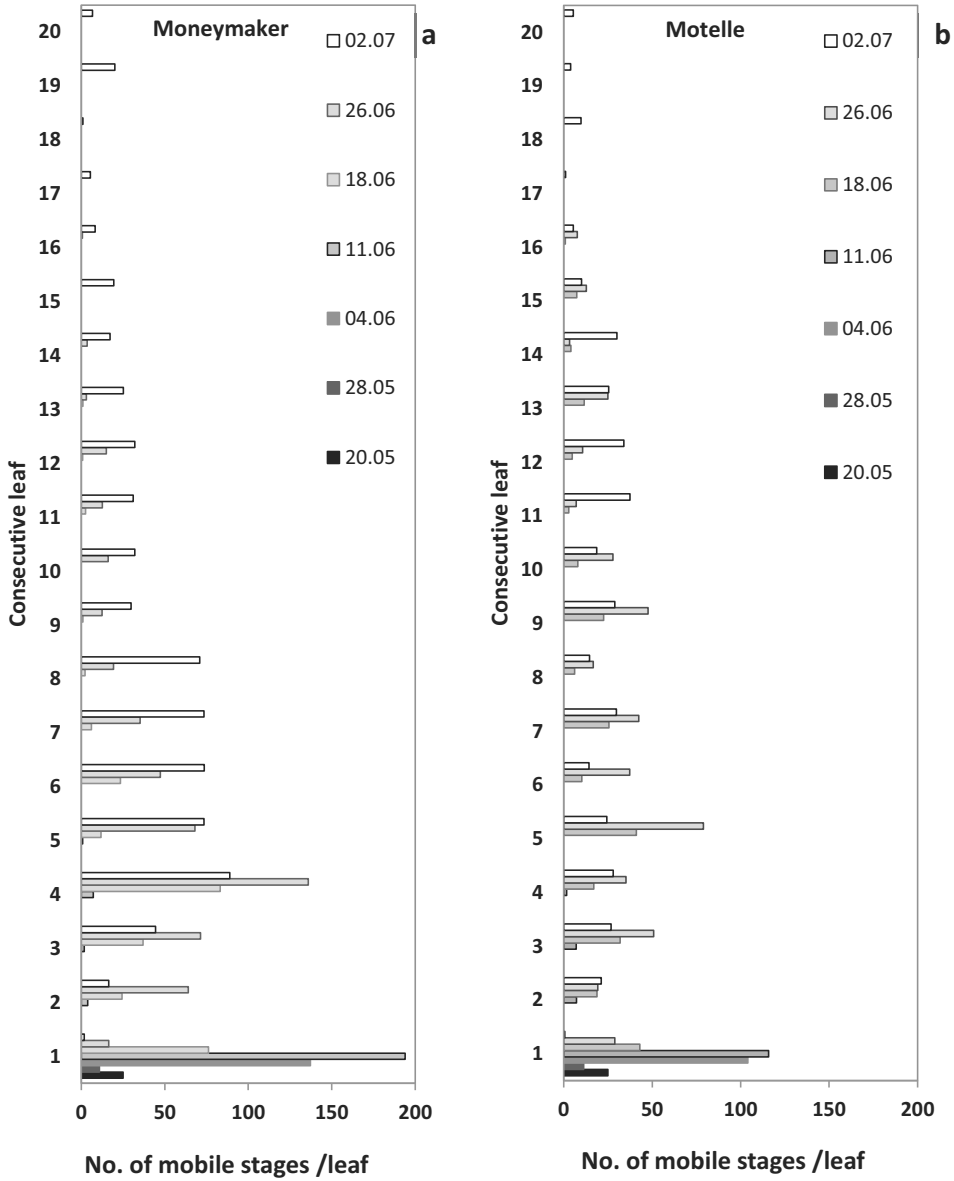


Fig. 2. Dispersal of *T. urticae* mobile stages on tomato plants of cultivars ‘Moneymaker’ (a) and ‘Motelle’ (b) during 6 weeks of population development. The initial number of *T. urticae* was 25 females per leaf (20 May 2009)

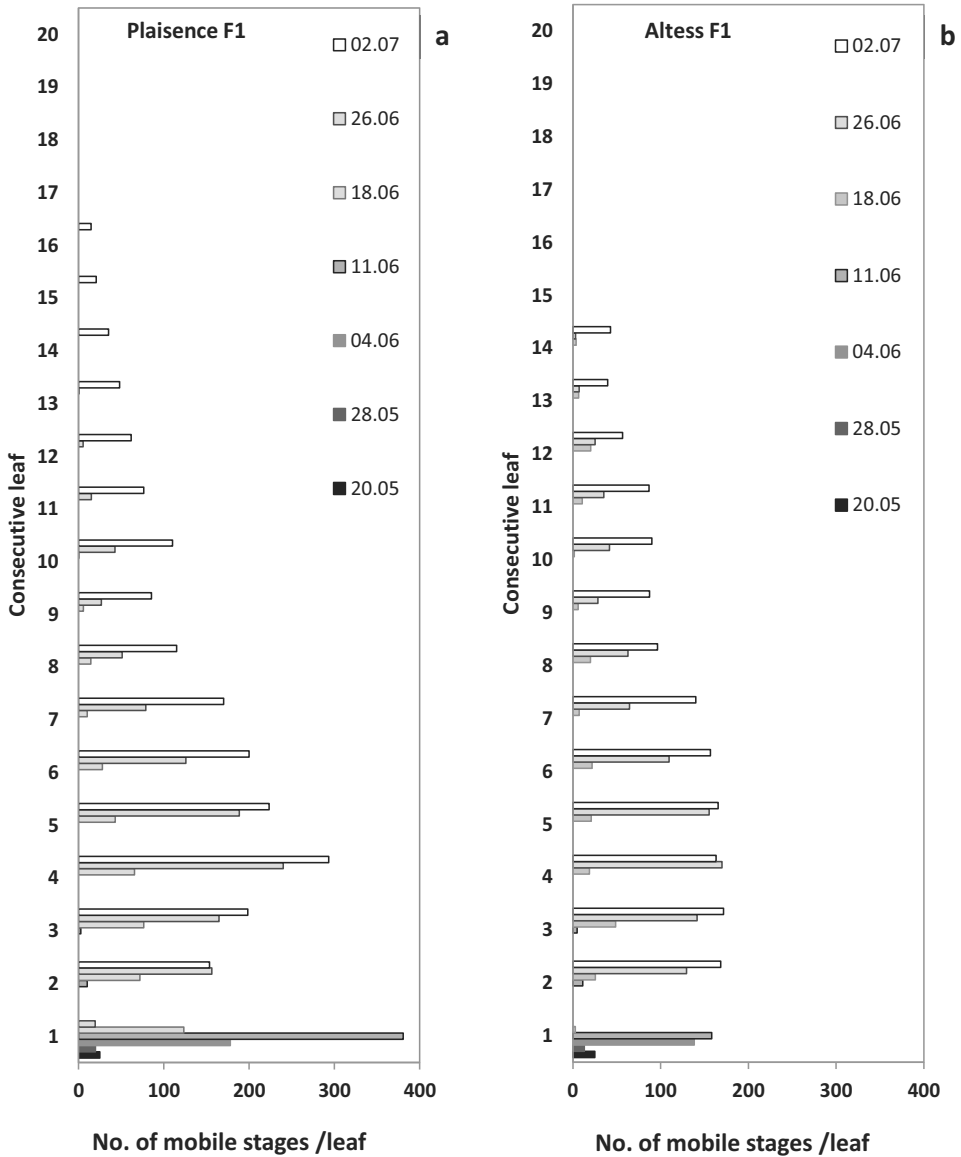


Fig. 3. Dispersal of *T. urticae* mobile stages on tomato plants of cultivars 'Plaisence F1' (a) and 'Altess F1' (b) during 6 weeks of population development. The initial number of *T. urticae* was 25 females per leaf (20 May 2009)

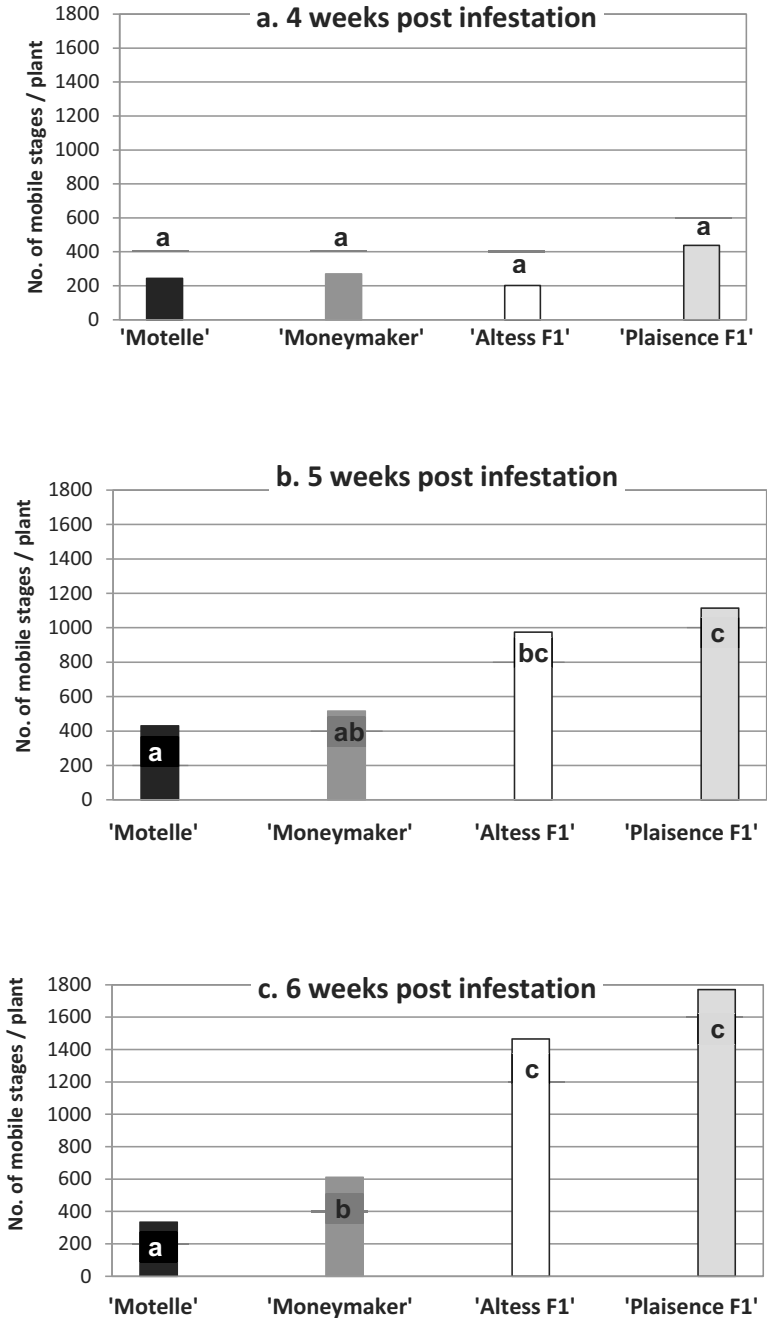


Fig. 4. Comparison of average numbers of *T. urticae* mobile stages per plant in 4 tomato cultivars at 4 (a), 5 (b) and 6 (c) weeks post infestation. Different letters indicate significant differences (Tukey HSD test)

'Moneymaker' and 'Plaisence F1' plants followed a similar pattern – the mites were most abundant in the middle parts of the shoots (Table 1; Fig. 2a; Fig. 3a). In contrast, on 'Motelle' and 'Altess F1' plants, the mites were spread more evenly (Table 1; Fig. 2b; Fig. 3b). Evidently, the average density of *T. urticae* on 'Altess F1' and 'Plaisence F1' plants significantly exceeded the average density of mites on 'Motelle' and 'Moneymaker' plants at 6 weeks post infestation ($F = 13.28$; $P = 0.0041$) (Fig. 1; Fig. 4). However, the average number of leaves on 'Altess F1' and 'Plaisence F1' plants was lower than on 'Motelle' and 'Moneymaker' plants (data not shown).

DISCUSSION

Previous results indicated that tomato plants carrying the *Mi-1.2* gene are resistant not only to nematodes (MILLIGAN et al. 1998) but also to some insect herbivores of the order Hemiptera, with a piercing-sucking mode of feeding, that take in nutrients from phloem tissues (KALOSHIAN et al. 1995; ROSSI et al. 1998; GOGGIN et al. 2001; Nombela et al. 2003; CASTEEL et al. 2006). The question arises if the presence of the *Mi-1.2* gene affects *T. urticae*, which is a common pest of tomatoes and feeds from leaf mesophyll cell content. We have previously observed that under laboratory conditions, population parameters of *T. urticae* on leaves detached from tomato plants carrying dominant or recessive *Mi-1.2* alleles did not differ (GODZINA et al. 2010a). Furthermore, a similar value of the intrinsic rate of natural increase (r_m) of *T. urticae*, observed on both tomato genotypes, suggested a comparable increase of mite population capacity. Contrary to that assumption, the present study demonstrates that *T. urticae* population density and distribution on intact tomato plants growing under greenhouse conditions varies depending on the allelic combination of the *Mi-1.2* gene. The results obtained here, for the first time, indicate that the mite-pest develops more slowly on tomato plants of cultivar 'Motelle', carrying 2 dominant alleles for the *Mi-1.2* gene, than on heterozygous 'Altess F1' tomatoes and both cultivars carrying only recessive alleles of this gene: 'Moneymaker' and 'Plaisence F1'. However, the differences in the performance of *T. urticae* on tomato plants with and without the *Mi-1.2* gene were not as spectacular as in the case of differences in the performance of potato aphids that fed on dominant or recessive homozygous tomato plants (KALOSHIAN et al. 1995; ROSSI et al. 1998; GOGGIN et al. 2004; GODZINA et al. 2010b). The strong inhibition of aphids' feeding on *Mi*-tomato plants may be a result of the *Mi-1.2* gene influence on phloem structure and content (KALOSHIAN et al. 2000). Thus *T. urticae*, as a mesophyll-feeder, may be less sensitive to tomato plant resistance activated by the *Mi-1.2* gene. However, recently it has been found that *Mi*-mediated aphid resistance also involves effective factors acting possibly in the mesophyll, epidermis and/or in the intercellular spaces (PALLIPARAMBIL et al. 2010).

Numerous studies have shown that plant resistance affects pest performance by single or combined effects of antixenosis, antibiosis and/or tolerance (SMITH 2005). For example, type VI trichomes on the leaf surface of cultivated tomatoes contribute to their resistance to arthropod herbivores, including mite-pests, by: (1) mechanical entrapment of pest in metabolites exuded by trichomes; and/or (2) the direct toxic/repellent effect of trichome metabolites on the pest (SIMMONS & GURR 2005; KANG et al.

2010). Therefore, these morphological/biochemical features of *Mi*-tomato cultivars can potentially have a negative effect on *T. urticae* population development. Currently, both the density and chemical composition of type VI glands of *Mi*-tomatoes are under investigation. Further study is also needed to assess the interactions between *Mi-1.2*-gene-mediated tomato resistance against nematodes or aphids and its resistance to mites.

During the experimental period, the smallest population of *T. urticae* evolved on 'Motelle' plants (dominant homozygotes for the *Mi-1.2* gene) and the largest on 'Plaisence F1' plants (recessive homozygotes). In relation to the *T. urticae* density on 'Motelle' and 'Plaisence F1' plants, the mite population density on 'Altess F1' (heterozygote) and 'Moneymaker' (recessive homozygote) plants reached intermediate values. Furthermore, *T. urticae* developed much better on commercial cultivars ('Altess F1', 'Plaisence F1') than on those from the gene bank ('Motelle', 'Moneymaker'). 'Altess F1' and 'Plaisence F1' are common greenhouse cultivars. Therefore, we presume that they may offer much better nutritional qualities to mites than 'Motelle' and 'Moneymaker' cultivars.

Studies on the behaviour and development of *T. urticae* and the carmine spider mite (*T. cinnabarinus* Boisduval, 1867) in greenhouse conditions on commercial cultivars of cucumber and tomato, respectively (KIELKIEWICZ & TOMCZYK 1987; KIELKIEWICZ 1996, 2003), demonstrate that the host-plant species and cultivar greatly affect its population dynamics and dispersal. In the present study, the distribution of mobile stages on tomato plants varied depending on the presence of the *Mi-1.2* gene. On the tomato cultivars 'Moneymaker' and 'Plaisence F1' (recessive homozygotes), mites found the best conditions to feed in the middle parts of the plant. This is in line with the earlier results of KIELKIEWICZ (1996, 2003) proving that *T. cinnabarinus* finds the best conditions to feed and multiply in the middle part of tomato shoots in greenhouse conditions. By contrast, in the present study, on the tomato plants with 1-2 dominant alleles of the gene *Mi-1.2* ('Altess F1' and 'Motelle', respectively), mite-pests settled rather evenly on all available leaves.

In conclusion, it has been shown for the first time that the same initial number of *T. urticae*, under greenhouse conditions, develops a population that varies in abundance and distribution depending on the allelic composition of the *Mi-1.2* gene. Generally, mite population densities on the commercial tomato cultivars were higher than on plants from the gene bank. The smallest population of mites developed on tomato plants of the cultivar with 2 dominant alleles for the *Mi-1.2* gene, and the largest on plants of commercial cultivar with 2 recessive alleles. In relation to the above-mentioned homozygous cultivars, the mite population density on a heterozygous cultivar had intermediate values. This suggests that the *Mi-1.2* gene may be involved in the resistance of the tomato plants against *T. urticae* when this dominant gene is expressed homozygously. Further advances in the understanding of the mechanisms of this phenomenon are needed.

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