Direct and indirect adverse effects of tomato on the predatory mite *Neoseiulus californicus* feeding on the spider mite *Tetranychus evansi*

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Abstract

Plants may defend themselves against herbivores via morphological traits, chemical traits, or a combination of both. Herbivores that overcome the defensive mechanisms of a plant tend to specialize on this plant due to enhanced protection from natural enemies. Well-known examples of plants possessing a suite of defensive mechanisms are found in nightshades (Solanaceae), especially in the tomato genus *Lycopersicon*. The spider mite *Tetranychus evansi* Baker and Pritchard (Acari: Tetranychidae) is specialized on solanaceous plants and is an invasive pest of tomato in Europe and Africa. Biological control of *T. evansi* with currently available natural enemies, such as the predatory mites *Phytoseiulus persimilis* Athias-Henriot and *Neoseiulus californicus* McGregor (both Acari: Phytoseiidae), is unsuccessful, with the underlying mechanisms only vaguely known. We hypothesized that *T. evansi* is a key pest of tomato because this host plant provides a two-pronged protection from natural enemies. Direct adverse effects of tomato on predators may arise from morphological traits and/or trichome exudates, whereas indirect effects are prey-mediated through the accumulation of toxic plant compounds. Using a 2×3 factorial design, we assessed and separated direct and indirect effects of tomato on the life history of *N. californicus* feeding on two strains of *T. evansi* (reared on bean or tomato) on three substrates (tomato leaf, bean leaf, and an artificial cage). Developmental time and oviposition rate of *N. californicus* were both directly and indirectly negatively affected by tomato whereas offspring sex ratio and survival of juveniles and adult females were unaffected. The direct and indirect, prey-mediated adverse effects of tomato on *N. californicus* with *T. evansi* prey had similar magnitudes and were additive. We conclude that *T. evansi* per se is a suitable prey species for *N. californicus* and discuss the results with respect to the potential use of *N. californicus* as biological control agent of *T. evansi* on tomato and other host plants.

Introduction

Plants may defend themselves against herbivores via various mechanisms. Defensive mechanisms acting directly on herbivores include morphological traits such as plant architecture, thorns, trichomes, or surface waxes as well as chemical traits such as secondary plant metabolites (for reviews, see Price et al., 1980; Agrawal et al., 1999; Ananthakrishnan, 2001). Herbivores that overcome direct defensive mechanisms of a given plant tend to specialize on this plant and may benefit by reduced competition and/or predation (Price et al., 1980; Bernays & Graham, 1988; Agrawal, 2007). Some plants are known to possess a suite of defensive mechanisms against herbivores (Agrawal, 2007). Well-known examples are found in the tomato genus *Lycopersicon* (for a review, see Kennedy, 2003).

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The cultivated tomato *Lycopersicon esculentum* Miller (Solanaceae) is a highly important vegetable crop (FAO, 2005) and attacked by a wide range of arthropod pests (Lange & Bronson, 1981; Kennedy, 2003). Among these, the spider mite *Tetranychus evansi* Baker and Pritchard (Acari: Tetranychidae) is an important invasive pest in Africa and southern Europe. The mite is probably of South American origin (Gutierrez & Etienne, 1986) and was first recorded in continental Africa in Zimbabwe in 1979 (Blair, 1983) from where it spread northwards (Knapp, 2003; Knapp et al., 2003). Since 1991, it has also been spreading in southern Europe (Ferreira & Carmona, 1995; Ferragut & Escudero, 1999; EPPO, 2004; Migeon, 2005; Castagnoli et al., 2006). *Tetranychus evansi* is polyphagous but preferentially feeds on wild and cultivated solanaceous plants (Quereshi et al., 1969; Blair, 1983; Moraes et al., 1987; Bolland et al., 1998; Rosa et al., 2005).

Biological control of spider mites using predatory mites has been successfully implemented on numerous vegetables and ornamentals (Hoy, 1982; Helle & Sabelis, 1985; McMurtry & Croft, 1997). However, in contrast to many other tetranychid mites such as the two-spotted spider mite *Tetranychus urticae* Koch, biological control of *T. evansi* with predatory mites, in particular *Neoseiulus californicus* McGregor and *Phytoseiulus persimilis* Athias-Henriot (both Acari: Phytoseiidae), is not efficacious (Moraes & McMurtry, 1985a,b, 1986; Knapp et al., 2003; Escudero & Ferragut, 2005). The mechanisms causing the unsuitability of *T. evansi* as prey for predatory mites are only vaguely known. Moraes & McMurtry (1985b) found neither toxic substances produced by *T. evansi* per se nor morphological or behavioural prey characteristics (Moraes & McMurtry, 1986) as possible explanations for the malperformance of the predatory mite *P. persimilis* when feeding on this prey. A common assumption is that *T. evansi* accumulates toxic compounds of solanaceous plants, which in turn affect the predators feeding on them (Moraes & McMurtry, 1986, 1987; Escudero & Ferragut, 2005).

Constitutive morphological and chemical traits of plants not only affect the herbivores feeding on them but may also directly and indirectly affect the natural enemies of the herbivores (Duffey, 1980; Price et al., 1980; Bottrell & Barbosa, 1998; Cortesero et al., 2000; Roda et al., 2001; Seelmann et al., 2007). Direct effects of tomato on predators may arise from morphological traits and/or trichome exudates. Tomato possesses a variety of glandular and non-glandular trichomes (e.g., Simmons & Gurr, 2005). Non-glandular trichomes may act as a physical barrier impeding predator movements, thereby increasing the searching times and reducing the encounter rates with prey (Krips et al., 1999; Skirvin & Fenlon, 2001; Stavrinides & Skirvin, 2003). Glandular tomato trichomes release sticky and toxic exudates, which may negatively affect the performance of natural enemies, including the predatory mite *P. persimilis* (van Haren et al., 1987; Nihoul, 1993; Kennedy, 2003; Simmons & Gurr, 2005). Compounds from tomato trichome exudates such as methyl ketones and zingiberene are not only toxic to spider mites (Chatzivasileiadis & Sabelis, 1997, 1998; Chatzivasileiadis et al., 1999; Maluf et al., 2001), but also to *P. persimilis* (Gillespie & Quiring, 1994). Cédola & Sánchez (2003) reported direct negative effects of increased tomato trichome density on *N. californicus* but left open whether these effects were caused by the physical or chemical properties of the trichomes or both.

Indirect effects of tomato on predators are mediated by herbivores that accumulate toxic plant compounds rendering them unsuitable prey (hereafter termed indirect, prey-mediated effects). Besides the toxic exudates of glandular trichomes, three other compounds of tomato leaves, namely, α-tomatine, chlorogenic acid, and rutin, have been documented as being toxic to various insect herbivores (Elliger et al., 1981; Chan & Tam, 1985; Hare, 1987; Bloem et al., 1989) and to indirectly affect predators and parasitoids (Campbell & Duffey, 1979; Stamp et al., 1997). Unambiguous evidence of indirect, prey-mediated effects of toxic compounds of tomato plants on predatory mites is lacking.

Based on the general hypothesis that living on tomato provides herbivores a two-pronged protection from natural enemies, our objective was to assess the mechanisms impairing the suitability of *T. evansi* as prey for the predatory mite *N. californicus* on tomato. Previous studies suggested either indirect, prey-mediated effects of nightshades such as *Solanum douglasii* Dunal (Moraes & McMurtry, 1986, 1987) and potato (Escudero & Ferragut, 2005) or a combination of both direct and indirect effects of *S. douglasii* (Moraes & McMurtry, 1985a), *Solanum americanum* Miller (Ferrero et al., 2007), and tomato (Nihoul, 1993; Drukker et al., 1997; Castagnoli et al., 1999, 2001; Cédola et al., 2001; Cédola & Sánchez, 2003) on predatory mites feeding on spider mite prey. In contrast, to the best of our knowledge, there are no studies investigating the relative contribution of those two mechanisms to the overall adverse effect of nightshades, including tomato, on any natural enemy (for reviews, see Kennedy, 2003; Simmons & Gurr, 2005). In particular, we tested if and to what extent tomato as host plant of *T. evansi* affects the life history of the predatory mite *N. californicus* (i) through morphological traits and/or trichome exudates (direct effects) and/or (ii) through host-plant compounds accumulated by the prey (indirect, prey-mediated effects). To separate direct and indirect effects, we used a 2×3 factorial design consisting of two strains of *T. evansi* (reared on bean or tomato) offered on three substrates (tomato leaf, bean leaf, and artificial cage).

Materials and methods

Experimental animals and treatments

Neoseiulus californicus used for experiments were drawn from a laboratory-reared population founded with specimens collected on carnation (*Dianthus caryphyllus* L.) in Naivasha, Kenya. The population was maintained on artificial rearing units (McMurtry & Scriven, 1965) and fed with a mix of *T. urticae* and *Tetranychus lombardinii* Baker and Pritchard. *Tetranychus evansi* used as prey in experiments was reared on two host plants, bean (*Phaseolus vulgaris* L.) and tomato (*L. esculentum*). The bean-reared population of *T. evansi*, hereafter called B-*T. evansi*, was reared for at least three generations on the bean variety 'Rosecoco' before being used in experiments. The tomato-reared population of *T. evansi*, hereafter called T-*T. evansi*, was reared on the tomato variety 'Moneymaker'.

In both experiments described below, 'adult female survival and oviposition' and 'juvenile survival and development', we used a 2×3 factorial design. Treatments were all possible combinations of prey type (B-*T. evansi* and T-*T. evansi*) and substrate (bean leaf, tomato leaf, and artificial cage). Tomato and bean leaf arenas consisted of single, detached leaves placed upside down on moist cotton wool. The edges of the leaf were covered with moist tissue paper. A strip of non-toxic glue (Raupenleim; Avenarius-Agro GmbH, Wels, Austria) was applied on the tissue paper to prevent the mites from leaving the arena. Each artificial cage consisted of a circular opening (1.5 cm in diameter) laser-cut into an acrylic plate (0.5 cm thick). The openings were closed at the bottom with a gauze and on the upper side with a microscope slide secured with a rubber band (Schausberger, 1997). Prey on the leaf arenas and in the cages was always available in surplus and replenished as needed. Rearing and experimental units were kept at 25 ± 1 °C, $70 \pm 10\%$ r.h., and 12-h photophase.

Adult female survival and oviposition

Mixed stages of *T. evansi* were brushed onto the leaf arena or into the cage and a gravid female predator, randomly chosen from the rearing units, was added. Each treatment (substrate-prey type combination) was repeated 10–14 times. The predator female was left for 11 days on/in the arena/cage and predator survival and number of eggs laid were monitored daily. Only females that laid at least one egg on the 1st day were used for the subsequent experimental period. The eggs laid on the 1st day were omitted from analysis. During the remaining 10 days, the eggs of the predators were removed daily and placed on separate artificial rearing units. These rearing units were stored in a refrigerator at 8 °C to decelerate egg development until the end of the 10-day experimental period. Afterwards, the arenas were taken out of the refrigerator and offspring were reared to adulthood with a mix of *T. urticae* and *T. lombardinii* prey to assess offspring sex ratio.

Juvenile survival and development

Newly picked leaves infested with spider mite prey were placed on the stock colony of *N. californicus* 12 h before the start of the experiment. Numerous female predators moved to these leaves and laid eggs. Eggs were then randomly selected and isolated on a bean or tomato leaf arena or in an artificial cage and fed with mixed stages of either B-*T. evansi* or T-*T. evansi* as prey. Subsequently, the developmental stage was recorded twice per day in 12-h intervals. Developmental progress was determined by the presence of the shed skin of the previous life stage, which was then removed. Upon reaching adulthood, individuals were sexed. Each treatment (substrate–prey type combination) was repeated 15–20 times.

Intrinsic rate of natural increase (r_m)

Data on juvenile survival and developmental time, female survival and oviposition rate, and offspring sex ratio were used to estimate the intrinsic rate of natural increase (r_m) of *N. californicus* for each treatment (combination of substrate and prey) (Birch, 1948; Hulting et al., 1990). The pre-reproductive period needed for estimations but not examined in the experiments was calculated by adding a 1.5-day pre-oviposition period (Gotoh et al., 2004; Walzer et al., 2007) to the measured egg–adult period (assuming that *N. californicus* starts laying eggs on the 2nd day after reaching adulthood at 25 °C).

Statistical analyses

We used SPSS 11.0 (SPSS Inc., Chicago, IL, USA) for all statistical analyses. The effects of prey type (B-*T. evansi* or T-*T. evansi*) and substrate (tomato, bean, or cage) on developmental time and oviposition rate were analysed using univariate analysis of variance (ANOVA) and repeated measures ANOVA, respectively, followed by pairwise Bonferroni tests to compare the estimated marginal means among prey types and substrates. Sex was used as covariate in the analysis of the developmental time. Time was used as inner-subject factor in the analysis of the oviposition rate. The requirements of variance homogeneity (Levene's test, P>0.05) and normal distribution (Kolmogorov–Smirnov, P>0.05) were met for both parameters, oviposition rate and developmental time. Binary logistic regression with the covariates prey type and substrate was used to analyse adult female survival, offspring sex ratio, and juvenile survival.
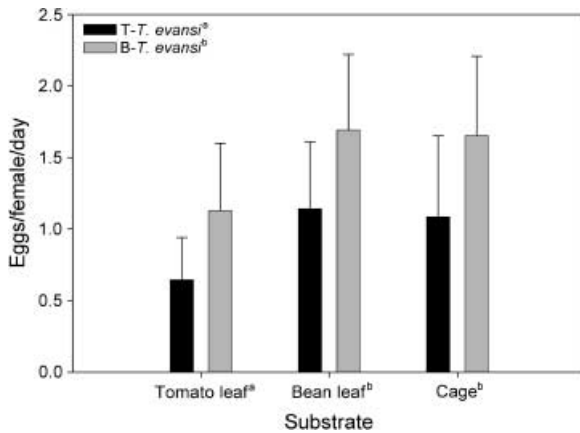
Figure 1 Oviposition rate (mean + SD) of *Neoseiulus californicus* held on tomato, bean, or in an artificial cage for 10 days and fed with *Tetranychus evansi*, previously reared on bean (B-*T. evansi*) or tomato (T-*T. evansi*). Different superscript letters following prey and substrate types indicate significant differences within either factor (Bonferroni tests following analysis of variance, P<0.05).

Results

Adult survival and oviposition

Survival of *N. californicus* during the 10-day experiment ranged from 48% on tomato with B-*T. evansi* to 70% in the cage with B-*T. evansi* and was neither influenced by prey type (logistic regression: Wald = 0.160, d.f. = 1, P = 0.689) nor substrate (logistic regression: Wald = 0.865, d.f. = 1, P = 0.352). In contrast, the oviposition rate of *N. californicus* was affected by both prey type and substrate but not by the interaction of the two sources of variation (Table 1 and Figure 1). Overall, the predators laid the most eggs on the

Table 1 Repeated measures analysis of variance (ANOVA) for the effects of prey type (*Tetranychus evansi* previously reared on tomato or bean) and substrate (tomato leaf, bean leaf, or artificial cage) on the oviposition rate of *Neoseiulus californicus* over a 10-day period

Source of variation	d.f.	Mean square	F	P-value
Between-subject factors				
Prey type	2	1.925	8.056	0.001
Substrate	1	5.309	22.218	<0.001
Prey type*substrate	2	0.036	0.151	0.861
Error	66	0.239		
Inner-subject factor				
Time	9	5.606	11.279	<0.001
Time*substrate	18	0.523	1.053	0.398
Time*prey type	9	0.430	0.865	0.556
Error (time)	594			

bean leaf with B-*T. evansi* prey and the least on the tomato leaf with T-*T. evansi* prey (Figure 1). The estimated marginal mean oviposition rate of *N. californicus* fed with T-*T. evansi* was 0.56 eggs/female/day lower than the corresponding rate of *N. californicus* fed with B-*T. evansi* (Bonferroni, P<0.001). Among the three substrates, the predators had the lowest estimated marginal mean oviposition rate on the tomato leaf, which was ~0.5 eggs/female/day lower than the rate estimated for predators on the bean leaf (Bonferroni, P = 0.002) and in the cage (Bonferroni, P = 0.002). The indirect, prey-mediated negative effect of tomato was particularly apparent in the cage, which excluded any direct plant effect. In the cage, *N. californicus* laid ~0.6 eggs/female/day more when fed with B-*T. evansi* than when fed with T-*T. evansi* (Figure 1). The direct and indirect, prey-mediated effects of tomato on the oviposition rate of the predators had the same magnitude and were additive. Furthermore, time had a significant effect on the oviposition rate irrespective of
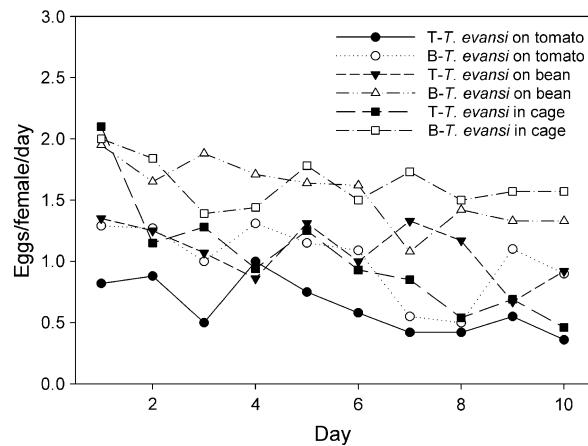

Figure 2 Mean daily oviposition rate of *Neoseiulus californicus* held on tomato, bean, or in an artificial cage and fed with *Tetranychus evansi,* previously reared on bean (B-*T. evansi*) or tomato (T-*T. evansi*), during a 10-day period.

prey type and substrate (Table 1 and Figure 2). In each treatment, that is, each substrate–prey type combination, the oviposition rate decreased more or less continuously during the 10-day experiment (Figure 2). Offspring sex ratio was neither influenced by prey type (logistic regression: Wald = 1.506, d.f. = 1, P = 0.220) nor substrate (logistic regression; Wald = 1.255, d.f. = 1, P = 0.263) and ranged from 60.1% female offspring on tomato with T-*T. evansi* to 71.1% female offspring on bean with B-*T. evansi*.

Juvenile survival and development

Neoseiulus californicus was able to successfully complete development in all treatments. Mortality in the juvenile
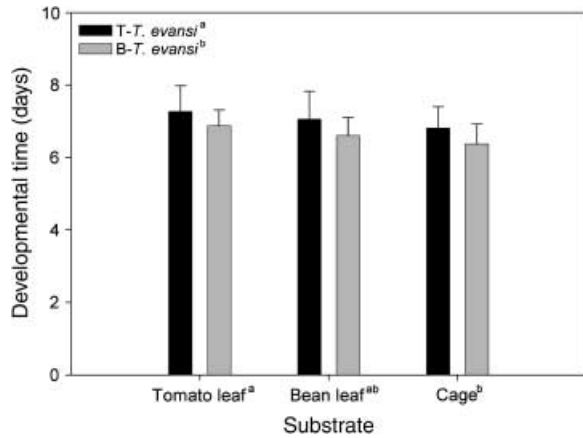
Figure 3 Developmental time (egg to adult; mean + SD) of *Neoseiulus californicus* held on tomato, bean, or in an artificial cage and fed with *Tetranychus evansi*, previously reared on bean (B-*T. evansi*) or tomato (T-*T. evansi*). Different superscript letters following prey and substrate types indicate significant differences within either factor (Bonferroni tests following analysis of variance, P<0.05).

phase was low (<17%) and neither influenced by prey type (logistic regression; Wald = 1.620, d.f. = 1, P = 0.203) nor substrate (logistic regression; Wald = 2.050, d.f. = 1, P = 0.152). However, the developmental time from egg to adult was significantly affected by both prey type and substrate, whereas the interaction between the two sources of variation did not have an effect (Table 2 and Figure 3). Comparison of the estimated marginal means revealed that *N. californicus* needed ~0.4 days longer to develop from egg to adult when fed with T-*T. evansi* than when fed with B-*T. evansi* (Bonferroni, P<0.001). The estimated marginal mean developmental time of *N. californicus* was ~0.5 days longer on tomato than in the cage (Bonferroni, P = 0.001), whereas the estimated marginal mean developmental times did not differ between tomato and bean (Bonferroni, P = 0.232) and bean and cage, respectively (Bonferroni, P = 0.105). The differences in developmental

Table 2 Analysis of variance (ANOVA) for the effects of prey type (*Tetranychus evansi* previously reared on tomato or bean) and substrate (tomato leaf, bean leaf, or artificial cage) on the developmental time (egg to adult) of *Neoseiulus californicus*

Source of variation	d.f.	Mean square	F	P-value
Prey type	2	2.353	6.895	0.002
Substrate	1	4.604	13.491	<0.001
Prey type*substrate	2	0.024	0.070	0.933
Sex (covariate)	1	2.104	6.167	0.015
Error	99	0.341		

times were exclusively determined by the feeding stages, that is, the proto-, and deutonymph. As with the oviposition rate, the indirect, prey-mediated effect of tomato on the total developmental time of *N. californicus* was especially visible in the cages. In the cages, *N. californicus* needed significantly more time to develop from egg to adult with T-*T. evansi* prey than with B-*T. evansi* prey (Figure 3). Sex as a covariate had an influence on the total developmental time. The estimated marginal mean developmental time of males (7.103 ± 0.684 days; n = 15) was somewhat longer than the corresponding time of the females (6.789 ± 0.634 days; n = 91) (Table 2).

Intrinsic rate of natural increase
The estimated intrinsic rate of increase (r_m) was the lowest for *N. californicus* feeding on T-*T. evansi* on the detached tomato leaflet (0.093/female/day) and the highest for *N. californicus* feeding on B-*T. evansi* on the detached bean leaf (0.189) or in the cage (0.193). The rate was intermediate and similar for predators feeding on T-*T. evansi* on bean (0.147) and in the cage (0.166) and predators feeding on B-*T. evansi* on tomato (0.150).

Discussion

Direct effects of tomato on *Neoseiulus californicus*
The host plant tomato had a direct negative effect on fecundity and developmental time of *N. californicus* irrespective of the rearing history of the prey. Both the sticky and toxic trichome exudates and the trichome density of *L. esculentum* may have negatively affected the performance of *N. californicus*. The longer developmental time of the predator on tomato than on bean or in the cage was mainly observed in the active nymphal stages but not in the larval stage. Probably, the larger size and higher activity of nymphs as compared to larvae (Schausberger & Croft, 1999) led to an increased encounter rate with the tips of the glandular trichomes and with that to increased contact with the exudates. Increased light intensity and temperature have been shown to alter the morphology of glandular trichomes on tomato stalks, promoting the entrapment of another predatory mite, *P. persimilis*, by the trichome exudates (Nihoul, 1993). A negative effect of glandular tomato trichomes on *N. californicus* has also been suggested by Castagnoli et al. (1999), Cédola et al. (2001), and Cédola & Sánchez (2003). However, none of these studies excluded indirect, prey-mediated effects of tomato.

The density of non-glandular trichomes has been shown to affect predatory mites other than *N. californicus*. *Typhlodromus pyri* Scheuten and *Kampimodromus aberrans* Oudemans perform better on densely haired leaves whereas the opposite is true for *Euseius finlandicus* Oudemans and

P. persimilis (Krips et al., 1999; Roda et al., 2001; Seelmann et al., 2007). There are no such studies available for *N. californicus*.

Unlike spider mites (Chatzivasileiadis & Sabelis, 1998; Chatzivasileiadis et al., 1999), the progression of the oviposition rate of *N. californicus* over time does not suggest any accumulation of toxic compounds via contact with trichome exudates. There was a more or less continuous decrease in the oviposition rate, but this decline occurred on all three substrates, tomato, bean, and cage (Figure 2). Possible explanations for the declining oviposition rate are the diet shift from *T. urticae* to *T. evansi* (Castagnoli et al., 2001) and/or the aging of females (Gotoh et al., 2004).

Indirect, prey-mediated effects of tomato on *Neoseiulus californicus*

In addition to the direct effect of tomato on *N. californicus*, our study revealed an indirect, prey-mediated host-plant effect. The tomato-reared strain of *T. evansi* negatively influenced the reproductive performance and development of the predator compared to the bean-reared strain. Similarly, Moraes & McMurtry (1987) found an indirect, prey-mediated effect of the nightshade *S. douglasii* on *P. persimilis* feeding on the spider mite *T. urticae*. Toxic compounds of tomato were apparently not transmitted from *N. californicus* females to their eggs. No difference in survivorship or sex ratio was observed between offspring of females that had been kept on the substrates tomato, bean, or cage and fed with the tomato or bean strain of *T. evansi*. The indirect effects of tomato via toxic compounds accumulated by the prey are in line with the results of Escudero & Ferragut (2005). They kept *N. californicus* on bean and offered *T. evansi* reared on potato as prey. The observed oviposition rate (0.8 eggs/female/day) and developmental time (183 h) of their strain were inferior to the corresponding values determined in the present study with a similar host plant–prey combination (1.2 eggs/female/day; 169 h).

Our study clearly indicates that the suitability of *T. evansi* as prey for predatory mites is mediated by the host plant. The oviposition rate of the predators was higher and the developmental time was shorter when fed with the bean strain of *T. evansi* on bean or in the artificial cage compared to the tomato strain. Consequently, the feeding deterrent in/on eggs of *T. evansi* but not *T. urticae* suggested by Moraes & McMurtry (1986, 1987) is a host plant-dependent defensive mechanism of the mites. Together, those findings strongly indicate that *T. evansi* not only accumulates toxic plant compounds from tomato like the spider mite *T. urticae* does (Chatzivasileiadis & Sabelis, 1998; Chatzivasileiadis et al., 1999), but may additionally alter those chemicals to a feeding deterrent. This suggests a higher level of adaptation to tomato in *T. evansi* than in

T. urticae. Sequestration and synthesizing of phytochemicals for defence against natural enemies has been reported for a number of herbivores (Duffey, 1980), especially *Lepidoptera* (for review, see Nishida, 2002).

Synthesis and biocontrol aspects

Our study provides a mechanistic explanation for the unsuitability of *T. evansi* as prey for predatory mites on tomato. Sorting out the direct and indirect adverse effects of tomato on *N. californicus* revealed that tomato confers a two-pronged protection from predators to *T. evansi*. The direct and indirect effects of tomato on *N. californicus* had the same magnitude and were additive. Our findings suggest that *T. evansi* may be successfully controlled on non-solanaceous plants, raising the hypothesis that tomato provides enemy-free space for *T. evansi* (Jeffries & Lawton, 1984). This hypothesis is supported by the occurrence of *T. evansi* together with the predatory mite *N. californicus* on runner beans, *Phaseolus coccineus* L., in Kenya. In contrast, *T. evansi* has never been observed associated with predatory mites on Solanaceae in eastern and southern Africa (M Knapp, unpubl.). The use of enemy-free space on tomato has also been suggested for other arthropods such as the potato tuber moth *Phthorimaea operculella* Zeller (Mulatu et al., 2004).

In the present study, the number of offspring was only recorded for a 10-day period but not throughout life, which led to a slight underestimation of the r_m. However, the r_m of *N. californicus* feeding on tomato-reared *T. evansi* on tomato leaflets is extremely low compared to that reached on more favourable host plant–prey combinations (e.g., Gotoh et al., 2004). In contrast, the r_m of *N. californicus* with bean-reared *T. evansi* on bean and in the cage approaches that determined for *N. californicus* feeding on other spider mite species on non-solanaceous host plants (Gotoh et al., 2004; Escudero & Ferragut, 2005). Due to the documented plasticity in life history of *N. californicus* (e.g., Gotoh et al., 2004; Walzer et al., 2007), adaptation to tomato resulting in efficacious control of *T. evansi* might be possible. Most remarkably, Castagnoli et al. (1999) observed a more than two-fold increase in the estimated r_m of *N. californicus* (from 0.118 to 0.256/female/day) after numerous generations feeding on *T. urticae* on tomato.

For developing a successful biological control strategy against *T. evansi* and other pest mites on tomato, further studies scrutinizing the tritrophic interactions in the tomato–herbivore–predator system, especially the mechanisms causing the adverse effects of this host plant on *N. californicus* and other predatory mites are required. Promising results for control of *T. evansi* have been recently reported for a Brazilian *Phytoseiulus longipes* Evans strain (Furtado et al., 2007). However, to optimize the use of this strain the

mechanisms responsible for its variability in coping with *T. evansi* on solanaceous plants (Ferrero et al., 2007) need to be investigated. Questions to be addressed in future studies are (i) which plant compounds of tomato accumulated by the herbivores cause the indirect effects, (ii) whether the direct adverse effects of tomato are due to the stickiness of the trichome exudates, their toxicity, or the trichome density, and (iii) which mechanisms and to what extent – genetic predisposition, maternal effects, and/or learning – allow to cope with the hostile tomato environment. Such information may then be used to pinpoint and improve predator traits required for successful biological control.

Acknowledgements

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