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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Down-regulation of plant defence in a resident spider mite species and its effect upon con- and heterospecifics

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Abstract Herbivorous spider mites occurring on tomato plants (*Solanum lycopersicum* L.) cope with plant defences in various manners: the invasive *Tetranychus evansi* reduces defences below constitutive levels, whereas several strains of *T. urticae* induce such defences and others suppress them. In the Mediterranean region, these two species co-occur on tomato plants with *T. ludeni*, another closely related spider mite species. Unravelling how this third mite species affects plant defences is thus fundamental to understanding the outcome of herbivore interactions in this system. To test the effect of *T. ludeni* on tomato plant defences, we measured (1) the activity of proteinase inhibitors, indicating the induction of plant defences, in those plants, and (2) mite performance on plants previously infested with each mite species. We show that the performance of *T. evansi* and *T. ludeni* on plants previously infested with *T. ludeni* or *T. evansi* was better than on clean plants, indicating that these two mite species down-regulate plant defences. We also show that plants attacked by these mite species had lower activity of proteinase inhibitors than clean plants, whereas herbivory by *T. urticae* increased the activity of these proteins and resulted in reduced spider mite performance. This study thus shows that the property

of down-regulation of plant defences below constitutive levels also occurs in *T. ludeni*.

Keywords *Tetranychus ludeni* · Spider mites · Plant defences · Proteinase inhibitors · Plant–herbivore interactions

Introduction

Plants are attacked by a variety of antagonistic biotic agents that can cause severe damage (Zangerl and Bazzaz 1992; Baldwin and Preston 1999). Plants have consequently evolved a range of defences against a broad range of enemies (Kessler and Baldwin 2002; Glazebrook 2005). Because such defensive traits may be costly (Karban and Myers 1989; Herms and Mattson 1992), many defences are only mounted upon the occurrence of a given stress, such as herbivory. Moreover, defences often appear specific, depending on the herbivore species (Karban and Carey 1984; Walling 2000; Kessler and Baldwin 2002). These defences are aimed at reducing herbivore performance, thus benefitting the plant. However, selection also acts upon herbivores to avoid induction or to become resistant to plant defences (Karban and Agrawal 2002; Zhu-Salzman et al. 2005; Alba et al. 2011).

How herbivores and plant pathogens cope with plant defences is highly variable. Whereas most species induce defences, species of several taxonomical groups do not, e.g. viruses (Burgyán and Havelda 2011), bacteria (Zhao et al. 2003; Abramovitch et al. 2006), nematodes (Haegeman et al. 2012), and several species of arthropods (Musser et al. 2002; Lawrence et al. 2008; Sarmento et al. 2011a; Kant et al. 2015). Moreover, the induction of and resistance to plant defences may vary within species. Indeed, different

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populations of the aphid *Myzus persicae* (Sauge et al. 2006) and of the spider mite *Tetranychus urticae* (Kant et al. 2008; Alba et al. 2015) induce or supress plant defences to different levels and are differently affected by them.

This specificity of plant defences and responses to them are likely to affect interactions among plant pests and diseases in different ways (Denno et al. 1995; Agrawal 2000; Kant and Baldwin 2007; Poelman and Dicke 2014). Indeed, a herbivore that induces defences reduces the quality of host plants, but it may also reduce the likelihood of competition with other herbivores, as these might avoid induced plants (Pallini et al. 1997; Kessler and Baldwin 2001; Rostás and Hilker 2002). Conversely, down-regulating plant defences increases the quality of plants as a resource, but it may also increase the performance of competitors (Sarmento et al. 2011a). Additionally, given the specificity of induced defences and the negative cross-talk between defensive pathways (Walling 2000), some herbivore species may benefit from previous attack by other species (Belliure et al. 2005, 2010; Poelman et al. 2008). This may have complex consequences for species attacking the same plant, especially if the system is composed of some species that induce plant defences and others that down-regulate them. In such cases, the effect of plant defences on herbivores and pathogens may vary with local species composition and order of arrival (de Oliveira et al. 2015).

As in many other species, induced responses in tomato plants (*Solanum lycopersicum* L.) are regulated by phytohormones such as ethylene, salicylic acid and jasmonic acid. In general, salicylic acid is the key regulator of the pathways involved in the response against biotrophic pathogens and phloem-feeding insects. Both jasmonic acid and ethylene are responsible for the regulation of the pathways involved in defence against necrotrophic pathogens, chewing herbivores and cell-content feeders (Walling 2000; Koornneef and Pieterse 2008; Thaler et al. 2012). The spider mite *Tetranychus urticae* is a cell-content feeder which, in general, induces defences of both the salicylic acid and jasmonic acid pathways, which interfere with feeding by herbivores (Ozawa et al. 2000; Li et al. 2002; Kant et al. 2004). However, this induction is not universal: some *T. urticae* lines down-regulate tomato defences (Kant et al. 2008; Alba et al. 2015). Moreover, *T. evansi*, a congeneric of *T. urticae* specialized on Solanaceous plants, down-regulates tomato defensive compounds, such as proteinase inhibitors, to lower levels than those of un-infested plants, and this is correlated with a significantly better performance of herbivores on plants previously attacked by mites of this species (Sarmento et al. 2011a, b; Alba et al. 2015). *T. evansi* is endemic in South America and has recently invaded the whole Mediterranean region at a rapid pace (Boubou et al. 2012). In this region, it has affected the distribution of resident spider mites (Ferragut et al. 2013), which may be related to this property of down-regulating plant defences.

Given the contrasting mode of coping with plant defences of most *T. urticae* strains versus that of *T. evansi*, knowing how other spider mite species co-occurring with them behave toward such defences becomes pressing. Here, we address this issue by analysing how tomato plant defences are affected by *T. ludeni*, another spider mite commonly found on tomato plants and other Solonaceae in the Mediterranean region (Migeon et al. 2011; Ferragut et al. 2013). Recent studies suggest that this species may potentially become an important crop pest in the context of global warming (Gotoh et al. 2015). Additionally, we assess how this defence, or lack of it, affects the performance of other mite species sharing this host plant. Addressing this issue will contribute to our understanding of the interaction between invasive and resident herbivorous spider mites on tomato plants.

Materials and methods

Mites and plants

Tomato (*Solanum lycopersicum*, var Moneymaker) and bean (*Phaseolus vulgaris*, var Prelude) plants were sown in a greenhouse, where they grew for 4 weeks, (25 °C, light:dark = 16:8). Tomato plants used for experiments and for mite rearings had at least four fully expanded leaves.

Tetranychus evansi was collected from tomato plants in a greenhouse in Brazil in 2002 and maintained since then on the same host plant species (Sarmento et al. 2011a). A subset of this population was transferred to the University of Amsterdam in 2009 and subsequently to the University of Lisbon in 2013. *Tetranychus urticae* was collected from *Ricinus communis* in the Netherlands in 2009. *Tetranychus ludeni* was collected from *Datura stramonium* in Portugal in 2013. The two latter species were reared on bean plants. All mites have been maintained on detached leaves kept on top of wet cotton in isolated boxes under controlled conditions (25 °C, light:dark = 16:8) in a climate room at the University of Lisbon since September 2013. New leaves of the same host plant species were added and overexploited leaves were removed twice a week.

To ensure that females used in the experiments were approximately of the same age, adult females where isolated on separate leaves and allowed to lay eggs for 48 h. In all experiments, we used the adult females resulting from this cohort, 12 days after egg hatching.

All experiments were performed using 4-week-old tomato plants with at least four fully expanded leaves.

Effect of herbivory upon proteinase inhibitor activity

The second true leaf of each plant was isolated by applying lanolin paste on the petiole to prevent mites from moving to different parts of the plant. Subsequently, each plant was infested with 100 female mites of either *T. evansi, T. ludeni* or *T. urticae*. Mites were distributed over all leaflets of the above-mentioned leaves. Plants were infested for 12, 24 or 48 h. After this period, mites, eggs and web were removed with a thin brush and leaf material was stored at −80 °C. This was done in order to analyse the leaf material specifically, without any potential contamination by mite products. Equivalent leaves of clean plants were also stored at each time point, under the same conditions as experimental leaves and were used as control. Proteinase inhibitor (PI) activity was determined as the percentage of trypsin activity (Broadway and Duffey [1986]). An amount of ca. 300 mg of each leaf sampled was ground in liquid nitrogen, homogenized with 0.6 ml of extraction buffer (0.1 M Tris–HCl, pH 8.2; 20 mM $CaCl_2$; 1:3) and centrifuged at 4 °C, 5000 rpm, for 35 min. Subsequently, 50 µl of the supernatant (or 50 µl of water as control) were mixed with 50 µl trypsin solution (4.7×10^{-5} M) and 500 µl buffer and incubated for 5 min at room temperature. 100 µl buffer and 100 µl Na-benzoyl-D,L-arginine-4nitroamilide hydrochloride (1.2 mM) were added to 100 µl of the mixture. The absorbance (410 nm) was measured at 60 and 150 s, repeated in triplicate per sample. Trypsin activity was determined as the difference between the two measurements and converted to mg of trypsin per gram protein (Kakade et al. [1974]). The total amount of protein in each sample was determined using the Bradford method (Bradford [1976]). This analysis was repeated in two blocks through time, each including three plants per infesting treatment (i.e., replicates).

Effect of herbivory upon herbivore performance

The second true leaf of each plant was isolated by applying lanolin paste on the petiole to prevent mites from moving to different parts of the plant. Subsequently, 100 adult females of either *T. evansi, T. ludeni* or *T. urticae* were placed on this leaf. Mites were allowed to feed and oviposit on the plants for 48 h. Subsequently, females, eggs and web were removed from the leaves and 10 small arenas of ca. 4 cm^2 (a size large enough for it to stay fresh during the entire procedure) were made from those leaves. Similar arenas from clean plants of the same age, also treated with lanolin paste, were used as control. This was repeated in three blocks of time with, in total, 10 plants per treatment. Each arena was put on top of wet cotton wool in a Petri dish and one adult female spider mite was placed on each arena and

allowed to oviposit for 4 days. Half of the discs were used to measure oviposition by females of *T. evansi*, the other half for females of *T. ludeni*. The number of eggs on each arena was then assessed and used as a measure of mite performance. In the statistical analysis we used only the offspring of the females that were alive at the end of these 4 days. ($n = 189$ and $n = 156$ for *T. evansi* and *T. ludeni*, respectively) Additionally, female survival was compared between treatments. We could not measure fecundity of *T. urticae* as the majority of females were dead by the end of the experiment.

Statistical analysis

All statistical analyses were performed with the software R v.3.0.2. The effect of the species that previously attacked the plants (referred to as "infesting species" below) on oviposition of *T. evansi* and *T. ludeni* was analysed using a Generalized Linear Mixed Model (glmer of the lme4 package; Bates et al. [2013]) with a Poisson error distribution. Infesting species and ovipositing species were used as fixed factors and replicate (plant) as a random factor. The effect of the infesting species on the proportion of individuals of *T. evansi* and *T. ludeni* surviving was also assessed using the glmer function of lme4 package, but with a Binomial error distribution. Infesting species was used as a fixed factor and replicate as a random factor. The effect of the infesting species on plant proteinase inhibitor activity was also assessed using a glmer, but with a Gaussian error distribution. Infesting species and time of infestation (12, 24 and 48 h) were used as fixed factors and block as a random factor. Non-significant factors and interactions were sequentially removed from the models. Contrasts among treatments were assessed using Tukey HSD using the glht function of the multcomp package (Hothorn et al. [2008]).

Results

Effect of herbivory on proteinase inhibitor activity

The activity of proteinase inhibitors was significantly different across plants infested with different species (glmer: $F_3 = 30.4$; $p < 0.001$). Nonetheless, infestation through time did not differ significantly among species (interaction of treatment with time: $F_6 = 1.83$; $p = 0.11$). There was no significant difference in the activity of proteinase inhibitors in plants infested with *T. evansi* or *T. ludeni* (Fig. 1; Tukey HSD: $z = 0.35$; $p = 0.98$). Both these activities were significantly lower than the activity of proteinase inhibitors from clean plants (Fig. 1; *T. evansi*, $z = 3.31$; $p = 0.004$, *T. ludeni*, $z = 3.68$; $p < 0.001$). In contrast, the proteinase
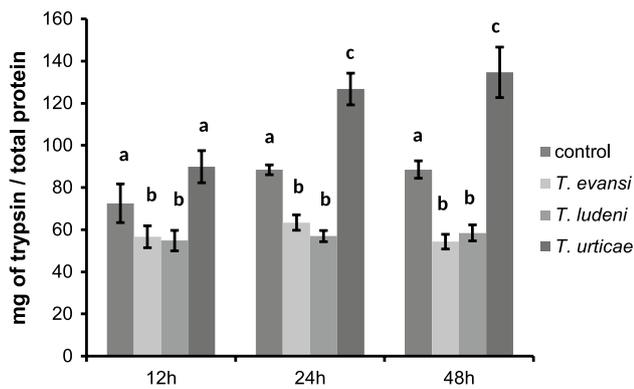
**Fig. 1** Proteinase inhibitors analysis. Mean proteinase inhibitor activity (±SEM; 2 blocks, 3 plants per block) in tomato leaves previously infested with 100 *Tetranychus evansi* females, 100 *T. ludeni* females, 100 *T. urticae* females for 12, 24 or 48 h and leaves of clean tomato plants. Different *letters* represent significantly differences in the Tukey HSD contrasts

inhibitor activity in plants infested with *T. urticae* was significantly higher than that of clean plants (Fig. 1; $z = 4.72$; $p < 0.001$).

Effect of previous attacks on herbivore performance

The oviposition rate of *T. evansi* and *T. ludeni* was similarly affected by the species previously attacking the plants: the interaction between ovipositing species and infesting species was not significant (glmer: $X_3^2 = 1.21$; $p = 0.75$). The performance of both species was significantly different on plants previously infested with different species ($X_3^2 = 86.3$; $p < 0.001$). The oviposition rate of *T. evansi* and T. *ludeni* on tomato plants previously infested with *T. evansi* or T. *ludeni* was significantly higher than that on clean plants (Fig. 2; Tukey HSD: $z = 5.54$; $p < 0.001$ and $z = 3.69$; $p = 0.035$ for plants infested with *T. evansi* or T. *ludeni*, respectively). Moreover, the fecundity of both species on plants previously infested with *T. evansi* was significantly higher than that on plants previously infested with *T. ludeni* (Fig. 2; $z = 2.71$; $p = 0.02$). In contrast, the oviposition rate was significantly lower on tomato plants previously infested with *T. urticae* than on clean plants (Fig. 2, $z = 3.27$; $p = 0.006$).

The survival of *T. evansi* was significantly different across plants infested with different species (glmer: $F_3 = 4.39$; $p = 0.01$). Infestation by conspecifics increased the survival of *T. evansi* as compared to clean plants ($z = 2.5$; $p = 0.05$) whereas infestation by *T. ludeni* or *T. urticae* did not ($z = 1.0$; $p = 0.72$ for *T. ludeni* and $z = 1.3$; $p = 0.57$ for *T. urticae*). Mean survival of *T. evansi* females was 0.88 ± 0.04. The survival of *T. ludeni* (mean 0.74 ± 0.04) was not significantly affected by the infesting species (glmer: $F_3 = 1.53$; $p = 0.22$). Similarly, survival
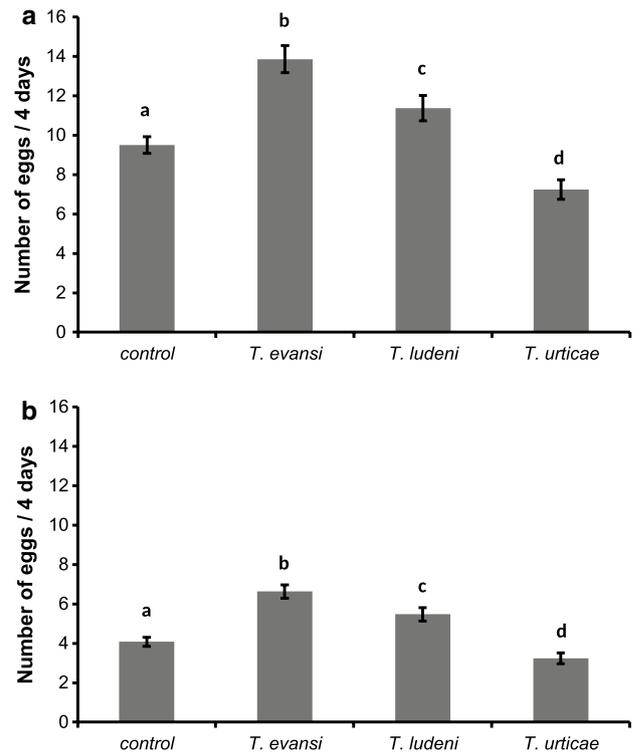
Fig. 2 Performance of *T. evansi* and *T. ludeni* on tomato plants. Mean oviposition (±SEM *whiskers*; 10 plants, 5 mites of each species per plant) of **a** *T. evansi* or **b** *T. ludeni* on plants previously infested with 100 *T. evansi* females, 100 *T. ludeni* females, 100 *T. urticae* females and clean (control) plants. Different *letters* represent significantly differences in the Tukey HSD contrasts

of *T. urticae* was unaffected by the infestation treatment (glmer: $F_3 = 1.95$; $p = 0.18$).

Discussion

In this study, we show that (1) the performance of spider mites was enhanced on plants previously infested by *T. evansi* or *T. ludeni* and decreased on plants previously infested by *T. urticae* relative to that on clean plants, and (2) the proteinase inhibitor activity showed the opposite pattern. We conclude that *T. ludeni* down-regulates tomato plant defences, with effects on the performance of both conspecifics and heterospecifics. Additionally, our results confirm earlier findings that most strains of *T. urticae* induce plant defences in tomato (Li et al. 2002; Kant et al. 2008) and that *T. evansi* down-regulates such defences (Sarmento et al. 2011a). The variability of plant-defence induction and suppression in the *Tetranychus* genus is, thus, further confirmed by our study.

T. ludeni had a weaker effect on tomato plant defences than its congeneric *T. evansi*: the effect of previous

infestations by *T. ludeni* on mite oviposition was weaker than that by *T. evansi*. In addition, the survival of *T. evansi* was higher on plants infested with conspecifics than on clean plants, whereas infestation by *T. ludeni* did not affect this trait. However, the effect on proteinase inhibitor activity was the same for both species. Although this trait is often used as proxy for the quality of plants as a resource for herbivores (Green and Ryan 1972), other defensive compounds are also produced by the plant upon herbivore attack and the activity of proteinase inhibitors may not directly correlate with performance of herbivores (Sarmento et al. 2011a; Kant et al. 2008; de Oliveira et al. 2015; Silva et al. 2015). Possibly, the differences in the degree of down-regulation pertain to the rearing conditions, as *T. ludeni* was reared on bean plants whereas *T. evansi* was reared on tomato plants and may thus have been acclimated to this host plant. In addition, *T. evansi* has been exclusively reared on this plant species since 2002, and we have no information about the short-term evolutionary history of *T. ludeni* before its collection. In line with this, we found that fecundity of *T. evansi* was higher than that of *T. ludeni* on tomato. Moreover, the effect of spider mites upon the transcriptome of their host plant is known to vary with the recent evolutionary history of contact between mites and plant species (Dermauw et al. 2013; Wybouw et al. 2015). Alternatively, the above-mentioned difference is an intrinsic characteristic of each species.

Nonetheless, *T. ludeni* and *T. evansi* share the remarkable ability of down-regulating plant defences to levels below those found in un-infested plants. Although some strains of *T. urticae* down-regulate tomato plant defences (Kant et al. 2008; Alba et al. 2015), this characteristic is not commonly found in most strains (Li et al. 2002; Ament et al. 2004; Kant et al. 2004), and this down-regulation never goes below levels of clean plants. Possibly, the ability to down-regulate plant defences below constitutive levels is phylogenetically clustered within the spider mite tree, as *T. evansi* and *T. ludeni* are more closely related to each other than to *T. urticae* (Matsuda et al. 2013). Testing this hypothesis requires addressing (1) within-species variability for this trait in these species, and (2) measuring this trait in closely-related species, such as *T. piercei*, *T. phaselus* and *T. turkestani*.

Another possibility is that host range affects the ability to cope with plant defences. Since plant defences differ according to the plant taxon (Wink 2003; Agrawal 2007), it may well be that the ability to down-regulate some defences trades off with resistance to other defences, hence herbivores that attack several plant families, such as *T. urticae*, may not have evolved means to manipulate different plant defences. Indeed, because generalists spend less time on a particular resource than specialists, the latter are expected to be better adapted to that resource than

generalists (Whitlock 1996). Although *T. ludeni* is as yet poorly studied, so far data concerning its host range do not contradict this hypothesis, as our field surveys (Diogo Godinho and Sara Magalhães, personal observations) and most publications associate this species with Solanaceous plants, in particular eggplant (*Solanum melongena*) (Reddy 2001, 2002; Reddy and Baskaran 2006). This strong interaction between *T. ludeni* and Solanaceous plants may have selected for the ability to down-regulate tomato plant defences. Note that the two hypotheses proposed above cannot be disentangled, since the phylogenetic distance between the two specialist species and *T. urticae* may be the cause or the consequence of their specialization. If specialization on Solanaceous plants does underlie the property of down-regulating tomato defences, then we expect no down-regulation of defences of non-solanaceous plants by these mites, a hypothesis that awaits a clear test.

The above reasoning suggests that down-regulating plant defences is beneficial for the herbivore species that performs this. However, a species that down-regulates plant defences improves resources not only for conspecifics but also for heterospecifics (Sarmento et al. 2011a). In agreement with this, we found that both *T. evansi* and *T. ludeni* similarly benefited from previous attacks by conspecifics or heterospecifics. It was also recently found that the tomato russet mite (*Aculops lycopersici*), a herbivore known to suppress plant defences, increases the performance of *T. urticae* when co-infesting the same plant (Glas et al. 2014). Moreover, this study shows that the population growth of the russet mite is reduced in the presence of *T. urticae*. Hence, it is not clear that down-regulating plant defences is a better strategy than inducing them. Therefore, the potential benefit of each strategy needs to be analysed in its adequate ecological context.

In the Mediterranean, the spider mite community is composed of several species that have overlapping distributions. In field surveys conducted in 2013 in Portugal, only three *Tetranychus* species were found: the two resident species *T. urticae* and *T. ludeni*, and the invasive *T. evansi*. Given their overlap in distribution and host range, the three species are likely to co-occur on the same plants. Unravelling the outcome of the interactions between these herbivore species with different strategies in coping with plant defences will help us understand the structure of the spider mite community in the Mediterranean and the impact of the invasive *T. evansi* on the resident species (note, however, that we need to confirm that other populations of *T. evansi* also down-regulate plant defences). Although information regarding the outcome of interspecific competition between *T. evansi* and *T. ludeni* is lacking, field surveys suggest that the distribution of the latter is not compromised by competition with the invasive *T. evansi* (Ferragut et al. 2013). Indeed, whereas other spider mite species such as *T. urticae*

and *T. turkestani* were affected by the invasion of the Mediterranean basin by *T. evansi*, and changed their host use, *T. ludeni* maintained its host range, even though it was overlapping with that of *T. evansi* (Ferragut et al. 2013). This difference between *T. ludeni* and the other resident congenerics may result from the fact that (1) *T. ludeni* has the ability to down-regulate tomato defences, and (2) it is able to cope with the strategies that *T. evansi* uses to protect the resources. These indirect interactions through plant defences with a competitor that displays similar strategies may hamper the invasion of *T. evansi*.

Our results support the mounting evidence that the strategy of down-regulating plant defences is more common than previously thought (Sarmento et al. 2011a), and not restricted to invasive species. Moreover, our data confirm that this strategy may provide benefits to other species (Glas et al. 2014), reinstating the need for an ecological contextualisation of its potential costs (Sarmento et al. 2011a, b).

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