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ORIGINAL ARTICLE

Phytophagous mite performance on intact plants and leaf discs with different defence levels

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Abstract

Plant quality for herbivores is usually evaluated with molecular and physiological techniques and with herbivore performance bioassays. These performance assays are usually done either on intact plants or on detached plant parts, such as leaves, leaflets, and leaf discs. It is thus far unclear how performance experiments on intact plants and on plant parts compare. Plant quality may change in detached plant parts because of the mechanical wounding inflicted, which may induce plant defences. Moreover, plant defences are often systemic, i.e., involving the entire plant, and may not be fully expressed in leaf discs. We investigated the effects of plant quality on the performance of a phytophagous mite on intact plants and on leaf discs. Plant quality was manipulated by infesting intact tomato plants (*Solanum lycopersicum* L., Solanaceae) either with a strain of the spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) that induces plant defences, or with *Tetranychus evansi* Baker & Pritchard, which suppresses defences, and using uninfested tomato plants as control. We subsequently evaluated the oviposition rate and survival of individual females of *T. evansi* on intact plants and on leaf discs as a measure of herbivore performance. The mites produced fewer eggs on detached leaf discs than on intact plants. However, the oviposition rate of *T. evansi* was lower on plants infested with the inducer *T. urticae* than on plants infested with the suppressor *T. evansi*, and than on uninfested plants, both on leaf discs and on intact plants. We conclude that both intact plants and leaf discs can be used to evaluate the effects of plant quality on performance of this herbivore.

KEYWORDS

induced plant defence, performance assay, *Tetranychus evansi*, *Tetranychus urticae*, tomato, oviposition, Acari, Tetranychidae, *Solanum lycopersicum*, Solanaceae, assay comparison, systemic response

INTRODUCTION

In response to herbivory, plants have evolved a wide range of defensive mechanisms to protect themselves against herbivore attacks (Walling, 2000; Kessler & Baldwin, 2002;

Howe & Jander, 2008; Wu & Baldwin, 2010; Kant et al., 2015). Such plant defences can be present continuously and are then referred to as constitutive defences, or they are increased when the plant is under herbivore attack, so-called induced defences (Karban & Baldwin, 1997; Baldwin &

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Preston, 1999; Sabelis et al., 2001, 2007). Defences can vary from morphological changes of plants to synthesis of secondary metabolites, which all negatively affect herbivores (Karban & Baldwin, 1997; Walling, 2000; Kessler & Baldwin, 2002; Howe & Jander, 2008; Alba et al., 2011, 2015). Together, constitutive and induced defences often result in a decrease of herbivore performance (Karban & Baldwin, 1997; Walling, 2000). However, several herbivores seem to have mechanisms to prevent the induction of plant defences or become less sensitive to them (Musser et al., 2002; Kant et al., 2008; Lawrence et al., 2008; Sarmiento et al., 2011; Godinho et al., 2016).

The evaluation of plant responses to herbivore attack is often done through measurements of genetic, molecular, and physiological activity in the plant and through experiments assessing the performance of herbivores (Kessler & Baldwin, 2002; Howe & Jander, 2008; Zheng & Dicke, 2008). These latter herbivore performance assays, also referred to as antibiosis assays (Stenberg & Muola, 2017), are done either on intact plants (Stout & Duffey, 1996; Agrawal, 2000a,b) or on detached plant parts, such as leaves, leaflets, and leaf discs (Stout & Duffey, 1996; Musser et al., 2002; Sarmiento et al., 2011; Orsucci et al., 2017). This is often influenced by the herbivore under study: the performance of larger arthropods such as caterpillars is often, but not always, assessed on intact plants, whereas the performance of smaller herbivores often requires the use of smaller arenas to allow observations using stereomicroscopes.

Because mechanical wounding can activate the production of defence genes and proteins (Graham et al., 1986; Ryan, 1990; Stout et al., 1994; Karban & Baldwin, 1997; Reymond & Farmer, 1998; Schmelz et al., 2001), assays performed on detached plant parts can be affected by this mechanical wounding (Reynolds & Smith, 1985; Smith, 1985; Howe et al., 1996; Stratmann & Ryan, 1997; Ryan, 2000; Strassner et al., 2002; Glawe et al., 2003; Schimmel et al., 2017b). Some of these defence genes and proteins are the same as those induced by herbivory (Stout et al., 1994; Howe et al., 1996; Stratmann & Ryan, 1997; Ryan, 2000; Strassner et al., 2002; Glawe et al., 2003). Thus, herbivore assays performed on detached plant parts may be affected by changes in plant resistance induced after mechanical wounding. Moreover, plant responses to herbivory are often systemic and require integration with other plant parts or organs (Karban & Myers, 1989; Ryan, 1990), and it is questionable whether such systemic responses occur to the same extent in detached plant parts as in intact plants. There are strong indications that the performance of aphids differs on intact plants vs. leaf discs, which is likely correlated with aphids being phloem feeders – phloem flows are probably interrupted in detached leaf discs, resulting in differences in their nutritional value (Cao et al., 2018). Despite these possible differences between intact plants and detached plant material, to our knowledge, there has been no study comparing the effects of plant defences on herbivore performance on intact plants and on detached plant parts in a single experiment.

We propose that this is essential to compare the results of studies that use one of these two methods.

Here, we compared the performance of a spider mite (Acari: Tetranychidae) on intact tomato plants (*Solanum lycopersicum* L., Solanaceae) vs. leaf discs. To generate variation in the level of plant defences, we used uninfested plants, plants with defences induced by a defence-inducing strain of the spider mite *Tetranychus urticae* Koch, and plants with defences suppressed by the species *Tetranychus evansi* Baker & Pritchard (Sarmiento et al., 2011; Alba et al., 2015; de Oliveira et al., 2016, 2019; Schimmel et al., 2017a). The induction and suppression of these defences in the plants has been amply documented elsewhere (Kant et al., 2004; Paschold et al., 2008; Sarmiento et al., 2011; Alba et al., 2015; Ataide et al., 2016; Villarroel et al., 2016; Liu et al., 2017; Schimmel et al., 2017a; Knecht et al., 2020) – here we use the inducing and suppressing spider mites merely to generate variation in plant quality. Thus, we evaluated the performance of *T. evansi* on intact plants and on leaf discs made from plants that had received one of these treatments.

MATERIAL AND METHODS

Study system

Tetranychus urticae and *T. evansi* are small (adult females are ca. 0.5 mm) phytophagous mites. They insert their stylet-shaped mouthparts into individual leaf cells to suck up their contents (van der Geest, 1985). Whereas *T. urticae* is found on over 1100 plant species (Migeon & Dorkeld, 2020), *T. evansi* is specialised on Solanaceae. Both mite species are pests on tomato plants, where *T. urticae* induces defence responses of the jasmonic acid (JA) and methyl salicylate (MeSa) pathways (Kant et al., 2004), and *T. evansi* suppresses these defences (Sarmiento et al., 2011a; Alba et al., 2015).

In spider mites, the rate of oviposition is strongly related to their population growth rate (Sabelis, 1991) and is therefore often used as a measure for performance (Yano et al., 1998; Egas et al., 2003; Magalhães et al., 2011; Sarmiento et al., 2011) and host plant quality (Li et al., 2002); therefore, we measured the oviposition rate on intact plants and leaf discs.

Rearing methods

Tomato plants (*S. lycopersicum* var. Santa Clara I-5300) were grown from seeds in pots (14 cm diameter) filled with a standard fertilized peat mixture for young plants (50% coco peat, 15% white peat, 35% frozen black peat; Jongkind Grond, Aalsmeer, The Netherlands). The plants were kept in a climate room under controlled conditions at the University of Amsterdam (25 ± 1 °C, 60–70% r.h., L16:D8 photoperiod), were fertilized once a week with EC fertilizer NPK (Ca, Mg), 15-5-15 (+7+3) (Peters Excel, Everris International, Heerlen, The Netherlands), and watered by

filling the trays under the pots with water 3× per week. The spider mites *T. evansi* and *T. urticae*, both Viçosa strains (Sarmiento et al., 2011), were reared on detached tomato leaves. The rearing units consisted of small trays (18 × 12 cm), placed upside down inside larger trays (40 × 25 cm). The larger trays were filled with tap water, thus isolating the cultures on the small trays. A tomato leaf containing spider mites was placed on the small tray with the petiole touching the water in the big tray to maintain leaf turgor. A clean tomato leaf was added to the rearing 3× per week. The rearing units were cleaned once per month, the water in the big trays was replaced and old leaves without spider mites were removed. To avoid contamination, the *T. evansi* and *T. urticae* rearing units were kept in separate climate rooms (both at 25 ± 1 °C, 60–70% r.h., L16:D8 photoperiod).

Performance of *Tetranychus evansi*

We evaluated the performance of *T. evansi* on intact tomato plants and on leaf discs from plants of the same age that had received the same treatment. We did not test the performance of *T. urticae* because earlier research has shown that its performance on plants treated similar to the plants used here parallels that of *T. evansi* (de Oliveira et al., 2016, 2019). To obtain plants with different levels of defences, 45-day-old plants with four completely developed leaves were infested by releasing 20 adult female *T. urticae* per leaflet (a total of 400 per plant) (induced defences), infested with the same densities of *T. evansi* (suppressed defences), or were not infested (control). Four days later, i.e., after sufficient time to affect plant defences (de Oliveira et al., 2016), a circle (2.4 cm diameter) was drawn on the abaxial surface of leaflets one, three and five of the third and fourth leaves of the plants. Subsequently, spider mites, their eggs and the webbing were carefully removed from within the circle with a soft brush, and a thin barrier of non-drying glue (Tanglefoot, Grand Rapids, MI, USA) was applied on top of the drawn circle. Half of the plants were left intact, and leaf discs (3 cm diameter) were cut around the circle from the other half. The leaf discs were placed abaxial surface up on wet cotton wool in a Petri dish. An adult female *T. evansi* from a cohort, aged 2 days since becoming adult, was released inside each circle and the eggs deposited were counted after 3 days. Young adult females of the same age were used because the oviposition rate of spider mites varies considerably with age (Sabelis, 1981). To prepare cohorts, we transferred around 30 adult males and 50 last resting stages before adulthood of females (so-called teleochrysalids) of *T. evansi* from the culture to tomato leaflets arranged on wet cotton wool in Petri dishes. The females were allowed to develop into adults and to mate and were used 2 days after turning adult.

The experiment was performed in six blocks through time, each consisting of a group of six plants; with all three levels of plant treatment crossed with the two experimental arena types (intact plants vs. leaf discs). From each plant,

there were six experimental arenas that received one adult female of *T. evansi* each. The females were allowed to oviposit for 3 days, after which the eggs were counted. Eggs of females that had died during the 3 days of oviposition were not included in the analysis. Because each plant is a true replicate, the oviposition rate of the surviving females was averaged, yielding one average oviposition rate per plant. These averages were compared with a linear mixed effects model (lme of the package ‘NLME’; Pinheiro et al., 2017) with plant treatment (uninfested or infested with *T. urticae* or *T. evansi*) and experimental arena type (intact plant vs. discs) as fixed factors and block as random factor. When the use of intact plants or leaf discs would differentially affect the plant defence and consequently the performance of the mites, this would result in a significant interaction between plant treatment and arena type, and we therefore specifically included this interaction in the analysis. Contrasts among treatments were assessed using general linear hypothesis testing (package ‘emmeans’; Lenth, 2019). All statistical analyses were performed with R v.3.6.0 (R Core Team, 2019). Although differences in adult female survival caused by differences in plant quality or on leaf discs and intact plants were not expected (Agrawal et al., 2002; Magalhães et al., 2007, 2011), we verified this by comparing the survival of adult females between leaf discs and intact plants during the oviposition test with a generalized linear mixed effects model (function ‘glmer’ of the package ‘LME4’; Bates et al., 2015) with a binomial error distribution (logit link) with the proportion of mites surviving as dependent variable, type of arena and plant treatment as factors, and block as random effect.

RESULTS

Mortality of females during the oviposition test did not differ significantly between leaf discs and intact plants (glmer: $\chi^2 = 0.61$, d.f. = 1, $P = 0.43$; Figure 1) or among plant

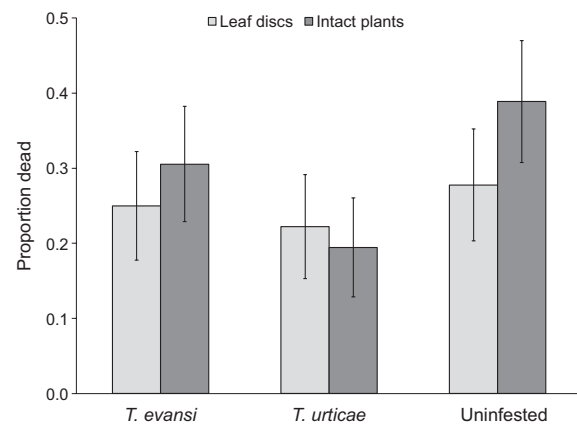


FIGURE 1 Mean (± SE) mortality of *Tetranychus evansi* on tomato leaf discs or intact plants. Previously, plants were either infested with *T. evansi*, with *T. urticae*, or uninfested. Shown is the mortality of adult females of *T. evansi* that were put inside circular arenas, either on leaf discs or on intact plants, over a total of 3 days, averaged over plants.

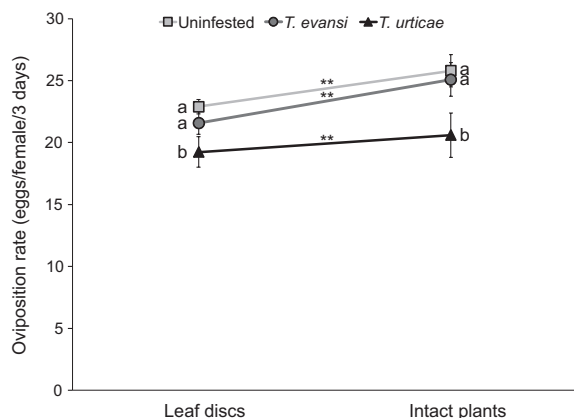


FIGURE 2 Mean (\pm SE) oviposition rate (no. eggs per female per 3 days) of *Tetranychus evansi* on tomato leaf discs or intact plants. Previously, plants were either infested with *T. evansi* (dots), with *T. urticae* (triangles), or were not infested (squares). Shown is the oviposition rate of individual females, averaged per plant, during 3 days. Means within an experimental arena type marked with different letters are significantly different among treatments, and asterisks indicate significant differences between arena types within a treatment (contrasts after lme: $P < 0.05$).

treatments ($\chi^2 = 2.98$, d.f. = 2, $P = 0.23$) and showed the same trends on leaf discs and intact plants (arena type*plant treatment interaction: $\chi^2 = 0.80$, d.f. = 2, $P = 0.67$). The oviposition rate of *T. evansi* showed the same trends on leaf discs and intact plants [lme, arena type*plant treatment: LR (likelihood ratio) = 2.097, d.f. = 2, $P = 0.35$; Figure 2], but was significantly higher on intact plants than on leaf discs (LR = 13.36, d.f. = 1, $P = 0.0003$). As expected, plant treatment significantly affected herbivore oviposition rate (LR = 23.6, d.f. = 2, $P < 0.0001$). *Tetranychus evansi* laid more eggs on plant material that had previously been infested with conspecifics and on plant material from uninfested plants than on plant material that had been infested with *T. urticae* (induced plants) (Figure 2). Contrary to expectation, previous attacks of plants by *T. evansi* did not result in increased oviposition on plant material of these plants (Figure 2).

DISCUSSION

Herbivore performance assays are common experiments in studies of plant defences (Karban & Carey, 1984; Thaler et al., 1996; Van Zandt & Agrawal, 2004). They are either done on intact plants or on plant parts (leaves or parts of leaves), but it is questionable whether these different methods yield the same results or whether different types of arena interact with plant defences in different manners. Here, we show the absence of such interaction for tomato plants and spider mites, suggesting that either of these two types of arenas can be used for performance experiments with spider mites.

Leaf discs may consist of a larger or smaller proportion of the preferred leaf tissue of the herbivores, and this may

account for differences in feeding rates and performance among leaf discs, leaflets, or leaves or intact plants. We found that the performance of *T. evansi* was lower on leaf discs than on intact plants. De Ponti (1977) found no significant difference in oviposition on leaf discs and on the mechanically damaged leaves on the plant from which these discs were taken, but he did not measure oviposition on intact plants. Kavousi et al. (2009) found that the growth rate of *T. urticae* was higher on detached leaves than on leaf discs, but they did not test performance on intact plants. Huang et al. (2003) tested herbivory by the cucumber beetle, *Diabrotica balteata* LeConte, on intact lettuce plants, detached leaves, and leaf discs, and found that the amount of tissue consumed differed among treatments, but they did not assess survival or reproduction of the herbivores. Likewise, Boiça Junior et al. (2015) showed that caterpillars of *Anticarsia gemmatilis* Hübner and *Spodoptera frugiperda* Smith & Abbot larvae consumed less foliage of leaflets of soybean than of leaf discs. Nam & Hardie (2012) found no differences in performance of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), on detached leaves and on leaves on intact plants, but they did not compare host plants that differed in defences. To our knowledge, our study is the first to show that variation in plant quality translates to comparable differences in herbivore performance on intact plants and leaf discs in a single, controlled experiment.

It has been suggested that detached leaf parts are lower quality food than intact leaves because of the chemical changes at the cutting site (Jones & Coleman, 1988). These changes may deter herbivores because of locally increased defences, but they may also be feeding stimulants (Boiça Júnior et al., 2015). This 'edge' effect may be more pronounced in herbivores that start feeding from the leaf edge, such as many caterpillars. The mites we used here are small relative to the leaf disc size (adult females are 0.5 mm long, ca. 50× smaller than the diameter of the leaf disc), and had ample opportunity to choose a feeding site away from the disc edge. Earlier experiments have shown that spider-mite oviposition on leaf discs does not decrease during 3–4 days (de Ponti 1977; EF de Oliveira & A Janssen, unpubl. data, 2016), suggesting that the leaf disc quality does not decrease with time. Another reason for differences in oviposition rates on leaf discs vs. intact plants may be the constant evaporation of water from the wet cotton wool and leaf discs, which may cause lower temperatures in the boundary layer of the leaf discs.

Plants infested with *T. urticae* were expected to have induced defences, resulting in reduced herbivore performance, whereas plants infested by *T. evansi* should have suppressed defences, resulting in increased performance (Sarmiento et al., 2011; Alba et al., 2015; de Oliveira et al., 2016, 2019; Godinho et al., 2016; Schimmel et al., 2017a). Whereas we did find evidence for induction of defences by *T. urticae*, we did not observe increased performance on plants or leaf discs previously attacked by *T. evansi*. A recent meta-analysis of published and unpublished studies on defence suppression by *T. evansi* showed that the capacity

to suppress tomato plant defences decreased during cultivation of *T. evansi* in laboratories (Knecht, 2019), and the experiments reported here were done with a strain that has been in culture for ca. 14 years. This reduced capacity to suppress plant defences could in theory have been caused by the mites being cultured on detached leaves. Upon being detached, mechanical wounding may induce defences in these leaves, and this induction could then restrict the capacity of the mites to suppress defences, resulting in reduced selection for defence suppression in the culture. However, when plants were induced by *T. urticae*, *T. evansi* was seen to suppress defences in tomato plants even more than in clean plants (Schimmel et al., 2017a), suggesting that it can cope with such induction. It should be noted that the strain used here was still capable of preventing induction of defences.

In this study, we evaluated the oviposition of the spider mites only once, after 3 days. In bioassays with mites, it is common to evaluate oviposition rates on a daily basis, but this was not feasible here because of the impossibility to accurately count mite eggs on intact plants. When oviposition rates are assessed daily, a normal procedure with mites is to discard the oviposition of the 1st day, because this is partly determined by the previous diet of the mite (Storms, 1971). Furthermore, it is easier to adjust oviposition for mortality of the adult female with daily observations (Zhang et al., 2018). In conclusion, there are several advantages of assessing performance of mites, and probably of other small herbivores, on leaf discs rather than on intact plants.

Based on our results, we suggest that the use of detached leaves and leaf discs is a valuable method for small herbivores such as mites and thrips that feed on plant cell contents. It should be noted that *T. urticae*, one of the species used here, induces both major biochemical pathways involved in plant defences, i.e., the jasmonate and the salicylate pathways (Kant et al., 2004). It is conceivable that mechanical wounding interferes differently with these pathways (Reymond & Farmer, 1998; Mithöfer et al., 2005). It is therefore advisable to run similar experiments as done here for herbivores that induce either of the two pathways separately.

It is advisable to carry out herbivore performance experiments as much as possible on intact plants, knowing that this allows for expression of the full gamut of plant responses. This seems especially important for phloem-feeding herbivores such as aphids (Cao et al., 2018; but see Nam & Hardie, 2012). Concern has also been raised whether the use of leaf discs is suitable for larger, chewing herbivores such as caterpillars, which will likely also feed on the mechanically damaged edges of the leaf discs (Jones & Coleman, 1988). The use of leaf discs or detached leaves with the aim of increasing the numbers of replicates (i.e., testing six mites on one plant as was done here) is misguided, because the plant is the natural unit of replication, not the individual mite. It is for this reason that we averaged the oviposition rate per plant, resulting in one observation per replicate. Needless to say that testing more individuals per plant does increase the reliability of this

average performance on a particular plant. In conclusion, both whole plants and leaf discs may be used to evaluate the effects of plant defences on the performance of small herbivores.

AUTHOR CONTRIBUTIONS

Cleide Rosa Dias: Conceptualization (equal); data curation (lead); formal analysis (equal); investigation (lead); methodology (equal); validation (lead); writing – original draft (lead); writing – review and editing (lead). **Lívia Maria Silva Ataíde:** Conceptualization (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Tomas Tjalling Meijer:** Investigation (equal); methodology (equal); writing – review and editing (equal). **Madelaine Venzon:** Conceptualization (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal). **Angelo Pallini:** Funding acquisition (lead); project administration (lead); supervision (lead); writing – original draft (supporting); writing – review and editing (supporting). **Arne Janssen:** Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (equal); supervision (lead); writing – original draft (lead); writing – review and editing (lead).

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available at DOI 10.21942/uva.20477178.

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