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The effect of host plants on *Tetranychus evansi*, *Tetranychus urticae* (Acari: Tetranychidae) and on their fungal pathogen *Neozygites floridana* (Entomophthorales: Neozygiteaceae)

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ABSTRACT

In a series of tritrophic-level interaction experiments, the effect of selected host plants of the spider mites, *Tetranychus evansi* and *Tetranychus urticae*, on *Neozygites floridana* was studied by evaluating the attachment of capilliconidia, presence of hyphal bodies in the infected mites, mortality from fungal infection, mummification and sporulation from fungus-killed mite cadavers. Host plants tested for *T. evansi* were tomato, cherry tomato, eggplant, nightshade, and pepper while host plants tested for *T. urticae* were strawberry, jack bean, cotton and *Gerbera*. Oviposition rate of the mites on each plant was determined to infer host plant suitability while host-switching determined antibiosis effect on fungal activity. *T. evansi* had a high oviposition on eggplant, tomato and nightshade but not on cherry tomato and pepper. *T. urticae* on jack bean resulted in a higher oviposition than on strawberry, cotton and *Gerbera*. Attachment of capilliconidia to the *T. evansi* body, presence of hyphal bodies in infected *T. evansi* and mortality from fungal infection were significantly higher on pepper, nightshade and tomato. The highest level of *T. evansi* mummification was observed on tomato. *T. evansi* cadavers from tomato and eggplant produced more primary conidia than those from cherry tomato, nightshade and pepper. Switching *N. floridana* infected *T. evansi* from one of five Solanaceous host plants to tomato had no prominent effect on *N. floridana* performance. For *T. urticae*, strawberry and jack bean provided the best *N. floridana* performance when considering all measured parameters. Strawberry also had the highest primary conidia production. This study shows that performance of *N. floridana* can vary with host plants and may be an important factor for the development of *N. floridana* epizootics.

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1. Introduction

Spider mites are considered to be major pests of commercial crops and often require costly control measures due to development of resistance to most available pesticides (Cranham and Helle, 1985). The twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is a worldwide pest of numerous crops with tomato, bean and cucurbit crops being attacked most often (Jepson et al., 1975) while the tomato red spider mite, *Tetranychus evansi* Baker & Pritchard (Acari: Tetranychidae) attacks host plants such as nightshade, tomato, eggplant and potato (Moraes et al., 1987). However, both spider mites are web spinning and occur during prolonged, hot and dry periods (Huffaker et al., 1969; Moraes et al., 1987; Knapp et al., 2003). Because of difficulties associated

with their control and huge economic losses thereof, there is much interest in the search for alternative control measures especially biological control.

Effort is currently being devoted to the search for natural enemies of *T. evansi* because most predatory phytoseiids used in the control of other spider mites such as *T. urticae* are not effective for its control especially in regions where it is considered exotic (Moraes and McMurtry, 1985, 1986; Fiaboe et al., 2006; Furtado et al., 2006, 2007). Interest in the use of acaropathogenic fungi for the control of spider mites has also increased in recent years (Chandler et al., 2000; Van der Geest et al., 2000; Wekesa et al., 2005). However, biological control can be challenging as spider mites are known to perform differently on different host-plant species in terms of survival and fecundity (Gould, 1978). For instance, Agrawal (2000) collected several hundred *T. urticae* from cotton, bean, roses, and morning glory (*Convolvulus arvensis* L.) and maintained them on cotton and cucumber (*Cucumis sativus* L.) for several generations before using the reversion lines on cotton and

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concluded that local adaptation to host plants may be genetically correlated with reduced performance on other hosts and with altered host-plant preference. Generally, most herbivorous arthropods are restricted to feeding on relatively few plant families, and it is believed that this host-range limitation may be due to fitness costs associated with alternative hosts (Fox and Morrow, 1981). Trade-offs in fitness arises from differential adaptations to plant defenses such as ability to detoxify toxic allelochemicals and the benefits derived from these chemicals (Gould, 1979).

Neozygites floridana (Weiser and Muma) Remaudière and S. Keller (Zygomycetes: Neozygitaceae) is a fungal pathogen that is an important natural enemy of *T. urticae* and *T. evansi* and it is a major mortality factor that causes decline in field populations of *T. urticae* attacking different crops such as corn (Smitley et al., 1986), peanuts (Boykin et al., 1984), soybean (Klubertanz et al., 1991), lima beans (Brandenburg and Kennedy, 1983), cotton (Carner and Canerday, 1970), strawberry (Klingen and Westrum, 2007) as well as *T. evansi* attacking tomato (Humber et al., 1981; Duarte et al., 2009). This fungus develops inside spider mites as hyphal bodies, kills its hosts, sporulates and produces primary conidia on conidiophores on the outside of the dead mite when conditions are favorable. Primary conidia are actively ejected from swollen brown desiccated cadavers, referred to as mummies. These conidia germinate to form the infective and more persistent capilliconidia that infects new mites (Carner, 1976; Elliot, 1998; Delalibera et al., 2006). It only takes one attached capilliconidium to produce a lethal infection (Oduor et al., 1997), and capilliconidia attached to the mite body indicate a strong infection potential and hence a good estimate for the infection level (Delalibera et al., 2000).

Abiotic factors such as relative humidity, temperature, photoperiod and light intensity have been proven to affect production, germination and viability of fungal conidia of *N. floridana* (Carner, 1976; Klingen and Nilsen, 2009; Castro et al., 2010; Wekesa et al., 2010a, 2010b). Also the use of pesticides are known to affect this beneficial fungus (Klingen and Westrum, 2007; Wekesa et al., 2008). Although several factors are known to influence *N. floridana*, the role of host plants and their impact on the development of epizootics are largely unknown. In order to maximize the potential of fungal pathogens in the management of spider mites, it is therefore necessary to understand the effects of host plants on fungal efficacy.

Phytochemical differences among host plants can determine their suitability to arthropod herbivores and susceptibility to entomopathogens which increases as host plant suitability decreases (Felton and Dahlman, 1984; Richter et al., 1987; Hare, 1992). Insect- and mite pathogenic fungi are known to be affected by the arthropod host plants through tritrophic-level interactions (Hajek and St. Leger, 1994). Hare (1992) suggested that pest control strategies that seek to decrease the suitability of crop plants for the growth and development of arthropod herbivores should ensure compatibility with entomopathogens as the two strategies of pest control should be additive or synergistic. Several studies have established that host plants can alter susceptibility of arthropod pests to microbial pathogens and result to variation in efficacy for the pathogens used in their control (Hare and Andreadis, 1983; Ramoska and Todd, 1985; Benz, 1987; Costa and Gaugler, 1989a). However, some studies showed no effect of host plants on susceptibility of invertebrate hosts to fungal pathogens (Costa and Gaugler, 1989a; Vidal et al., 1998) and these differences in results from various fungal-invertebrate-host plant systems shows that there is a need for more studies for possible effects on the variation of host plants on spider mites.

This study therefore aimed at revealing whether different host-plant species of *T. urticae* and *T. evansi* influence the mortality, mummification, sporulation, and attachment of capilliconidia and presence of hyphal bodies in the infected mites of two *N. floridana* isolates specific to each of the two mite species. In addition,

oviposition was evaluated to establish host plant suitability to *T. urticae* and *T. evansi* and to establish the relationship between their suitability and mummification by the fungus. The effects of host plant switching on the spider mites as well as on *N. floridana* were also evaluated to yield information that may help in the management of these pest mites.

2. Materials and methods

2.1. Mites

Two spider mite species, *T. urticae* and *T. evansi* were used in this study. *T. urticae* was collected on cotton at the University of São Paulo farm, Piracicaba, Brazil on February 2007 and the colony was maintained on jack bean, *Canavalia ensiformis* (L.) (DeCandolle). *T. evansi* was collected in the same period on the American nightshade, *Solanum americanum* Mill in a greenhouse in the same farm and the colony was maintained on tomato, *Lycopersicon esculentum* Mill.

2.2. Fungal cultures

Two isolates of *N. floridana* were used in this study: isolate ESALQ1418 and ESALQ1419. Both were collected as fungus-killed cadavers of *T. urticae* and *T. evansi* on jack bean and tomato, respectively in a greenhouse at the University of São Paulo in September 2004. The isolates were previously stored as desiccated cadavers on cotton in vials containing silica gel at -10°C . After retrieval from storage, the cadavers from the two fungal isolates were thawed by keeping them at room temperature for 10 min and used in the production of new cadavers. Cadavers used in the experiment were produced by exposing healthy *T. urticae* or *T. evansi* females to sporulated cadavers from the stock culture of ESALQ1418 and ESALQ1419 respectively. Sporulation from fungus-killed mite cadaver was obtained by keeping cadavers at 25°C in darkness on leaf disks (1.2 cm diameter) placed onto wet sponge in closed Petri dishes (9 cm diameter) at 100% RH for 24 h. Afterwards, exposed mites were maintained in an incubator at 25°C and 50% RH under natural light-dark regime (12D:12L) and cadavers were collected 3–7 days later in accordance with to the method described by Delalibera and Hajek (2004). The collected cadavers were stored as previously described and in all the experiments, cadavers were stored no more than 4 weeks before use.

2.3. Rearing of spider mites on different host plants

The twospotted spider mite, *T. urticae* originally maintained on jack bean (*C. ensiformis* L.) was transferred to four test plants namely strawberry (*Fragaria* × *ananassa* Duch. var. Santa Clara), jack bean (*C. ensiformis*), cotton (*Gossypium hirsutum* L. var. Delta Pine 404) and, *Gerbera jamesonii* L. var. Tonga. The tomato red spider mite, *T. evansi* originally maintained on tomato (*Lycopersicon esculentum* var. Santa Cruz) was transferred to new five Solanaceous test plants, including tomato (*L. esculentum* var. Santa Cruz), cherry tomato (*L. esculentum* var. *cerasiforme*), eggplant (*Solanum melongena* L. var. 'Natu Nobilis'), nightshade (*S. americanum* Mill – a wild variety) and pepper (*Capsicum annuum* var. Black pearl). All the plants were maintained in the greenhouse in plastic pots and were fertilized with NPK fertilizer and watered appropriately. Mites were maintained on test plants for at least three weeks before use in the experiment.

2.4. Effect of host plant on the performance of *N. floridana*

To infect *T. urticae* and *T. evansi* reared on different host plants with *N. floridana*, cadavers from storage cultures were placed

individually on leaf disks (1.2 cm in diameter) that were punched out from each test plant. Leaf disks with cadavers were then placed on wet sponges soaked in distilled water inside Petri dishes (9 cm in diameter). Dishes were kept closed for 24 h in darkness at 25 ± 2 °C to encourage sporulation. Sporulation was confirmed under a compound microscope (100 \times) before introducing 20 females of either *T. evansi* or *T. urticae* per disk of each plant. The mites were maintained on these disks for 24 h to allow maximum contamination with fungal conidia and then transferred to new and larger leaf disks (2.5 cm in diameter) placed in Petri dishes (3 \times 1.5 cm, diameter \times height) and covered with PVC stretch film. To ensure fresh leaf disks at all times, disks were changed after 4 days. Attachment of capilliconidia, presence of hyphal bodies in the infected mites, mortality from fungal infection and mummification were recorded daily for 8 days. Mites were considered to have been killed by the fungus if hyphal bodies and mummies were observed on dead mites or dead mites formed desiccated mummified cadavers. Ten leaf disks were used for each host plant in each experiment involving *T. evansi* while five leaf disks were used for host plants of *T. urticae* and the experiments were repeated three and four times respectively.

2.5. Effect of host plants on sporulation of *N. floridana* cadavers

To determine the effect of host plants on sporulation from fungus-killed mite cadaver, 15 mummified *N. floridana* cadavers of *T. evansi* and *T. urticae* produced in the host plant experiment were used for evaluation of spore production. Cadavers were placed individually on clean tomato disks (1.2 cm in diameter) resting on a wet sponge inside Petri dishes (9 cm diameter) at 100% RH and 25 °C in darkness for 24 h. The number of conidia discharged per cadaver was estimated directly under a compound microscope according to an arbitrarily chosen categorical scale (0 = indicates no sporulation, 1 = 1–100, 2 = 101–500 and 3 \geq 501 conidia). The experiments were repeated three times at similar conditions.

2.6. Effect of host plant switching on fungal infection of *T. evansi*

Tomato (*L. esculentum* var. Santa Cruz) had in previous experiments shown a high percentage of *N. floridana* caused mummification of *T. evansi* (data not shown). In this experiment we therefore wanted to test whether host plant switching after the *N. floridana* inoculation of *T. evansi* on five different host plants (nightshade, eggplant, pepper, cherry tomato, tomato) would change the performance of *N. floridana* to *T. evansi*. The host plant switching experiment was conducted with *T. evansi* that was first reared and inoculated with *N. floridana* on one of the five different host plants for at least two weeks before adult females were tested on tomato leaf disks. The inoculation process and evaluation of results was conducted as described in previous experiment. Evaluation of *N. floridana* performance in terms of hyphal bodies in infected mites, fungal mortality, and mummification followed the same procedure as described in Section 2.4.

2.7. Effect of host plant on reproduction of *T. evansi* and *T. urticae*

This experiment was performed to establish the relationship between host plant suitability and *N. floridana* performance on *T. evansi* and *T. urticae* reared on different host plants.

Individuals of known age were obtained from the stock colony and allowed to oviposit on tomato or jack bean leaf disks, respectively. After 12 h, females were removed and the eggs laid were kept at 25 ± 2 °C. Eggs were allowed to hatch and larvae were transferred to respective host plants at 25 ± 2 °C until they reached the deutonymphal stage. Deutonymphs were sexed and females were transferred singly in arenas containing leaf disks (2.5 cm in

diameter) of tomato, cherry tomato, nightshade, eggplant and pepper in case of *T. evansi*. *T. urticae* females were assayed on jack bean, strawberry, cotton and *Gerbera* under similar conditions. In total, eight female mites were used for each host plant and oviposition recorded daily for 2 weeks. The experiments were repeated three times for each mite host plant combination.

2.8. Statistical analysis

Treatment mortality was corrected using the Abbott's formula (Abbott, 1925) to adjust for natural control mortality (5–10%). Mummification was calculated as the proportion of the total number of dead fungus-killed mites that formed desiccated cadavers. Differences in contamination, infection, mortality and mummification of mites reared on different host-plant species (both for direct experiments where spider mites were reared and tested on respective host plants or host-switch where mites were reared on different host plants and tested on tomato) were compared with analysis of variance (ANOVA) and means were separated using Duncan multiple range test (DMRT) after Arcsine transformations of percent contamination, infection, mortality and mummification data. Oviposition rate of both *T. evansi* and *T. urticae* reared on their respective host plants was also compared with ANOVA with the aim of determining host suitability. Categorical data for sporulating cadavers were compared by Mann Whitney U test in relation to the host plants upon which the mycosed mites were reared.

3. Results

3.1. Effect of host plant on *N. floridana* performance

A significant effect of Solanaceous host plants of *T. evansi* on *N. floridana* performance was recorded for attachment of capilliconidia ($F = 30.37$; $df = 4, 145$; $p = 0.0001$), presence of hyphal bodies ($F = 26.51$; $df = 4, 145$; $p = 0.0001$), mortality from fungal infection ($F = 25.85$; $df = 4, 145$; $p = 0.0001$) and mummification ($F = 40.98$; $df = 4, 145$; $p = 0.0001$). Mummification of *T. evansi* reared on tomato was more than three times higher than those reared on nightshade and two times higher than those on cherry tomato (Table 1). Attachment of capilliconidia, presence of hyphal bodies in the infected mites and mortality from fungal infection were also high for tomato, pepper and nightshade. A significant effect of host plants of *T. urticae* on *N. floridana* performance was also recorded for attachment of capilliconidia ($F = 5.29$; $df = 3, 63$; $p = 0.0026$), presence of hyphal bodies ($F = 6.76$; $df = 3, 63$; $p = 0.0005$), fungal-mediated mortality ($F = 2.91$; $df = 3, 63$; $p = 0.0413$) and mummification ($F = 6.49$; $df = 3, 63$; $p = 0.0007$). Strawberry and jack bean were the plants which resulted in significantly better performance of *N. floridana* when considering all measurements (attachment of capilliconidia, presence of hyphal bodies, mortality from fungal infection and mummification) (Table 2). Host plant did not affect time to death for *N. floridana* infected *T. evansi* ($F = 1.40$; $df = 4145$; $p = 0.2364$) or *T. urticae* ($F = 0.63$; $df = 3, 51$; $p = 0.6008$).

3.2. Effect of host-plant species on sporulation of cadavers

T. evansi cadavers from eggplant and tomato produced more conidia than those from cherry tomato, nightshade and pepper but sporulation did not vary between tomato and eggplant or between cherry tomato and nightshade. Cadavers produced on pepper sporulated poorest among all the host plants (Table 3). *T. urticae* cadavers from strawberry produced the highest number of spores followed by jack bean. While cadavers from cotton and jack bean did not differ in sporulation, sporulation in strawberry

was significantly different with cotton. Cadavers from *Gerbera* sporulated poorest among the host plants tested for *T. urticae* (Table 4).

3.3. Effect of host plant switching on *N. floridana* performance on *T. evansi*

Proportion of *T. evansi* with hyphal bodies were lower in mites that switched from cherry tomato than from nightshade ($F = 5.68$; $df = 1, 38$; $p = 0.0223$) and did not differ from pepper, tomato and eggplant ($F = 1.47$; $df = 4, 95$; $p = 0.2161$) (Table 5). Similarly, mortality from fungal infection was lower in cherry tomato than nightshade ($F = 5.72$; $df = 1, 38$; $p = 0.0218$) and was not different from

Table 1
Host plant effect on *N. floridana* activity on *T. evansi*. Data are percentage means for fungal performance (\pm standard error) of 30 replicate leaf disks with *T. evansi* ($n = 600$) referring to attachment of capilliconidia, presence of hyphal bodies in the infected mites, mortality from fungal infection, and mummification of fungus-killed mite cadaver.

Host plant	Attached capilliconidia	Hyphal bodies	Fungal mortality	Mummification
Nightshade	92.2 \pm 0.9a	81.3 \pm 1.4a	80.3 \pm 1.4a	20.1 \pm 2.1e
Eggplant	76.8 \pm 2.0b	66.7 \pm 2.5b	64.8 \pm 2.7b	45.5 \pm 2.7c
Pepper	95.1 \pm 1.1a	84.5 \pm 1.7a	83.2 \pm 1.9a	52.8 \pm 2.5b
Tomato	89.8 \pm 1.2a	78.5 \pm 1.5a	77.4 \pm 1.5a	61.7 \pm 2.4a
Cherry tomato	70.2 \pm 3.4c	57.2 \pm 3.4c	54.6 \pm 3.6c	33.2 \pm 2.9d

Percentages of means followed by different letters in a column are significantly different ($P < 0.05$) according to Duncan multiple range test.

Table 2
Host plant effect on *N. floridana* activity on *T. urticae*. Data are percentage means for fungal performance (\pm standard error) of 20 replicate leaf disks with *T. urticae* ($n = 400$) referring to attachment of capilliconidia, presence of hyphal bodies in the infected mites, mortality from fungal infection, and mummification of fungus-killed mite cadaver.

Host Plant	Attached capilliconidia	Hyphal bodies	Fungal mortality	Mummification
Strawberry	93.1 \pm 2.1a	90.8 \pm 2.2a	59.7 \pm 4.8a	75.5 \pm 4.5a
Jack bean	92.4 \pm 2.4a	83.8 \pm 4.4ab	55.6 \pm 3.7a	76.1 \pm 5.2a
<i>Gerbera</i>	83.4 \pm 3.5ab	76.4 \pm 4.3bc	53.8 \pm 5.9a	50.7 \pm 6.8b
Cotton	76.9 \pm 5.2b	66.2 \pm 4.7c	38.1 \pm 6.7b	52.5 \pm 5.0b

Means followed by different letters in a column are significantly different ($P < 0.05$) according to Duncan multiple range test.

Table 3
Effect of host plant on conidia production of cadavers of *T. evansi* infected with *N. floridana*. Sporulation was based on an arbitrarily chosen categorical scale (0 = no sporulation, 1 = 1–100, 2 = 101–500 and 3 \geq 501 conidia) and mean ranks compared with Mann Whitney U test.

Host plant	Mann Whitney U	P-value
Tomato \times cherry tomato	68.5	0.045531
Tomato \times eggplant	101	0.578075
Tomato \times nightshade	39	0.00089
Tomato \times pepper	10.5	0.000011
Cherry tomato \times eggplant	63	0.02555
Cherry tomato \times nightshade	85	0.211730
Cherry tomato \times pepper	36.5	0.00094
Eggplant \times nightshade	37	0.000814
Eggplant \times pepper	51	0.006111

The difference in sporulation between cadavers from different host plant combinations is significant for $P < 0.05$ (asymptotic significance level) (2-tailed). Outcomes of the two compared treatments were quantified using an estimator i.e. the median of all possible differences in outcomes between the compared host plants that accompanies p , an estimate of the probability.

the other host plants ($F = 1.38$; $df = 4, 95$; $p = 0.2470$). Mummification was significantly different between host plants ($F = 7.82$; $df = 4, 95$; $P = 0.0001$) with the lowest being in pepper (35.0%) and highest in tomato (63.3%).

3.4. Effect of host plant on reproduction of *T. evansi* and *T. urticae*

T. evansi reared on eggplant, tomato and nightshade resulted in the highest production of eggs while cherry tomato and pepper both resulted in significantly less eggs ($F = 13.20$; $df = 4, 81$; $p = 0.0001$). The mean number of eggs per female during the entire period of evaluation varied from 2.9 eggs (pepper) to 36.8 eggs (eggplant) (Fig. 1). *T. urticae* reared on jack bean produced more eggs than when reared on strawberry, cotton and *Gerbera*

Table 4
Estimated conidia production of cadavers of *T. urticae* infected with *N. floridana* on different host plants. Sporulation was based on an arbitrarily chosen categorical scale (0 = no sporulation, 1 = 1–100, 2 = 101–500 and 3 \geq 501 conidia) and mean ranks compared with Mann Whitney U test.

Host plant	Mann Whitney U	P-value
Cotton \times jack bean	365	0.1149
Cotton \times strawberry	336.5	0.02137
Cotton \times <i>Gerbera</i>	282	0.0271
Jack bean \times Strawberry	398	0.2480
Jack bean \times <i>Gerbera</i>	149.5	0.0000
Strawberry \times <i>Gerbera</i>	149.5	0.0000

The difference in sporulation between cadavers from different host plant combinations is significant for $P < 0.05$ (asymptotic significance level) (2-tailed). Outcomes of the two compared treatments were quantified using an estimator i.e. the median of all possible differences in outcomes between the compared host plants that accompanies p , an estimate of the probability.

Table 5
Effect of switched host plant on *N. floridana* activity when *T. evansi* was reared on one host plant listed in the table and transferred to tomato. Data are percentage means for fungal performance (\pm standard error) of 30 replicate leaf disks ($n = 450$) referring to attachment of capilliconidia, presence of hyphal bodies in the infected mites, mortality from fungal infection, and mummification of fungus-killed mite cadaver.

Host plant	Attached capilliconidia	Hyphal bodies	Fungal mortality	Mummification
Nightshade	81.0 \pm 2.3 ^a	79.5 \pm 2.1a	78.5 \pm 2.2a	45.5 \pm 3.8bc
Eggplant	80.5 \pm 2.6 ^a	75.5 \pm 3.3ab	73.6 \pm 3.8ab	61.8 \pm 4.0a
Pepper	77.3 \pm 2.6 ^a	76.3 \pm 2.7ab	74.6 \pm 3.0ab	35.0 \pm 3.5c
Tomato	74.3 \pm 3.6 ^a	74.0 \pm 3.5ab	72.8 \pm 3.6ab	63.3 \pm 4.4a
Cherry tomato	74.3 \pm 4.1 ^a	69.0 \pm 3.9b	67.4 \pm 4.1b	52.3 \pm 5.2ab

Means followed by different letters in a column are significantly different ($P < 0.05$) according to Duncan multiple range test.

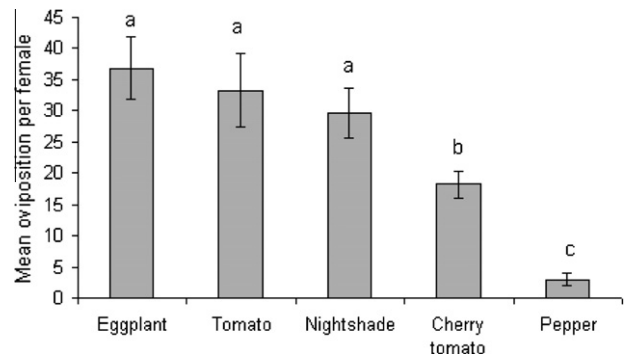


Fig. 1. Oviposition of *T. evansi* reared on five different host plants to determine host plant suitability for the mite reproduction.

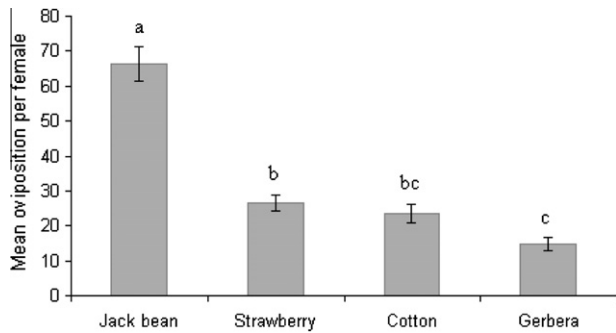


Fig. 2. Oviposition of *T. urticae* reared on four different host plants to determine host plant suitability for the mite reproduction.

($F = 52.74$; $df = 3, 73$; $p = 0.0001$). The mean number of eggs per female of *T. urticae* varied from 14.8 (*Gerbera*) to 66.4 (jack bean) (Fig. 2).

4. Discussion

In this study we found that mummification of *T. evansi* reared on tomato was higher than those reared on the other four host plants. Tomato, together with pepper and nightshade also resulted in the highest level of attachment of capilliconidia (contamination), presence of hyphal bodies (infection) and mortality from fungal infection. Furthermore, *T. evansi* cadavers from tomato and eggplant produced the highest number of primary conidia and at the same time, *T. evansi* reared on tomato, eggplant and nightshade resulted in the highest production of eggs. These results indicate that tomato is the plant most suitable both as a host plant for *T. evansi* and for *N. floridana* performance. The results for *T. urticae* showed that strawberry and jack bean were the plants which resulted in the best *N. floridana* performance when considering all measurements (mummification, attachment of capilliconidia, presence of hyphal bodies in the infected mites and mortality from fungal infection). Strawberry was also the host plant of *T. urticae* that resulted in the highest primary conidia production while *T. urticae* reared on jack bean resulted in the highest egg production.

Our results corroborate previous studies that demonstrate difference in spider mites performance on different host plants (Gould, 1978; Agrawal, 2000), and that they have higher oviposition rate on suitable host plants (Dabrowski and Bielak, 1978). Plant factors that might be important for their suitability to arthropod hosts are chemical plant compounds and plant trichomes. Tomato, cherry tomato and eggplant for example are characterized by the presence of trichomes that vary both in size and intensity with varying effects on spider mites (Rasmy, 1985; Maluf et al., 2001).

Insects and mites are known to be more susceptible to pathogens when they feed on sub-optimal hosts (Hajek and St. Leger, 1994; Mayer et al., 2002). However, effects of different host plants on *N. floridana* performance have not been studied. Degree of host plant hairiness is often considered an important characteristic that influences colonization and infestation by pests.

Since *N. floridana* does not host-search but depends on host's activities such as movement, reduction of spider mite movements due to trichomes, might negatively affect fungal infection rates. Numbers, structure and chemical content of trichomes might be of specific importance to attachment of capilliconidia to the spider mites as well as their infection. Trichomes may interfere with the movement of the spider mites resulting in low attachment of capilliconidia and their glands may also contain fungicidal chemicals

that reduce the germination of capilliconidia. Furthermore, the chemical content of the plant leaf itself might be important for the development of the fungus inside the spider mites. This was evident in a host-switching experiment where spider mites were reared on different host plants and tested on identical tomato leaf disks. However, further studies on the effect of types of trichomes and chemical content of host plants to quantify their effects on *N. floridana* performance are warranted.

Most Solanaceae species contain high concentrations of glycoalkaloids especially solanine and tomatine that have been shown to have considerable negative effects on entomopathogenic fungi within the Hypocreales and other natural enemies (Gallardo et al., 1990; Lacey and Mercadier, 1998; Poprawski and Jones, 2000). Infection process can be affected due to the action of allelochemicals that contribute to poor development of the fungi through effects on colonization and hyphal growth with resultant variation in mortality and mummification. However, our data on tomato and eggplant seems inconsistent with previous studies that indicate that tomatine and solanine negatively affect fungal entomopathogens (Arneson and Durbin, 1968; Costa and Gaugler, 1989b) because mummification and sporulation was high on these plants. Cotton also contains high concentration of gossypol that is known to affect fungal entomopathogens negatively. Poprawski and Jones (2000) established that germination of conidia *Paecilomyces fumosoroseus* and *Beauveria bassiana* was strongly inhibited (below 12% germination) on the cuticle of whitefly nymphs reared on cotton but was over 95% on the cuticle of nymphs reared on melon. The authors hypothesized that the terpenoid gossypol, produced by many cultivars of cotton, might have been involved in antibiosis. Our studies also shows that *N. floridana* performance is greatly affected when *T. urticae* is reared on cotton as compared to other hosts such as jack bean.

T. evansi cadavers from tomato and eggplant produced the highest number of conidia compared to cherry tomato, nightshade and pepper. Unexpectedly, we found that cadavers produced on pepper sporulated less despite a high mummification rate. This corresponds with other studies suggesting that poorly growing hosts, such as *T. evansi* on pepper, are detrimental to pathogen reproduction (Milner and Soper, 1981). In addition, nutritionally unsuitable host plants have previously been suggested to interfere with sporulation of *Nomurea rileyi* in cadavers of *Helicoverpa armigera* (Gopalakrishnan and Narayanan, 1989) and *Entomophaga maimaiga* in *Lymantria dispar* (Hajek et al., 1995).

Differences in mummification and sporulation may have several implications on the fungus and may affect its efficiency in the control of spider mites when feeding on different host plants. This is because the quality of the mummified cadavers determine sporulation which in turn influences horizontal transmission. High mummification and sporulation of spider mite cadavers in both tomato and eggplant or strawberry and jack bean would favor rapid development of epizootics while high mummification in pepper accompanied with poor sporulation will lead to decreased transmission rates. Nightshade and cherry tomato which had poor mummification and sporulation would also be expected to have low transmission rates. Decreased transmission rates may result in a slow epizootic development and affect the efficiency of the fungus in controlling the spider mites in these particular host plants. Therefore, the next step is to test our hypotheses on epizootic development in the greenhouse or field to establish performance of the fungus on spider mites feeding on various host plants.

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