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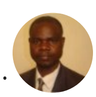

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Differential effects of various African nightshade species on the fecundity and movement of *Tetranychus evansi* (Acari: Tetranychidae)

L.K. Murungi[1,2]*, M. Knapp[2†], D. Salifu[2], J. Wesonga[1], A. Nyende[1], P. Masinde[1] and B. Torto[2]

[1]Jomo Kenyatta University of Agriculture and Technology (JKUAT), PO Box 62000-00200, Nairobi, Kenya and [2]International Centre of Insect Physiology and Ecology (icipe), PO Box 30772-00100, Nairobi, Kenya

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Abstract. The tomato red spider mite *Tetranychus evansi* Baker & Pritchard is a serious pest of solanaceous plants worldwide. Management of this oligophagous pest in African nightshades has been a challenge to smallholder African farmers due to its high reproductive rate and rapid development of resistance to synthetic pesticides. The aim of the present study was to determine the influence of leaf trichomes on *T. evansi* by comparing its fecundity and movement on the leaf surfaces of five African nightshade species, namely *Solanum sarrachoides* Sendter, *S. villosum* Miller, *S. tarderemotum* Bitter, *S. americanum* Miller and *S. scabrum* Miller. Data were recorded in the laboratory at 23 ± 1°C, 50–70% relative humidity and a 12 h light:12 h dark photoperiod for the effect of trichome type and density of the abaxial leaf surface on mite fecundity. Distances travelled by mites on the leaf surface from the edge of a thumbtack pin inserted on the leaf were also recorded. Different trichomes, glandular and non-glandular types, were identified. There was a significant negative correlation of fecundity and distance walked by mites with the density of glandular trichomes. Significantly fewer eggs were laid on *S. sarrachoides* in comparison with the other *Solanum* species. The distance walked by mites was also significantly shorter in this species, indicating that higher densities of glandular trichomes interfere with mite movements. These results suggest that African nightshade genotypes differ in their levels of resistance to *T. evansi*, which is partially associated with differences in trichome types and their densities.

Key words: resistance, *Solanum* spp, *Tetranychus evansi*, trichome

Introduction

The tomato red spider mite *Tetranychus evansi* Baker & Pritchard (Acari: Tetranychidae) is an invasive pest in Africa (Migeon *et al.*, 2009). Although commonly known to be a serious pest of tomato (*Lycopersicon esculentum* M.) and aubergine (*Solanum melongena* L.) (both Solanaceae), *T. evansi* is also a pest of several other solanaceous plants including nightshade (Moraes *et al.*, 1987; Fiaboe *et al.*, 2006). African nightshades have for long been considered as inedible poisonous plants and troublesome agronomic weeds (Schilling and Andersen, 1990; Edmonds and Chweya, 1997; Schippers, 2000); however, in western, eastern and southern Africa, the leaves are sold as vegetables in

*E-mail: lucykananu@yahoo.com
†Present address: Koppert Biological Systems, PO Box 155, 2650 AD Berkel en Rodenrijs, The Netherlands.

both rural and urban markets for dietary consumption (Edmonds and Chweya, 1997). In addition, their fruits and leaves are also used as a source of dye, and for various medicinal purposes (Schippers, 2000). In this regard, African nightshades are among the top priority indigenous vegetables earmarked for further research and improvement due to their role in improving the nutritional and economic status of marginalized and nutritionally vulnerable populations in Africa (Schippers, 2000).

In the last decade, *T. evansi* has become one of the most severe pests of solanaceous crops in Africa, causing crop losses of up to 90% in south-east Africa (Sibanda *et al.*, 2000; Saunyama and Knapp, 2003) and West Africa (Duverney and Ngueye-Ndiaye, 2005). A recent laboratory study revealed that some African nightshade species have considerable effects on life table parameters of *T. evansi* (Murungi *et al.*, 2010). In this study, *Solanum sarrachoides* Sendter negatively affected the doubling time and hence the intrinsic rate of the natural increase of *T. evansi*. However, the resistance mechanisms underlying the differential suitability of African nightshades to *T. evansi* have not been explored, although trichomes have been implicated in related solanaceous species (Simmons and Gurr, 2005).

Foliar trichomes are unicellular or multicellular structures arising from the epidermal tissues (Larkin *et al.*, 1996). They represent a plant morphological trait that can impose resistance to herbivores (Peters and Berry, 1980; Fernandes, 1994). Trichomes act as mechanical defence to small arthropods that impede the movement on the leaf surface, restrict access to food, diminish food digestibility and assimilation, and reduce fecundity (Valverde *et al.*, 2001; Kennedy, 2003; Simmons *et al.*, 2003; Handley *et al.*, 2005). In addition to the mechanical defence, some plant glandular trichomes secrete toxic chemicals and/or sticky exudates that may entrap and kill small insects (Gurr and McGrath, 2002). For instance, the hairy nightshade *S. sarrachoides* has been reported to confer some degree of resistance to the two-spotted spider mite *Tetranychus urticae* Koch (Rasmy, 1985). Leaves of this nightshade species have a high density of glandular hairs and mites quickly get entrapped in their exudates, which are released when the trichome cuticle breaks after being touched by the mites (Van Haren *et al.*, 1987; Chatzivasileiadis and Sabelis, 1997; Chatzivasileiadis *et al.*, 1999).

We hypothesized that the differential levels of nightshade preference by *T. evansi* are partially associated with the plant's trichome-based physical resistance. We tested this hypothesis using laboratory assays to study the influence of trichomes in different African nightshade species on a biological and a behavioural response of *T. evansi*.

Materials and methods

Plant material

The African nightshade species evaluated included *S. sarrachoides* (GBK 028726), which was obtained from the Gene Bank, Kenya, and *Solanum villosum* Miller (MW 13), *Solanum scabrum* Miller (SS 52), *Solanum americanum* Miller (SA) and *Solanum tarderemotum* Bitter (MW 03) that were sourced from the World Vegetable Centre (AVRDC, Arusha, Tanzania). To produce seedlings, seeds were sown in soil enriched with compost in plastic seedling trays kept in a greenhouse at the International Centre of Insect Physiology and Ecology (icipe), Nairobi, Kenya. The greenhouse temperature was monitored using a HOBO Pro Series Temp, relative humidity (RH) data logger (www.onsetcomp.com). The daily average temperature in the greenhouse during the experiments was 23 ± 1°C and 60–70% RH. Seedlings were transplanted into pots (29 cm in diameter) filled with a mixture of soil, compost and sand (3:2:1, v/v) 28 days after sowing. Plants were watered daily and each pot was fertilized with 3 g calcium ammonium nitrate (26% N) 2 weeks after transplanting.

Mites

Mites used in this study were sourced from a colony maintained on potted tomato plants (variety Moneymaker obtained from the East African Seed Company, Nairobi, Kenya), in a rearing room at a temperature of 25 ± 1°C, 50–70% RH and 12 h photoperiod.

Trichome identification and quantification

Twelve fully expanded young leaves were collected at random from 4-week-old plants of each respective nightshade species. Photographs of fully expanded leaves were taken with a 25× light microscope (Leitz Orthoplan; Leitz GmbH, Wetzlar, Germany) along the midrib. Identification and classification of the trichomes was made based on the presence or absence of glands according to the criteria established by Luckwill (1943) to classify trichomes in *Lycopersicon* spp. Trichome counts were made under a 32× dissecting microscope (Leica MZ8; Leica Microsystems, Wetzlar, Germany) fitted with a square grid to assist in counting. Ten squares (each 0.11 mm^2) were selected at random on the abaxial surface of each leaf. Densities were expressed as the number of trichomes/mm^2. Three replicates each with 36 leaves were carried out for respective plant species.

Effect of trichomes on mite fecundity

Fecundity tests were carried out on leaf disks of the same age as leaves on which the number of trichomes was counted and representing each investigated species. Four leaf disks (25 mm in diameter) of the respective species were maintained individually in one Petri dish (86 mm in diameter) stacked with cotton wool moistened with tap water and placed into plastic trays (36 × 23 × 2.3 cm). A single female deutonymph and two males were carefully picked from the colony and transferred to the respective leaf disks for oviposition. These rearing units were placed in an incubator maintained at 25 ± 1°C, 70–80% RH and a 12 h photoperiod. Males were removed 48 h later, after the female had emerged. The number of eggs laid per female was monitored daily during the first 10 days of the oviposition period. The leaf disks were changed every 4 days. A total of five replicates, each with 20 deutonymphs, were evaluated for each plant species.

Effect of trichomes on mite movement

The effects of trichomes on various African nightshade species on *T. evansi* movement were quantified with a no-choice thumbtack bioassay modified from that described by Weston and Snyder (1990). Young leaves of the respective species whose trichome density had previously been determined were used. One leaf of each species was attached to a board of Styrofoam® through a metallic thumbtack (9 mm in diameter) placed at the centre of its abaxial surface. One replicate consisted of four leaves of each species individually placed on the Styrofoam® boards. Ten female spider mites were transferred with a fine camel-hair brush to the head of each thumbtack. The trial was carried out on a laboratory bench at 23 ± 1°C. Distances travelled by each mite onto the leaf surface were measured as the shortest distance (in cm) between the mite and the thumbtack edge, and were recorded after 15, 30, 45 and 60 min. Mites that stayed on the thumbtack were considered to have travelled a distance equal to zero. Three replicates, each with 40 spider mites, were carried out for each plant species.

Data analysis

Data on fecundity (number of eggs laid by female *T. evansi*) were analysed using a generalized linear model with a negative binomial error and logarithmic link. Leaf trichome density was log-transformed $\{\log_{10}(x+1)\}$ prior to analysis of variance. Data on distances travelled by mites onto the respective species after the specified time duration were analysed using two-way analysis of variance where effect of plant species, time and the interaction were evaluated. Means were separated by Tukey's honestly significant difference (HSD) test. Distances travelled by mites and eggs laid onto the respective species were correlated with trichome densities, respectively. All data analyses were implemented using R-Development-Core-Team (2011).

Results

Trichome identification and quantification

A morphological description of the five trichome types, identified based on the presence or absence of glands and length, is given in Table 1. The range in the length of glandular trichomes (types T, W) was < 0.1–5.0 mm, while non-glandular trichomes (types X, Y) were shorter in size with a range of < 0.1–0.8 mm. The head of the trichome types T and W is swollen in a glandular vesicle, although larger in the latter (Fig. 1A and B). Non-glandular type X, found in *S. scabrum* and *S. tarderemotum*, stands on a single stalk base, is pointed at the tip and also long and appressed (Fig. 1C and D). Trichome type Y, found in *S. villosum*, is also appressed but stands on a large stalk base (Fig. 1B). Significant differences in densities of both glandular and non-glandular trichomes were detected among the species (Table 2). The range of glandular trichome density was 4.5–30.8 trichomes/mm^2, while there

Table 1. Description of the trichome types identified in five African nightshade species

Trichome type+	Description
T	Slender, long, glandular hairs, 0.2–5.0 mm long, standing on a single stalk base, tip swollen in a small glandular vesicle. Highly abundant in *S. sarrachoides*
W	Short, glandular hairs, < 0.1 mm long, standing on a single and thin stalk base, tip swollen in a large glandular vesicle. Sparsely distributed in *S. sarrachoides*, *S. villosum*, *S. tarderemotum* and *S. scabrum*
X	Non-glandular 0.1–0.8 mm long, tip pointed, standing on a single stalk base. Sparsely distributed in *S. scabrum* and *S. tarderemotum*
Y	Non-glandular appressed hairs, 0.4–0.8 mm long, tip pointed, standing on a large stalk base. Abundant in *S. villosum*

+ T, W, X and Y refer to randomly assigned letters to the identified trichome types.

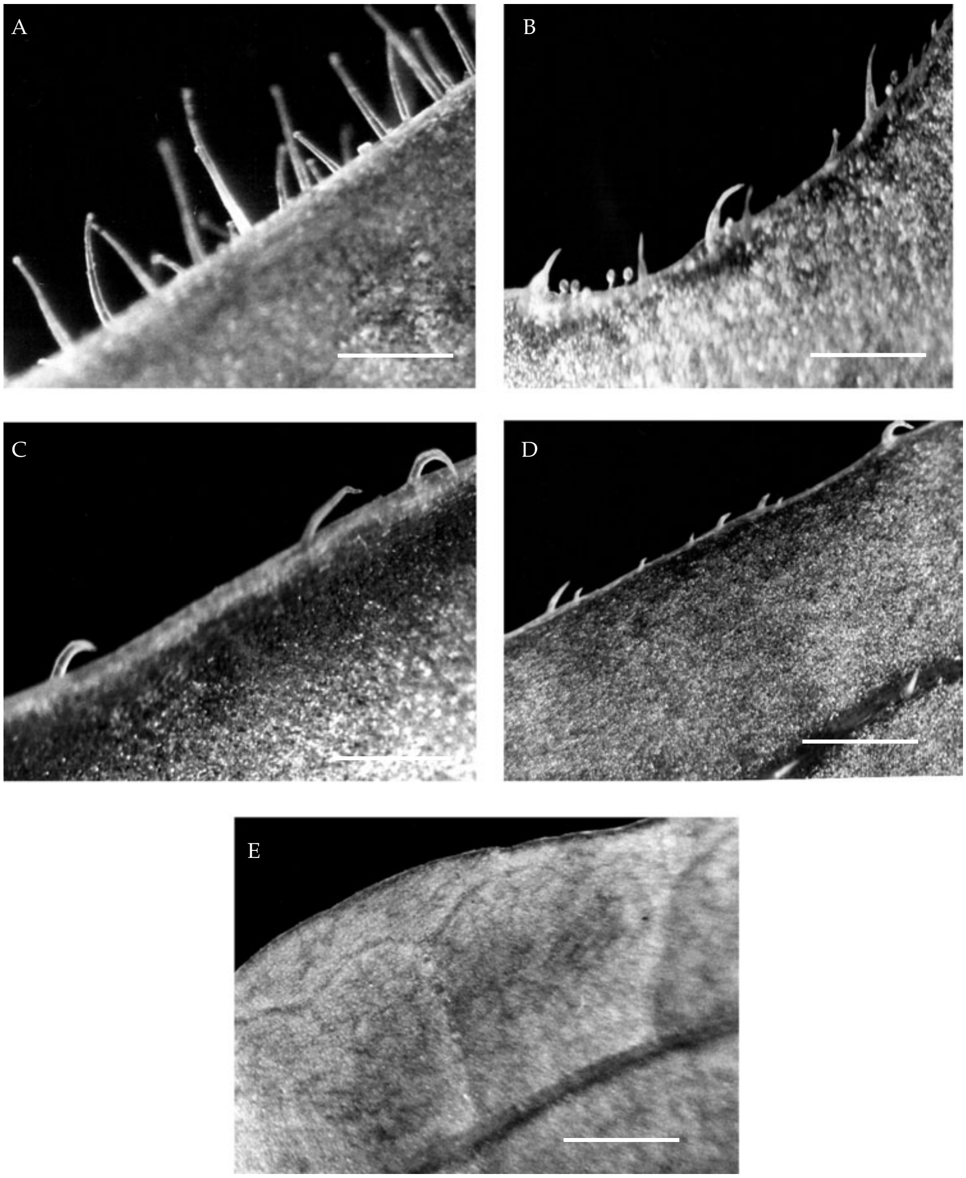

Fig. 1. Trichomes on the leaves of various *Solanum* species. A, *S. sarrachoides*, long glandular trichomes, type T; B, *S. villosum*, short glandular hairs, type W and non-glandular hairs, type Y; C, *S. scabrum*, non-glandular hairs, type X; D, *S. tarderemotum*, non-glandular hairs, type X; E, *S. americanum* is completely glabrous. Scale bars: A, 3000 μm; B, 100–600 μm; C, 700 μm; D, 300 μm; E, no trichomes.

was a narrower distribution of non-glandular trichomes with a range of 2.7–13 trichomes/mm^2. The highest number of glandular and non-glandular trichomes was recorded in *S. sarrachoides* (30.8 trichomes/mm^2) and *S. villosum* (13 trichomes/mm^2), respectively (Table 2).

Mite fecundity

Significant differences in the number of eggs laid per female within 10 days on various plant species were detected, with *S. sarrachoides* having the least number (Table 2). Correlation analysis revealed that the density of glandular hairs (types T, W) negatively affected fecundity ($r = -0.68$; $P = 0.001$). In contrast, the correlation between the density of non-glandular hairs and fecundity was not significant ($r = 0.08$; $P = 0.73$).

Mite movement

Significant differences in the distance walked by mites on various plant species were detected (Table 3). This indicates that repellence was highest

Table 2. Fecundity of *Tetranychus evansi* females and trichome density (number of trichomes/mm^2) in five *Solanum* species

Plant species	Fecundity (no. of eggs/female)	Trichome density/mm^2 Glandular[1,2] (types T, W)	Trichome density/mm^2 Non-glandular[2,3] (types X, Y)
S. sarrachoides	9.8 ± 2.02a	1.5 (30.8)a	0.0 (0.0)c
S. villosum	35.4 ± 5.91b	0.7 (4.8)b	1.2 (13.0)a
S. scabrum	57.4 ± 9.21b	0.8 (6.2)b	0.6 (2.7)b
S. tarderemotum	55.0 ± 8.85b	0.7 (4.5)b	0.7 (3.9)b
S. americanum	48.0 ± 7.80b	0.0 (0.0)c	0.0 (0.0)c
	Deviance (χ^2) = 53.7	SE = 0.075	SE = 0.045
	$P < 0.0001$	$F_{4,15} = 50.2$	$F_{4,15} = 117.9$
		$P < 0.001$	$P < 0.001$

Mean values with the same letter within a column are not significantly different (Tukey's HSD test; $\alpha = 0.05$).
[1] With 'heads'.
[2] Values in parentheses are untransformed means of trichome density.
[3] With no 'heads'.

on *S. sarrachoides* leaves and lowest on *S. scabrum*. However, different time durations and their interaction with the various species did not reveal any significant differences (Table 3). Correlation analysis showed that glandular trichome density reduced the distance travelled at 15 and 45 min, whereas there was no apparent relationship with non-glandular types (Fig. 2).

Discussion

The results of this study demonstrate that nightshade species may differentially influence *T. evansi* reproduction and movement on the leaf surface. Mite fecundity and distance travelled were negatively correlated with densities of glandular trichomes (types T, W), suggesting that resistance by the African nightshade species to *T. evansi* is associated with the plant's morphology. This concurs with Rasmy (1985) who reported that high densities of glandular trichomes deterred the oviposition of *T. urticae* on *Lycopersicon hirsutum* var. *glabratum* C.H. Mull, and on *S. sarrachoides* compared with the cultivated tomato *L. esculentum*. In addition, Maluf *et al.* (2007) reported that higher densities of glandular trichomes decreased distances walked by mites onto the leaf surface of interspecific crosses of *Lycopersicon* spp. Recently, Alba *et al.* (2009) also found an association between glandular trichomes of a population of recombinant inbred lines of tomato species and two-spotted spider mite resistance.

Reports on the role of non-glandular trichomes in resistance to arthropods are rare (Simmons and Gurr, 2005). In this study, we found that the density of non-glandular trichomes (types X, Y) associated with *S. scabrum*, *S. villosum* and *S. tarderemotum* was not significantly correlated with the movement and

Table 3. Average distance (in cm) travelled by *Tetranychus evansi* females on the abaxial leaf surface of five selected African nightshade species for a given period of time

Plant species	Time (min) 15	30	45	60	Mean
S. sarrachoides	0.19	0.22	0.27	0.30	0.24c
S. villosum	3.35	3.36	3.27	3.25	3.31b
S. scabrum	4.65	5.10	5.10	5.09	4.99a
S. tarderemotum	2.97	3.29	3.53	3.54	3.33b
S. americanum	2.58	2.81	2.34	3.07	2.70b
Mean	2.75	2.96	2.90	3.05	
SE of means					
Time = 0.26		$F_{3,40} = 0.25$	$P = 0.86$		
Plant species = 0.27		$F_{4,40} = 36.19$	$P < 0.0001$		
Time × plant species = 0.57		$F_{12,40} = 0.11$	$P = 0.999$		

Mean values with the same letter within a column are not significantly different (Tukey's HSD test; $\alpha = 0.05$).

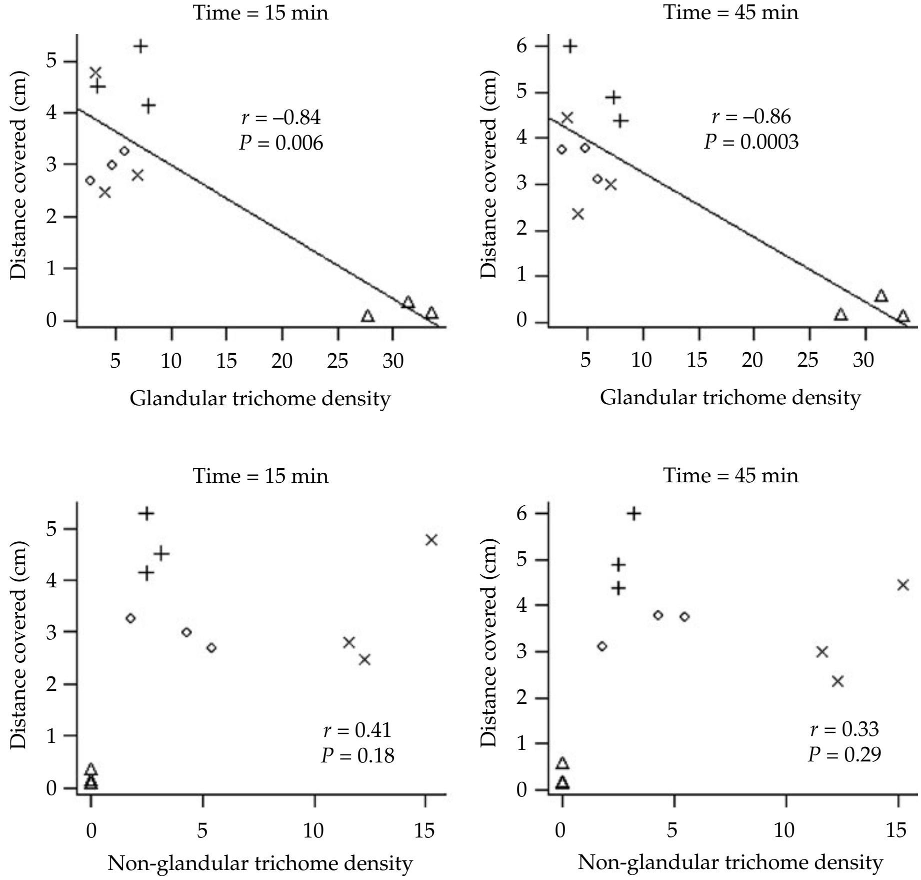

Fig. 2. Correlation between distances covered (cm) by *Tetranychus evansi* females and trichome density (trichomes/mm^2) in *Solanum* species. △, *S. sarrachoides*; +, *S. scabrum*; ×, *S. tarderemotum*; ◇, *S. villosum*

fecundity of *T. evansi*. Previous research has reported a positive effect of non-glandular trichomes (type V) on the larval survival of *T. evansi* in *L. esculentum* var. 'Money Maker' (Wosula *et al.*, 2009) and also a positive correlation between type V trichomes and larval survival of the potato tuber moth *Phthorimaea operculella* (Zeller), in *L. hirsutum* (Gurr and McGrath, 2002). However, Simmons and Gurr (2005) reported that this finding could possibly be an artefact, since plants with a high density of these non-glandular trichomes typically have a lower density of glandular trichomes (types IV and VI) and vice versa. Coincidentally, in our study, we found that *S. sarrachoides* had a high density of glandular trichomes but lacked non-glandular trichomes. Likewise, *S. scabrum*, *S. villosum* and *S. tarderemotum* lacked or had lower densities of glandular trichomes but higher densities of non-glandular trichomes. Contrary to these reports, experiments with beach strawberry cultivars *Fragaria chiloensis* L. (Mill.) (Rosaceae) revealed a negative correlation between non-glandular trichome densities and resistance against *T. urticae* (Luczynski *et al.*, 1990). The authors also reported a decrease in the number of eggs laid by *T. urticae* with an increase in the density of non-glandular trichomes.

Although some pests prefer hairy surfaces for oviposition, previous studies have reported a lower resistance to spider mites in glabrous leaves of petunia ecotypes (Griesbach *et al.*, 2002; Simmons and Gurr, 2005). In the present study, *S. americanum*, which is completely glabrous, compared favourably with *S. scabrum*, *S. villosum* and *S. tarderemotum*, which had a rather low density of trichomes, in relation to mite movement and fecundity. Mites walked freely on the leaf surface and oviposition was high, suggesting that *S. americanum* has a lower level of resistance to spider mite damage similar to those that had non-glandular hairs.

Conclusion

Results of the present study suggest that glandular trichome density may form a basis for the selection of African nightshade genotypes with higher resistance to spider mites. Since this study was conducted under laboratory conditions, further research is required to establish whether these African nightshade species affect reproduction and movement of mites when grown under greenhouse and field conditions. Furthermore, an evaluation of the effect of trichome chemistry on the plant–arthropod interaction as well as the organoleptic properties of these African nightshade species for consumer satisfaction is recommended.

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