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Effects of the invasive tomato red spider mite (Acari: Tetranychidae) on growth and leaf yield of African nightshades

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ABSTRACT

The tomato red spider mite, *Tetranychus evansi* Baker and Pritchard, is one of the most serious pests of solanaceous crops in Africa. Field experiments were conducted to investigate its effects on the growth and leaf yield of five African nightshade species viz. *Solanum americanum*, *S. sarrachoides*, *S. scabrum*, *S. tarderemotum* and *S. villosum* during the 2008 and 2009 growing seasons. Plants were infested with 2–4 day-old female spider mites which were allowed to multiply. The number of mite motiles increased throughout the growing season in unsprayed plots and this number varied significantly between the African nightshade species. Except for *S. sarrachoides*, leaf damage was high on the other four *Solanum* species irrespective of the spraying regime during both seasons. However, *S. scabrum* had a significantly greater leaf area ratio (ratio of leaf area to total plant weight) and specific leaf area (ratio of leaf area to total leaf dry weight) during both seasons. Overall yields were 1.5 times more in *S. scabrum* and *S. sarrachoides* compared to *S. americanum*, *S. tarderemotum* and *S. villosum*. Our results show that *T. evansi* infestation affects the leaf area ratio and specific leaf area of African nightshade species differentially which eventually determines the plant's overall leaf yield. These findings present an opportunity for evaluation and selection of African nightshade species that can withstand spider mite infestation in small holder farms for increased vegetable production in Africa.

1. Introduction

African nightshades (Solanaceae) comprise closely related leafy species which are grouped together in the '*Solanum nigrum*' complex (Edmonds and Chweya, 1997). Part of this group includes *Solanum americanum* Miller, *S. sarrachoides* Sendtner, *S. scabrum* Miller, *S. tarderemotum* Bitter and *S. villosum* Miller, which are consumed widely in parts of eastern and southern Africa as indigenous leafy vegetables (Schippers, 2000). Despite their role in food nutritional security (Grubben and Denton, 2004), African nightshades suffer severe damage from various arthropod pests (Fontem and Schippers, 2004; Rosa et al., 2005; Murungi et al., 2010). One of the most serious pests of solanaceous crops in Africa is the tomato red spider mite, *Tetranychus evansi* Baker and Pritchard. Spider mites feed by penetrating the leaf surface with their stylets and suck out the cell contents (Tomczyk and Kropczyńska, 1985). This leads to a reduction in the total chlorophyll content and net photosynthetic rate of leaves (Park and Lee, 2005) causing crop losses of up to 90% (Sibanda et al., 2000).

Laboratory studies have reported differential suitability of the five African nightshade species as hosts for *T. evansi* (Murungi et al., 2010). Of the five species, only *S. sarrachoides* negatively affected the intrinsic rate of increase and doubling time of *T. evansi*. However, little is known about the interaction of *T. evansi* and its effects on growth and productivity of African nightshades under field conditions. In this study, we present data from two field experiments showing that African nightshades have distinct yield differences as a result of *T. evansi* infestation, which is influenced by the plant's growth parameters (Hunt, 1990).

Abbreviations: RGR, Relative growth rate; ULR, Unit leaf rate; LAR, Leaf area ratio; SLA, Specific leaf area; LWR, Leaf weight ratio; REML, Restricted maximum likelihood.

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2. Materials and methods

2.1. Study site

Field experiments were conducted at the Jomo Kenyatta University of Agriculture and Technology (JKUAT) farm in Juja, Kenya (latitude 0° 10′ 48′ S, longitude 37° 07′ 12′ E, altitude 1525 m above sea level) during September to November, 2008 (Season I) and February to April, 2009 (Season II) to investigate the interaction of five African nightshade species and *T. evansi* populations. During both seasons, *S. sarrachoides* (accession number; GBK 028726), which was obtained from the Gene Bank, Kenya and *S. villosum* (accession number; MW 13), *S. scabrum* (accession number; SS 52), *S. americanum* (accession number; SA) and *S. tarderemotum* (accession number; MW 03) that were obtained from the World Vegetable Centre (AVRDC, Arusha, Tanzania) were used. Conditions at the study sites were as follows: soil: pH 6.4–6.8; N: 90–95 mg l^{-1}; weather: temperature 21–22 °C; relative humidity 70–73% were measured at JKUAT and Thika meteorological station (latitude 0° 59′ S, longitude 37° 04′ E, altitude 1548 m above sea level).

2.2. Treatments and experimental layout

Experiments were laid out as a split plot in a randomized complete block design with three replicates (Fig. 1). Main plots consisted of the spraying regimes at two levels; one sprayed with an acaricide (Abamectin 1.8%) purchased from a local agrochemical store in Nairobi, Kenya and the other was left unsprayed. Sub-plots consisted of the five species of African nightshade. Each subplot measured 2 m × 2 m with a 2.7 m distance between them and an inter- and intra-row plant spacing of 30 cm × 30 cm. A 2 m empty strip was left between the main plots to prevent any drift of acaricide spray which was applied at a rate of 0.5 ml l^{-1} of water using a knapsack sprayer fitted with a hollow cone nozzle.

2.3. Crop establishment

Seedlings of the respective African nightshade species were established in a greenhouse (temperature 23 ± 1 °C; relative humidity 60–70%) as previously described (Murungi et al., 2010). These plant species were transferred at the five leaf stage into polythene bags (5 cm in width × 15 cm in depth) filled with a mixture of soil: manure (3:1 v/v) and placed outside under a shade for three weeks to acclimatize to the field conditions. Plants were watered daily and fertilized only during the second week with 1.5 g of NPK plant^{-1}. Three weeks later, the plants were taken to the field and planted into treatment plots in a random manner for each species. The plants were watered daily and weeded on a weekly basis. After two weeks, 3 g of calcium ammonium nitrate (26% N) was applied to each plant.

2.4. Mites

Mites, *T. evansi*, were obtained from a colony maintained on tomato plants (variety ‘Money Maker’) in a rearing room at the International Centre of Insect Physiology and Ecology (*icipe*) at a temperature of 25 ± 1 °C, relative humidity 60–70% and 12:12 light: dark photoperiod.

2.5. Spider mite counts and damage assessment

Scouting for natural *T. evansi* infestation on African nightshade species was done on a weekly basis for three consecutive weeks after transplanting. Since no mites were found on the plants, artificial infestations were initiated. Tomato leaves that were heavily infested with two to four day-old young females of *T. evansi* were excised from the colony at *icipe* and transferred to JKUAT in ‘khaki’ envelopes placed in a cool box. Infestations were established by placing four tomato leaflets on the adaxial leaf surface of respective African nightshade species. Counting the number of mites began 14 days after infestation and continued at seven day intervals for six consecutive weeks. Three leaves were individually removed from the top, middle and bottom levels of respective plants, placed into khaki paper bags in cool boxes packed with ice and taken to the laboratory for processing. The motile stages namely, larvae, nymphs and adults were counted on both sides of the leaf under a dissecting microscope (×25). Leaf damage rating followed a method previously described (Hussey and Parr, 1963) on a scale of 0–5 where 0 = no damage, 1 = 0–20%, 2 = 20–40%, 3 = 40–60%, 4 = 60–80% and 5 = 80–100% damage.

2.6. Plant growth and yield analysis

Plants that were sampled for mite counts were harvested, placed into labeled polythene bags in cool boxes packed with ice and taken to the laboratory for processing. All the above ground parts including leaves, flowers, fruits and stems of each species were separated. Fresh weight of all leaves was determined using a weighing balance including those assessed for spider mite damage.

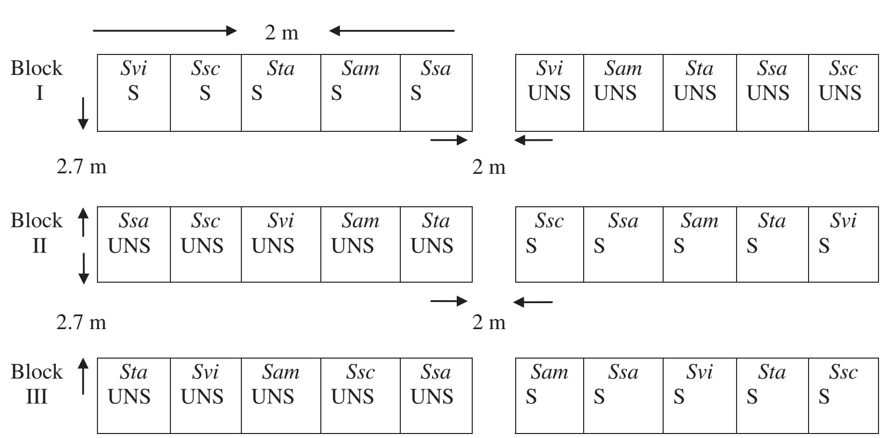

Fig. 1. Arrangement of main plots and sub-plots in the field season during season I and season II. *Svi* = *S. villosum*; *Ssc* = *S. scabrum*; *Sta* = *S. tarderemotum*; *Sam* = *S. americanum*; *Ssa* = *S. sarrachoides*; S = sprayed; UNS = unsprayed.

Plant parts of each African nightshade species were oven dried at 50 °C for a week upon which the dry weight was determined. The leaf area (in cm^2) was measured with a LI-COR Li-3000 leaf area meter (LI-COR, Lincoln, NE).

2.7. Statistical analysis

Mite counts were $\log_{10}$-transformed before analysis to ensure homogeneity of variance and normality of errors. To account for correlations and possible heterogeneous variances among observations taken on the same plot over time, a linear mixed model with random intercept was fitted to the data using the *lmer* function in R2.15.2 from the *lme4* package (Bates et al., 2013). The model was fitted using restricted maximum likelihood (REML) and factor effects were tested using Wald chi-square tests. The species, week and their interaction were considered as fixed effects and plot as the random effect. The analysis was done separately for the sprayed and unsprayed plots. Leaf damage scores were converted to percentage damage based on the definition of each damage score and percentage midpoints calculated. The percentages obtained were angular transformed prior to analysis of variance for split plot. Results at 42 days after transplanting (DAT), when damage was highest, are presented. Plant growth parameters namely relative growth rate, unit leaf rate, leaf area ratio, specific leaf area and leaf weight ratio were estimated by dry weights of one harvest interval (first and final harvest) using the software developed by Hunt et al. (2002). Mean estimates, their standard errors and 95% confidence limits for respective plant species per season and spraying regime are presented. The fresh weight of harvested leaves per plot was subjected to analysis of variance. Since there was no significant interaction between season and plant species ($P = 0.073$), means of respective plant species per spraying regimes are presented.

3. Results

3.1. Population dynamics of mites

3.1.1. Unsprayed plots

Spider mite populations increased throughout the growing season (Fig. 2a and b) and there were highly significant differences between the African nightshade species in Season I ($\chi^2 = 130.2$; df = 4; $P = <0.0001$) and season II ($\chi^2 = 101.0$; df = 4; $P = <0.0001$).

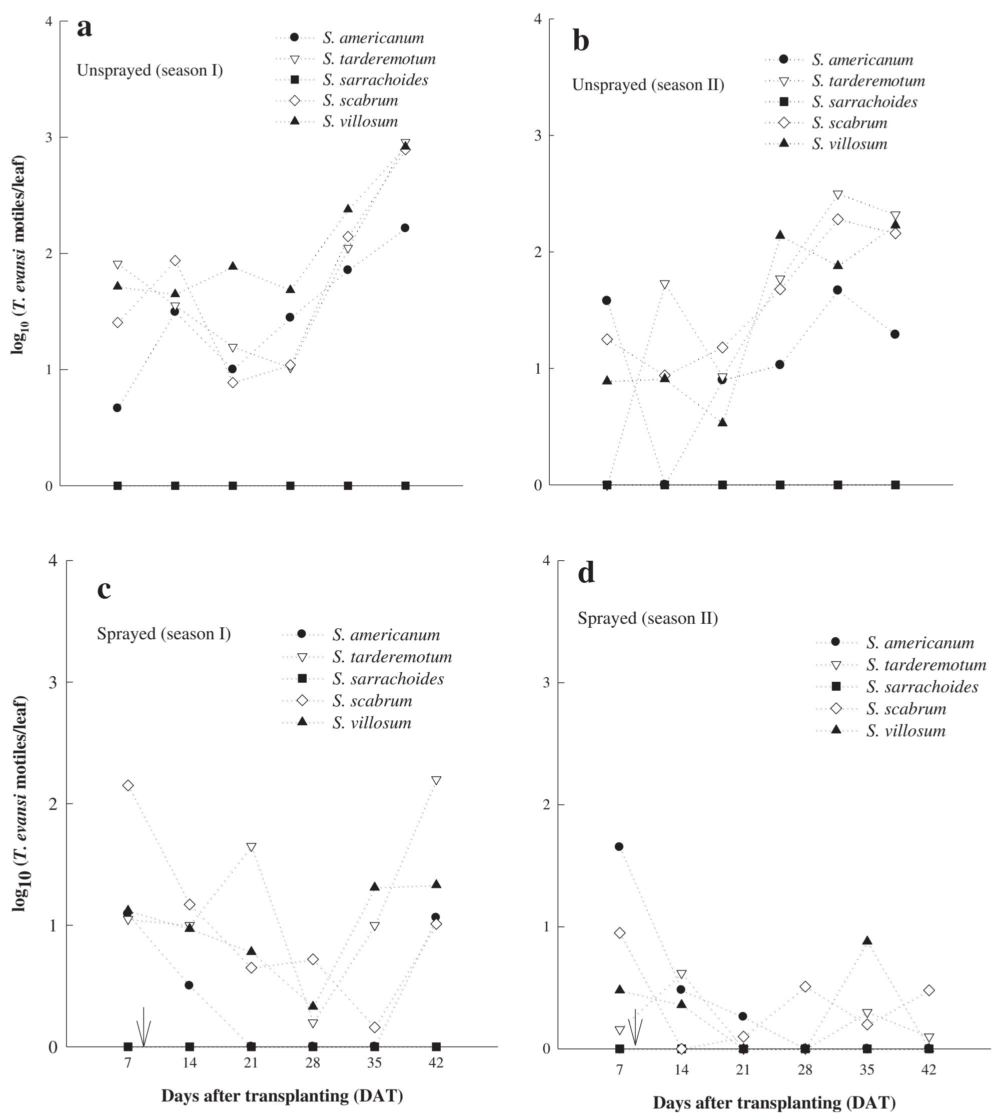

Fig. 2. Motile individuals of *Tetranychus evansi* per leaf on different African nightshade species in unsprayed and sprayed plots during 2008 (season I) and 2009 (season II): (a) unsprayed season I; (b) unsprayed season I; (c) sprayed season I; and (d) sprayed season II. Arrows indicate the point of acaricide spray application.

There was a significant interaction between days after transplanting (DAT) and plant species in season II ($\chi^2 = 19.69$; df = 4; $P = <0.0001$) but not in season I ($\chi^2 = 6.53$, df = 4, $P = 0.16$). However, the linear time effect was significant in both season I ($\chi^2 = 24.34$; df = 1; $P = <0.0001$) and season II ($\chi^2 = 42.9$; df = 1; $P = <0.0001$) with a remarkable increase in spider mite population on *S. americanum*, *S. scabrum*, *S. villosum* and *S. tarderemotum* at 28 DAT. *T. evansi* did not colonize and/or reproduce on *S. sarrachoides* throughout the growing season (Fig. 2a and b).

3.1.2. Sprayed plots

After spraying plants with an acaricide, significant variation in mite numbers between species was recorded in season I ($\chi^2 = 26.6$; df = 4; $P = <0.0001$), but not in season II ($\chi^2 = 5.41$; df = 4; $P = 0.25$) (Fig. 2c and d). A significant interaction between DAT and plant species was recorded in season II ($\chi^2 = 14.07$; df = 4; $P = <0.007$) but not in season I ($\chi^2 = 5.93$, df = 4, $P = 0.204$). Similarly, a linear time effect was significant only in season II ($\chi^2 = 9.59$, DF = 1, $P = 0.001$) with mite populations decreasing to zero in *S. scabrum* at 21 DAT, *S. americanum* at 28 DAT and *S. tarderemotum* and *S. villosum* at 42 DAT (Fig. 2d). Similar to unsprayed plots, *S. sarrachoides* was free of *T. evansi* infestation throughout the growing season (Fig. 2c and d).

3.2. Levels of leaf damage

Plant species showed a significant differential leaf damage in season I ($F_{4,16} = 11.85$; $P = <0.001$) and season II ($F_{4,16} = 16.0$; $P = <0.001$) although main effects of the spraying regime and their interaction with the plants were significant only in season II (Table 1). Leaf damage was highest on *S. tarderemotum* while there was no damage on *S. sarrachoides*. As expected, sprayed plants had markedly lower leaf damage compared to their unsprayed counterparts (Table 1).

3.3. Plant growth analysis

The parameters of plant growth are reported (Table 2). The relative growth rate (RGR) defines the dry weight increase per unit time, providing an overall index of plant growth. RGR did not vary significantly among species in season I which ranged between 0.03–0.06 g day^{-1} and 0.04–0.08 g day^{-1} in unsprayed and sprayed plots respectively. A similar trend was observed in season II with the RGR ranging between 0.03–0.06 g day^{-1} and 0.04–0.05 g day^{-1} in unsprayed and sprayed plots respectively. The unit leaf rate (ULR) defines the rate of increase in dry weight per unit leaf area. ULR did not also vary significantly between the species with values ranging between 0.01 and 0.03 cm^2 g^{-1} day^{-1} within the spraying regimes (Table 2).

The leaf area ratio (LAR) is the ratio of leaf area and total plant weight which indicates the fraction of plant weight allocated to the leaves. LAR differed significantly between the species in season I and II. Except for *S. scabrum*, LAR was relatively high in *S. americanum*, *S. sarrachoides*, *S. tarderemotum* and *S. villosum* in season I compared to season II when mite populations in these species were low. *S. scabrum* had significantly high LAR in both spraying regimes relative to other *Solanum* species in sprayed plots in season I and in both spraying regimes in season II. The Specific leaf area (SLA) measures the leaf area of a plant on the basis of total dry weight. SLA of *S. scabrum* was significantly greater than other *Solanum* species in sprayed plots in season I and unsprayed plots in both season I and II which ranged between 6.84–87.10 cm^2 g^{-1} and 7.84–46.5 cm^2 g^{-1} in unsprayed and sprayed plots respectively (Table 2). Leaf weight ratio (LWR) measures the leaf area of a plant on the basis of total dry weight of the plant. Although LWR did not vary significantly between the species, it was generally high in season I when mite populations were high in both unsprayed and sprayed plots (Table 2).

3.4. Fresh leaf yield

There were significant differences between the African nightshade species ($F_{4,38} = 26.06$; $P = <0.001$) in the overall weight of harvested fresh leaves (Table 3). However, there was no significant interaction between spraying regime and plant species ($F_{4,38} = 0.91$; $P = 0.470$) and the main effects of spraying regime ($F_{1,38} = 0.27$; $P = 0.607$) on overall fresh leaf yield. *S. scabrum* and *S. sarrachoides* had more than 1.5 times higher leaf yield compared to *S. americanum*, *S. tarderemotum* and *S. villosum* (Table 3).

4. Discussion

The economic damage caused by *T. evansi* populations depend primarily on the interactions with the growth of the host plant. In this study, the interaction between *T. evansi* infestation and the growth and productivity of African nightshades was investigated under field conditions. It was established that season and spraying regimes influenced *T. evansi* populations, but there was a distinction on how the African nightshades species responded in terms of leaf damage, plant growth and productivity. While *S. sarrachoides* did not support growth of any *T. evansi* populations throughout the crop growing seasons, *T. evansi* reproduced and multiplied on *S. americanum*, *S. scabrum*, *S. tarderemotum* and *S. villosum* causing significant leaf damage. This differential preference was partially associated with the high density of long glandular trichomes found in *S. sarrachoides* that interfere with *T. evansi* movement and hence slow its intrinsic rate of increase (Murungi et al., 2011).

When the overall leaf yield of African nightshade species was compared in both sprayed and unsprayed plots, *S. scabrum* compared favorably with *S. sarrachoides* suggesting that other plant factors play a role in *T. evansi*-African nightshade interactions (Georg and Gregg, 2008). For instance, LAR was predominantly high in *S. scabrum* compared to the other *Solanum* species indicating that the photosynthetic efficiency of *S. scabrum* is higher to compensate for leaf damage by *T. evansi*. The SLA of *S. scabrum* followed a similar trend suggesting further that this species has a high energy balance which compared favorably to the productivity of mite-free *S. sarrachoides*. Moreover, *S. americanum*, *S. tarderemotum* and *S. villosum* may require a higher leaf area to produce the same.

Table 1
Angular transformed percentage leaf damage (%) of African nightshades by *Tetranychus evansi* at 42 days after transplanting in season I and season II.

Plant species	Season I			Season II		
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean
S. tarderemotum	53.2	40.3	46.8a	2.5	46.3	24.4a
S. villosum	23.3	44.2	33.8ab	0.0	37.7	18.8a
S. scabrum	23.0	32.3	27.6b	2.5	35.5	19.0a
S. americanum	22.1	30.1	26.1b	0.0	22.0	11.0b
S. sarrachoides	0.0	0.0	0.0c	0.0	0.0	0.0c
Mean	24.3b	29.4a		1.0a	28.3b	
SE of means						
Plant species = ±4.96; $F_{4,16} = 11.85$; $P = <0.001$				Plant species = ± 2.37; $F_{4,16} = 16.00$; $P = <0.001$		
Spraying regime = ±12.29; $F_{1,16} = 0.09$; $P = 0.0798$				Spraying regime = ± 0.59; $F_{1,16} = 1078.84$; $P = <0.001$		
Regime × species = ±13.80 $F_{4,16} = 1.58$; $P = 0.227$				Regime × species = ±3.03; $F_{4,16} = 13.22$; $P = <0.001$		

Means followed by the same letter are not significantly different; Student Newman Keuls test, $\alpha = 0.05$.

Table 2
Relative growth rate, unit leaf rate, leaf area ratio, specific leaf area and leaf weight ratio of African nightshade species in unsprayed and sprayed plots during 2008 (season I) and 2009 (season II) growing seasons. Values in parenthesis indicate 95% confidence limit.

Spraying regime	Plant species	Season	Relative growth rate (g day^{-1})	Unit leaf rate (cm^2 g^{-1} day^{-1})	Leaf area ratio (cm^2 g^{-1})	Specific leaf area (cm^2 g^{-1})	Leaf weight ratio
Unsprayed	*S. americanum*	I	0.06 ± 0.02 (0.06)	0.01 ± 0.01 (0.02)	15.20 ± 9.01 (25.02)	26.24 ± 11.50 (31.94)	0.50 ± 0.18 (0.50)
		II	0.04 ± 0.01 (0.03)	0.02 ± 0.01 (0.03)	3.99 ± 1.40 (3.89)	10.51 ± 3.92 (10.91)	0.31 ± 0.05 (0.16)
	S. sarrachoides	I	0.03 ± 0.02 (0.07)	0.01 ± 0.00 (0.01)	16.70 ± 7.6 (21.10)	28.30 ± 15.20 (42.26)	0.65 ± 0.36 (1.00)
		II	0.03 ± 0.02 (0.07)	0.02 ± 0.01 (0.03)	2.63 ± 2.01 (5.59)	6.84 ± 4.91 (13.65)	0.41 ± 0.27 (0.74)
	S. scabrum	I	0.05 ± 0.01 (0.02)	0.01 ± 0.00 (0.00)	23.93 ± 12.3 (34.16)	39.70 ± 17.01 (47.37)	0.51 ± 0.09 (0.25)
		II	0.06 ± 0.02 (0.04)	0.01 ± 0.00 (0.00)	45.36 ± 20.97 (93.74)	87.10 ± 68.19 (189.32)	0.40 ± 0.15 (0.42)
	S. tarderemotum	I	0.05 ± 0.02 (0.06)	0.01 ± 0.01 (0.03)	12.80 ± 1.65 (4.59)	24.85 ± 7.18 (19.93)	0.50 ± 0.21 (0.59)
		II	0.06 ± 0.02 (0.06)	0.04 ± 0.01 (0.04)	3.60 ± 3.19 (8.88)	7.80 ± 3.50 (9.72)	0.41 ± 0.27 (0.75)
	S. villosum	I	0.05 ± 0.03 (0.08)	0.01 ± 0.01 (0.03)	15.42 ± 10.71 (29.72)	25.33 ± 16.91 (46.95)	0.58 ± 0.32 (0.09)
		II	0.04 ± 0.01 (0.03)	0.02 ± 0.01 (0.03)	3.82 ± 1.69 (4.68)	9.79 ± 4.36 (11.82)	0.33 ± 0.08 (0.21)
Sprayed	*S. americanum*	I	0.07 ± 0.02 (0.07)	0.03 ± 0.02 (0.04)	13.50 ± 8.80 (24.42)	22.39 ± 14.90 (14.37)	0.54 ± 0.24 (0.68)
		II	0.04 ± 0.01 (0.04)	0.01 ± 0.01 (0.02)	3.12 ± 1.77 (4.92)	9.50 ± 4.28 (11.87)	0.30 ± 0.08 (0.24)
	S. sarrachoides	I	0.03 ± 0.03 (0.08)	0.01 ± 0.01 (0.02)	11.00 ± 7.81 (21.71)	17.40 ± 12.93 (35.90)	0.64 ± 0.38 (1.06)
		II	0.04 ± 0.01 (0.04)	0.01 ± 0.01 (0.02)	5.87 ± 1.83 (5.08)	15.30 ± 4.94 (13.72)	0.36 ± 0.13 (0.36)
	S. scabrum	I	0.08 ± 0.00 (0.01)	0.01 ± 0.01 (0.00)	32.4 ± 6.56 (18.21)	46.5 ± 7.87 (19.07)	0.54 ± 0.08 (0.22)
		II	0.05 ± 0.01 (0.04)	0.01 ± 0.00 (0.00)	37.72 ± 15.50 (42.97)	74.10 ± 22.83 (63.39)	0.40 ± 0.13 (0.35)
	S. tarderemotum	I	0.04 ± 0.02 (0.07)	0.01 ± 0.01 (0.02)	16.01 ± 9.16 (33.51)	27.15 ± 10.48 (54.85)	0.58 ± 0.27 (0.76)
		II	0.05 ± 0.02 (0.06)	0.03 ± 0.01 (0.03)	3.15 ± 2.13 (5.92)	7.84 ± 4.23 (11.77)	0.40 ± 0.22 (0.63)
	S. villosum	I	0.05 ± 0.01 (0.04)	0.01 ± 0.00 (0.01)	13.90 ± 7.11 (19.75)	21.75 ± 11.80 (32.83)	0.60 ± 0.22 (0.62)
		II	0.04 ± 0.01 (0.03)	0.02 ± 0.00 (0.01)	3.89 ± 1.17 (3.26)	9.39 ± 2.04 (5.67)	0.34 ± 0.07 (0.21)

Values in parenthesis indicate 95% confidence limit.

These results are in agreement with those of (Poorter and Remkes, 1990) who reported a high variation in productivity of non-woody plants which is largely influenced by the differences in SLA.

The fact that LAR was mainly high in *S. americanum*, *S. tarderemotum* and *S. villosum* in season I when mite populations were high compared to season II indicates that these species require more leaf area to produce the same amount of photosynthetic product as those grown in season II. Similarly, the SLA was higher in season I than in season II, indicating that the plants' dry weight per unit leaf area was less in these species due to high *T. evansi* infestation which significantly reduced their productivity. These results concur with those of Park and Lee (2005) who reported a higher LAR and SLA in cucumber plants injured by *Tetranychus urticae* compared to mite free plants which varied with the season. Seasonal differences in *T. evansi* populations and their subsequent effects on plant growth could be attributed to changes in environmental conditions in the field.

To the best of our knowledge, this study provides the first field evidence of the interaction between African nightshades and *T. evansi*. These results suggest that there is a clear difference in the photosynthetic efficiencies of the different African nightshade species with respect to relative growth rate and unit leaf rate. The fact that *S. scabrum* is high yielding irrespective of whether it is protected with an acaricide spray or not, while *S. sarrachoides* does not support *T. evansi* at all, demonstrate presence of modalities of host plant resistance described by Painter (1951). It appeared that tolerance to *T. evansi* damage through increased photosynthetic rate was evident in *S. scabrum*. Previous studies have reported high yields in maize cultivars that are tolerant to damage by *Heliothis zea* Boddie (Lepidoptera: Noctuidae) (Wiseman et al., 1972) and *Ostrinia nubinalis* Hübner (Lepidoptera: Pyralidae) (Hudon et al., 1979) due to presumably an increased biomass which raised the plants economic injury level. Whether the mechanisms underlying tolerance in maize cultivars and non-woody plants (Poorter and Remkes, 1990) are similar to those in African nightshades need to be investigated further.

In summary, these findings suggest the possibilities of exploiting the unique properties of different African nightshade species by selecting those that have the potential to yield highly yet withstand spider mite damage in the small holder farmers' field and consequently reduce synthetic acaricide use.

Table 3
Overall fresh weights (kg/plot of 4 m^2) of harvested leaves of African nightshade species in sprayed and unsprayed plots during 2008/2009 growing seasons.

Plant species	Spraying regime		
	Sprayed	Unsprayed	Mean
S. scabrum	26.15	22.05	24.10a
S. sarrachoides	25.22	26.68	25.95a
S. americanum	15.06	15.75	15.40b
S. tarderemotum	15.41	14.94	15.17b
S. villosum	13.65	13.46	13.55b
Mean	19.10b	18.58b	
SE of means			
Plant species = ±1.37; $F_{4,38} = 26.06$; $P = <0.001$			
Spraying regime = ±0.30; $F_{1,38} = 0.27$; $P = 0.607$			
Regime × Species = ±1.76; $F_{4,38} = 0.91$; $P = 0.470$			

Means followed by the same letter are not significantly different; Student Newman Keuls test, $\alpha = 0.05$.

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