Sources of Resistance for Two-spotted Spider Mite (*Tetranychus urticae*) in Scarlet (*Solanum aethiopicum* L.) and Gboma (*S. macrocarpon* L.) Eggplant Germplasms

Dalia Taher
World Vegetable Center, Headquarters, 60 Yi-Min Liao, Shanhua, Tainan 74151, Taiwan; and Vegetable Crops Research Department, Agriculture Research Center, Horticulture Research Institute, Giza, Egypt

Mohamed Rakha[1]
World Vegetable Center, Headquarters, 60 Yi-Min Liao, Shanhua, Tainan 74151; and Horticulture Department, Faculty of Agriculture, University of Kafrelsheikh, Kafr El-Sheikh 33516, Egypt

Srinivasan Ramasamy
World Vegetable Center, Headquarters, 60 Yi-Min Liao, Shanhua, Tainan 74151

Svein Solberg
World Vegetable Center, Headquarters, 60 Yi-Min Liao, Shanhua, Tainan 74151; and Inland Norway University of Applied Sciences, Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, 2401 Elverum, Norway

Roland Schafleitner
World Vegetable Center, Headquarters, 60 Yi-Min Liao, Shanhua, Tainan 74151

Additional index words. Choice assays, mite leaf damage, *Solanum aethiopicum*, *S. macrocarpon*, trichome

Abstract. **The two-spotted spider mite, *Tetranychus urticae*, is a serious global pest of eggplants and other vegetables in the tropics and subtropics. The scarlet (*Solanum aethiopicum* L.) and gboma (*Solanum macrocarpon* L.) are two cultivated eggplants indigenous to sub-Saharan Africa. In this study, 120 accessions of *S. aethiopicum* and five accessions of *S. macrocarpon* from the World Vegetable Center's genebank collection were evaluated for spider mite resistance based on leaf damage scores and trichome types and densities. The highest levels of resistance were detected in *S. macrocarpon* accessions VI050393 and VI050444. In addition, two accessions of *S. aethiopicum*, VI042749 and VI042753, were moderately resistant. All other *S. aethiopicum* accessions were susceptible or highly susceptible. Spider mite resistance was significantly associated with the presence of type VII glandular trichome, but nonglandular stellate trichomes were not associated with resistance. The resistant *S. macrocarpon* accessions can be directly used as resistant cultivars or in prebreeding programs aimed at breeding resistant lines of the most commonly cultivated eggplant (*S. melogena*).**

The scarlet (*Solanum aethiopicum* L.) and gboma (*Solanum macrocarpon* L.) are two eggplant species commonly grown as vegetables in tropical Africa and elsewhere as minor crops (Daunay and Hazra, 2012; Plazas et al., 2014a; Schippers, 2000; Sunseri et al., 2010). According to the Global Biodiversity Information Facility (GBIF; 2017), the main clusters of *S. aethiopicum* and *S. macrocarpon* are in West Africa (Taher et al., 2017). Both *S. aethiopicum* and *S. macrocarpon* belong to the *Leptostemonum* clade (Knapp et al., 2013), which are native to the Old World and were domesticated from

Solanum anguivi (Lester and Niakan, 1986) and *S. dasyphyllum*, respectively (Bukenya and Carasco, 1994). In many African countries, their leaves and roots are used as traditional medicines for the treatment of several ailments; for example, they are used to help heal wounds and to treat high blood pressure, diabetes, and inflammatory tumors (Oboh et al., 2005). These species are therapeutically valuable because of their high content of phenolic acid and chlorogenic acid (Plazas et al., 2014b; San José et al., 2013). Globally, *S. aethiopicum* is the second most important cultivated eggplant after *S. melon-*

gena L., which is a well-known eggplant (Plazas et al., 2014a). Depending on the utilization type, *S. aethiopicum* can be classified into four main cultivar groups (Gilo, Kumba, Shum, and Aculeatum) (Lester, 1986). The *Gilo* group is cultivated for its fruits, the *Kumba* group is cultivated for its fruits and leaves, the *Shum* group is cultivated for its leaves, and the *Aculeatum* group is cultivated as an ornamental (Lester and Daunay, 2003; Prohens et al., 2012; Taher et al., 2017). *S. macrocarpon* is cultivated for its leaves and its fruits (Maundu et al., 2009; Plazas et al., 2014a). The use of its leaves, which are consumed similar to spinach, is common in the eastern and central parts of Africa (Nyadanu and Lowor, 2015; San José et al., 2016). Few studies have examined the diversity of *S. macrocarpon* (Polignano et al., 2010); however, in general, it is less morphologically diverse than *S. melongena* and *S. aethiopicum* (Plazas et al., 2014a; Taher et al., 2017).

The two-spotted spider mite [*Tetranychus urticae* Koch (Acari: Tetranychidae)] is one of the most damaging agricultural pests worldwide. This insect can cause potential damage to more than 1100 plant species, including different eggplant species (Adeniji and Aloyce, 2012; Rakha et al., 2017). High temperatures and dry conditions are suitable for the multiplication of spider mites, which live in colonies mostly on the underside of leaves. Foliar damage occurs because mites suck the chlorophyll, nutrients, and water from the leaf cells with their piercing and sucking mouthparts. Damage is seen as collections of tiny white or yellow spots and very thin webbing on the underside of leaves. Heavy infestation will result in leaf discoloration, often called bronzing and drop off, and will finally lead to stunting or plant death (Khanamani et al., 2014; Srinivasan, 2009). Chemical control of spider mites is often costly, and the excessive use of pesticides damages the environment and harms human health. Biological control by natural enemies is economical in greenhouses but is not feasible in the field (Bostanian et al., 2003; Khanamani et al., 2014). Therefore, resistant eggplant cultivars are considered an important component to managing the spider mite.

The relationship between insect resistance and trichome types and densities has been reported for many plant species (Mitchell et al., 2016; Tian et al., 2012). For the genus *Solanum*, eight types of trichomes have been identified, of which four (i.e., types I, IV, VI, and VII) are glandular trichomes and four (i.e., types II, III, V, and VIII) are nonglandular (Glas et al., 2012; Mărgineanu et al., 2014). Trichomes of cultivated eggplants *S. melongena* and *S. aethiopicum* are mostly nonglandular-type stellate (Hasanuzzaman et al., 2016; Stephenson et al., 2018). Nonglandular and glandular trichomes may act as a physical barrier that can deter pest movement on plants (Mitchell et al., 2016; Rakha et al., 2017). For instance, in wild tomato, spider mite resistance has been associated with high densities of certain glandular

trichomes (Rakha et al., 2017). In addition to a physical barrier, glandular trichomes store and secrete secondary metabolites that can prevent an insect attack or their feeding and oviposition on the plant (Glas et al., 2012; Rakha et al., 2017; Schilmiller et al., 2008). The role of trichomes in relation to pest resistance has been investigated, especially in Solanaceous crops such as tomato (*Solanum lycopersicum* L.) (Rakha et al., 2017) and potato (*Solanum tuberosum*) (Mărgineanu et al., 2014). However, to date, only limited data regarding trichome types and their relationship with insect resistance are available for African eggplants like *S. aethiopicum* and *S. macrocarpon*.

The objectives of the present study were to evaluate *S. aethiopicum* and *S. macrocarpon* accessions from the collection of the World Vegetable Center (WorldVeg) and to determine resistance to the spider mite based on leaf damage using choice assays. In addition, trichome type and density were characterized and correlated with mite resistance to study the possible mechanisms of resistance.

Materials and Methods

Location and seed sources. Experiments were conducted at WorldVeg in Taiwan. Seeds of 120 accessions of *S. aethiopicum* and five accessions of *S. macrocarpon* were obtained from the WorldVeg genebank (Table 1). The accession countries of origin were Bangladesh (1), Brazil (41), Burkina Faso (1), Cameroon (5), France (1), Ghana (5), Guinea (1), India (2), Ivory Coast (2), Kenya (2), Madagascar (2), Malaysia (1), Mali (1), Philippines (2), Senegal (1), Taiwan (1), Tanzania (5), Togo (1), Uganda (1), Yugoslavia (1), Zambia (1), and unknown (47). Two accessions (VI040627 and VI042040)

[1]Corresponding author. E-mail: mohamed.rakha@worldveg.org.

Table 1. Mean rating of *Tetranychus urticae* damage, type, and trichome density scores of *Solanum macrocarpon* and *S. aethiopicum* accessions and the two susceptible *S. melongena* checks.

Taxa and WorldVeg accession code	Spider mite damage (scale, 0–6)[z]	Trichome density (0–4)[y]		
		Nonglandular stellate	Type IV	Type VII
Solanum macrocarpon	2.9	0	0	2.6
VI050393	2.4 ± 0.2	0	0	3
VI050444	2.5 ± 0.2	0	0	3
VI050390	3.5 ± 0.2	0	0	2
VI047475	3 ± 0	0	0	2
VI042709	3 ± 0	0	0	3
S. aethiopicum	5.2	2.8	0.2	0.07
VI042749	3.5 ± 0.2	3	0	0
VI042753	3.6 ± 0.2	4	0	0
VI042447	4 ± 0	1	0	0
VI042710	4 ± 0	3	0	0
VI042748	4 ± 0	4	0	0
VI042754	4 ± 0	3.8	0	0
VI042755	4 ± 0	4	0	0
VI042770	4 ± 0	4	0	0
VI042771	4 ± 0	4	0	0
VI042772	4 ± 0	4	0	0
VI042796	4 ± 0	4	0	0
VI042797	4 ± 0	4	0	0
VI042798	4 ± 0	4	0	0
VI050378	4 ± 0	2	0	0
VI042751	4.2 ± 0.1	4	0	0
VI042783	4.4 ± 0.2	4	0	0
VI042795	4.4 ± 0.2	4	0	0
VI050384	4.5 ± 0.2	1	0	0
VI042252	4.6 ± 0.2	4	0	0
VI042750	4.6 ± 0.2	3	0	0
VI042752	4.6 ± 0.2	4	0	0
VI042786	4.9 ± 0.2	3	0	0
VI034895	5 ± 0	3.8	0	0
VI034972	5 ± 0	1.8	0	0
VI039605	5 ± 0	2	0	0
VI042253	5 ± 0	3	0	0
VI042711	5 ± 0	0	0	0
VI042735	5 ± 0	3	0	0
VI042736	5 ± 0	2.5	0	0
VI042742	5 ± 0	4	0	0
VI042743	5 ± 0	4	0	0
VI042774	5 ± 0	3	0	0
VI042775	5 ± 0	3	0	0
VI042777	5 ± 0	4	2	0
VI042782	5 ± 0	4	0	0
VI042785	5 ± 0	3	0	0
VI042787	5 ± 0	4	0	0
VI042788	5 ± 0	2	0	0
VI042790	5 ± 0	3	0	0
VI042791	5 ± 0	4	0	0
VI042792	5 ± 0	4	0	0
VI042793	5 ± 0	4	0	0
VI047459	5 ± 0	4	0	0
VI047460	5 ± 0	4	0	0
VI048579	5 ± 0	2	0	0
VI050156	5 ± 0	2	0	0
VI050324	5 ± 0	4	0	0
VI050338	5 ± 0	3	1	0
VI050340	5 ± 0	4	0	0
VI050341	5 ± 0	0	1	0.6
VI050354	5 ± 0	0	0	0
VI050355	5 ± 0	2	0	0
VI050361	5 ± 0	3	0	0
VI050371	5 ± 0	3	0	0
VI050372	5 ± 0	3	0	0
VI050377	5 ± 0	0	1	0
VI050380	5 ± 0	1	1	0
VI050382	5 ± 0	4	0	0
VI050386	5 ± 0	2	0	0
VI050388	5 ± 0	4	0	0
VI050389	5 ± 0	2	1	0
VI050391	5 ± 0	2	0	0
VI050404	5 ± 0	4	1	0
VI060303	5 ± 0	3	0	0
VI061526	5 ± 0	2	0	0

Table 1. (*Continued*) Mean rating of *Tetranychus urticae* damage, type, and trichome density scores of *Solanum macrocarpon* and *S. aethiopicum* accessions and the two susceptible *S. melongena* checks.

Taxa and WorldVeg accession code	Spider mite damage (scale, 0–6)[z]	Trichome density (0–4)[y]		
		Nonglandular stellate	Type IV	Type VII
VI062448	5.4 ± 0.2	1	1	0
VI042773	5.4 ± 0.2	2.3	2	0
VI042778	5.4 ± 0.2	4	0	0
VI042789	5.4 ± 0.2	4	0	0
VI044986	5.4 ± 0.2	3	0	0
VI047452	5.4 ± 0.2	3	0	0
VI050325	5.4 ± 0.2	4	0	0
VI050413	5.4 ± 0.2	1	1	2
VI042251	5.5 ± 0.2	3	0	0
VI042734	5.5 ± 0.2	2	0	0
VI042776	5.5 ± 0.2	4	0	0
VI042781	5.5 ± 0.2	4	1	0
VI044186	5.5 ± 0.2	3	0	0
VI050383	5.5 ± 0.2	2	0	0
VI050408	5.5 ± 0.2	3	0	0
VI050414	5.5 ± 0.2	4	0	0
VI042733	5.6 ± 0.2	4	0	0
VI042779	5.6 ± 0.2	3	2	0
VI047456	5.6 ± 0.2	4	0	0
VI050352	5.6 ± 0.2	2	0	0
VI047455	5.7 ± 0.2	4	0	0
VI050347	5.7 ± 0.2	0.8	1	0
VI050348	5.7 ± 0.2	3	0	0
VI050399	5.8 ± 0.1	4	0	0
VI034847	6 ± 0	0	0	0.5
VI038289	6 ± 0	0	0	0.6
VI042780	6 ± 0	4	0	0
VI042794	6 ± 0	4	0	0
VI042799	6 ± 0	4	0	0
VI044086	6 ± 0	2	0	0
VI047457	6 ± 0	4	0	0
VI047474	6 ± 0	3	0	0
VI050328	6 ± 0	0.8	1	0
VI050329	6 ± 0	4	0	0
VI050330	6 ± 0	0	1	0
VI050331	6 ± 0	4	1	0
VI050333	6 ± 0	4	0	0
VI050336	6 ± 0	4	0	0
VI050337	6 ± 0	4	0	0
VI050353	6 ± 0	3	0	1
VI050375	6 ± 0	0	2	0
VI050394	6 ± 0	4	0	0
VI050395	6 ± 0	4	0	0
VI050397	6 ± 0	2	0	0
VI050398	6 ± 0	4	0	0
VI050406	6 ± 0	0	2	3
VI051008	6 ± 0	1	0	0
VI059072	6 ± 0	3	0	0
VI061522	6 ± 0	0	0	0.6
VI061524	6 ± 0	0	0	0.5
VI061531	6 ± 0	1	0	0
VI062435	6 ± 0	1	1	0
S. melongena	6	3	0	0
VI040627	6 ± 0	2	0	0
VI042040	6 ± 0	4	0	0

[z]Spider mite damage was assessed visually 10 d after spider mite infestation and was based on the leaf damage using a scale of 0 to 6 (0 = no damage, 6 = dead plant). Values represent means (±SE; n = 10). *P* values indicate highly significant differences in the leaf damage levels among African eggplant accessions tested.
[y]Types of trichome densities were evaluated using a scale of 0 to 4 (Simmons and Gurr, 2005) with some modification: 4 = very abundant (>8 per mm^2); 3 = abundant (6–8 per mm^2); 2 = sparse (1–5 per mm^2); 1 = very sparse (<1 per mm^2); and 0 = absent. Scores were assessed using a stereo microscope on the interior middle abaxial surface of seven leaves from 4-week-old seedlings.

of common eggplant (*S. melongena*) were included as susceptible checks for *T. urticae*. Accessions and checks were first evaluated for trichome types and density in 4-week-old plants and later spider mite damage using choice assays for seedling trays of 6-week-old plants.

Trichome analysis. Seeds were sown in 50-plug seedling trays with 40 mL peat moss per cell in the WorldVeg greenhouse (26 ± 4 °C, 6 h/18 h day/night), where seedlings were grown for 4 weeks. Plants were watered daily and fertilized weekly with 15N–15P–15K. A stereo microscope (SZH-ILLB;

Olympus, Tokyo, Japan) equipped with a light system (LG-PS2; Olympus, Tokyo, Japan) was used to assess the trichome type and density of the leaves. Trichome-type classification was performed according to Luckwill (1943) and determined by the morphology and presence/absence of trichome glands. Four weeks after sowing, densities were determined from the interior middle section of the abaxial surface of the second leaf from the apex of seven randomly selected seedlings per accession using a 0 to 4 visual scale adapted from Simmons and Gurr (2005) with some modifications, where 4 = very abundant (>8 per mm^2); 3 = abundant (6–8 per mm^2); 2 = sparse (1–5 per mm^2); 1 = very sparse (<1 per mm^2), and 0 = absent. Cryo-scanning electron microscopy was performed with a JEOL JSM-6330F field emission scanning electron microscope (JEOL, Tokyo, Japan). Samples taken from young leaves had an area ≤7 mm and thickness ≤2 mm. Samples were frozen in slush, prepared in an Oxford Alto 2500 cryosystem (Catan), and examined with 15-kV accelerating voltage. The resulting images were captured digitally.

Spider mite colony and resistance evaluation. The colony of *T. urticae* was cultured and maintained on 2- to 3-week-old bean (*Phaseolus vulgaris* L.) plants in a growth room at 23 to 30 °C, as described by Rakha et al. (2017). Bean plants were replaced every 12 d by cutting an infested plant and placing it on top of a new plant for several days to allow spider mites to move onto the new plants. Bean leaves with a very high density of spider mites, eggs, and nymphs were used for choice assays in seedling trays. Six-week-old eggplants were evaluated for spider mite damage in the seedling trays. Ten seedlings per accession and the check were moved to new 50-plug seedling trays (5 rows × 10 columns) and randomly placed in cells of the tray; therefore, there were 50 plants per tray that contained five accessions. Once transplanted, the trays were moved onto stainless steel benches in growth rooms with a temperature of 26 ± 2 °C (conditions: 70% relative humidity, 16 h/8 h day/night). Two growth rooms were used, each with a capacity of 13 trays; therefore, a total of 1270 plants were evaluated for spider mite damage. Two days after being moved to growth rooms, the plants were covered by a net (60 mesh) and mass infested with a very high density of spider mites from bean leaves. Each plant was inoculated with ≈100 to 150 spider mite adults and a high number of eggs and nymphs. When the bean leaves wilted, the net was removed from the seedlings because the spider mites had moved onto the eggplant plants. Leaf damage was scored 10 d after spider mite infestation using a 0 to 6 visual scale based on the percentage of the leaf area damaged: where 0 indicates no symptoms (completely resistant); 1 indicates <5% leaf area affected (highly resistant); 2 indicates 6% to 15% leaf area affected (resistant); 3 indicates 16% to 30% leaf area affected

(moderately resistant); 4 indicates 31% to 60% leaf area affected and light webbing (moderately susceptible); 5 indicates 61% to 90% leaf area affected and intense webbing (susceptible); and 6 indicates 91% to 100% of leaf area affected, intense webbing, or a dead plant (highly susceptible). Statistical procedures were performed using the statistical software SAS (version 9.1; SAS Institute, Cary, NC). Linear correlations were calculated to test associations among trichome types and spider mite resistance based on spider mite damage.

Results

Trichome diversity. Four-week-old seedlings were characterized by the presence and densities of glandular (I, IV, VI, and VII) and nonglandular (II, III, V, and stellate) trichomes on the abaxial leaf surface (Fig. 1 and Table 1). Trichome types I, II, III, V, and VI were mostly absent or sparse in all *S. aethiopicum* and *S. macrocarpon* plants that were tested. Glandular trichome type IV was also absent in *S. macrocarpon* and in the susceptible checks (*S. melongena* accessions VI040627 and VI042040), whereas 18 accessions from *S. aethiopicum* had this trichome type but with a low density (≤2). The glandular trichome type VII was mainly found in *S. macrocarpon* accessions (with density ranging from sparse to abundant) and in some *S. aethiopicum* accessions (with a density ranging from very sparse to abundant). Both checks lacked this trichome type. Susceptible checks and most *S. aethiopicum* accessions had a high density of nonglandular stellate trichomes, whereas *S. macrocarpon* accessions lacked stellate trichomes.

Evaluation of the spider mite. The evaluation of spider mite resistance based on leaf damage from the choice assays for 125 accessions of *S. aethiopicum* and *S. macrocarpon* is presented in Table 1. Spider mites thrived well under controlled conditions (26 ± 2 °C, 70% relative humidity, 16 h/8 h day/night) in growth rooms, which enabled us to clearly observe and record spider mite damage 10 d after spider mite infestation. All susceptible check plants (*S. melongena* accessions VI040627 and VI042040) had severe damage, with a mean rating of 6 on a 0 to 6 scale. None of the *S. aethiopicum* and *S. macrocarpon* accessions showed complete resistance (no damage) to spider mites, even though two *S. macrocarpon* accessions demonstrated relatively high levels of resistance (Table 1). In general, *S. macrocarpon* accessions displayed lower spider mite damage compared with susceptible checks and *S. aethiopicum* accessions. The most resistant accessions were *S. macrocarpon* accessions VI050393 and VI050444, with a mean damage score of 2 on the given 0 to 6 scale. Three accessions of *S. macrocarpon* (VI050390, VI047475, and VI042709) were moderately resistant, with mean ratings of 3 or 3.5. Most accessions of *S. aethiopicum* (83%) were susceptible or highly susceptible, with mean ratings of ≥5; however, VI042749 and

VI042753 were moderately resistant, with mean ratings of 3.5 and 3.6, respectively.

Relationship between spider mite resistance and trichome types and density. Table 2 shows the Pearson *r* correlations between trichome types and density and the leaf damage caused by the spider mite. Type VII trichome density was especially negatively correlated with leaf damage caused by the spider mite (r = –0.37; $P \le 0.0001$). The correlation between stellate trichome density and leaf damage was not statistically significant. High negative correlations were detected between type VII trichome and stellate trichome density (r = –0.50; $P \le 0.0001$).

Discussion

Solanum macrocarpon and *S. aethiopicum* are popular vegetables in Africa. The longer crop stand period of African eggplant exposes them to a broad range of diseases and pests compared to most other vegetable crops (Adeniji and Aloyce, 2012). The two-spotted spider mite, *T. urticae*, is one of the most harmful and invasive pests of African eggplants, particularly in Southeast and West Africa. Mite control programs aim to decrease the spider mite population throughout the year, but *T. urticae* has a short life cycle (7 d at 27 °C) and the ability to develop resistance to a wide array of acaricides (Cazaux et al., 2014). Consequently, the identification of spider mite–resistant genetic resources that can be used to develop new cultivars is a high priority for eggplant breeders. The WorldVeg has the largest public germplasm collection of African eggplant, which includes 481 accessions of *S. aethiopicum* and 63 accessions of *S. macrocarpon* (Taher et al., 2017). Our strategy was to evaluate a large number of WorldVeg genebank accessions of *S. macrocarpon* and *S. aethiopicum* for spider mite resistance based on damage scores using choice assays, which would be very useful for identifying resistant sources and improving eggplant breeding. The use of choice assays for leaf
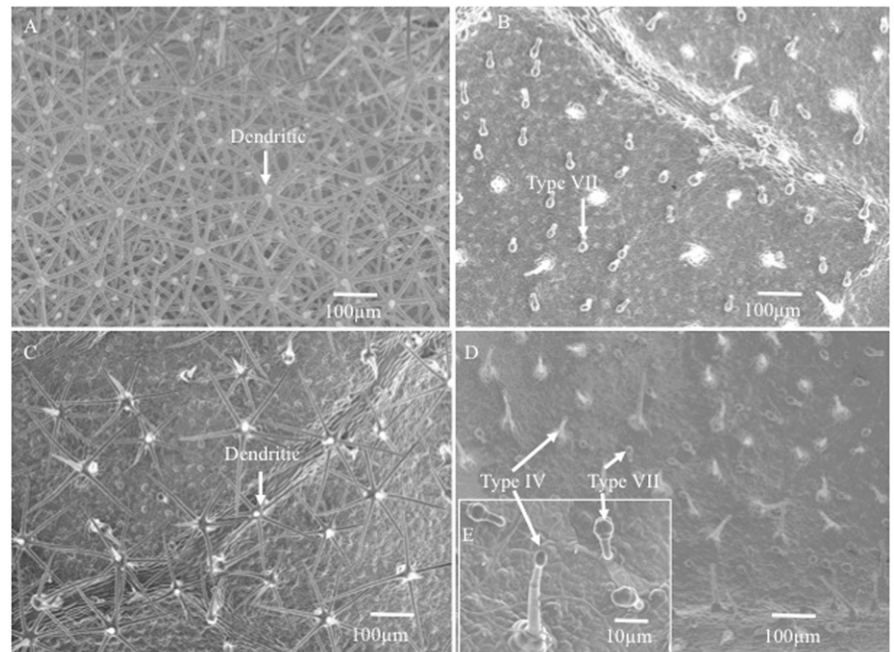

Fig. 1. Cryoelectron micrographs of leaf trichome on abaxial surfaces of four eggplant accessions (*Solanum* spp.): (**A**) spider mite–susceptible check *S. melongena* VI042040; (**B**) resistant *S. macrocarpon* VI050393; (**C**) susceptible *S. aethiopicum* VI050394; and (**D** and **E**) susceptible *S. aethiopicum* VI050406. Four-week-old plants were used for all images.

Table 2. Linear correlations between trichome types and *Tetranychus urticae* damage of *Solanum macrocarpon* and *S. aethiopicum* accessions evaluated using a choice bioassay.

Parameters	Trichome density (0–4)[z]	
	Nonglandular stellate	Glandular type VII
Damage of spider mite (scale, 0–6)[y]	0.05[NS]	–0.37**
Stellate		–0.50**
Type VII		

[z]Types and trichome densities were evaluated using a scale of 0 to 4 (Simmons and Gurr, 2005) with some modification: 4 = very abundant (>8 per mm²); 3 = abundant (6–8 per mm²); 2 = sparse (1–5 per mm²); 1 = very sparse (<1 per mm²); and 0 = absent. Scores were assessed by a stereo microscope on the interior middle abaxial surface of seven leaves from 4-week-old seedlings.
[y]Spider mite damage was assessed visually 10 d after spider mite infestation and was based on the leaf damage using a scale of 0 to 6 (0 = no damage, 6 = dead plant) at 6 weeks after sowing.

damage at the seedling stage could be an efficient method of evaluating large numbers of accessions to save money and efforts when trying to identify new resistant sources.

In our study, we identified and confirmed spider mite resistance in *S. macrocarpon* accessions VI050393 and VI050444; however, we do not know the relationship between these accessions and accessions reported to be resistant by Bletsos et al. (2004) and Rotino et al. (1997). In addition, we discovered moderate resistance by two accessions (VI042749 and VI042753) of *S. aethiopicum*. Furthermore, resistance to the spider mite has been reported in wild eggplant species (Rotino et al., 2014). *S. aethiopicum* and *S. macrocarpon* are cultivated eggplants; the introgression of resistant genes from cultivated eggplant should be easier and faster compared with wild species (Khan et al., 2013; Prohens et al., 2012; Rotino et al., 2014; Toppino et al., 2008). Both these cultivated species can be crossed with *S. melongena*, thus producing hybrids with intermediate fertility (Acquadro et al., 2017; Plazas et al., 2014a). Therefore, our identification of resistance by *S. macrocarpon* and *S. aethiopicum* accessions is highly useful for eggplant breeding.

Resistance to other biotic and abiotic stresses have also been reported for *S. macrocarpon* and *S. aethiopicum*. For example, *S. aethiopicum* presents resistance to root-knot nematodes (Hébert, 1985; Rotino et al., 1997). Resistance to shoot and fruit borers, such as the spider mite, has been reported for *S. macrocarpon* (Bletsosa et al., 2004; Gowda et al., 1990; Rotino et al., 1997). Furthermore, tolerance to *Fusarium oxysporum* f. sp. *melongenae* and *Ralstonia solanacearum* has been identified for both species (Collonnier et al., 2001; Daunay et al., 1991; Prohens et al., 2012; Rizza et al., 2002).

Adedeji et al. (2007) studied the foliar epidermal anatomy and organographic trichome distribution of the family Solanaceae. They found that *S. macrocarpon* was characterized by the presence of unicellular nonglandular and stalked glandular trichome, and that stellate nonglandular trichomes occurred in *Solanum torvum*. Our results demonstrated that nonglandular stellate trichomes were abundant in *S. aethiopicum* and the susceptible check (*S. melongena*), but that they were completely absent in *S. macrocarpon*. We observed that nonglandular trichomes were not associated with spider mite resistance. Similar observations have been reported for wild relatives of tomato and strawberry (Rakha et al., 2017; Steinite and Ievinsh, 2003).

Most previous studies showed that high densities of glandular trichomes, in contrast to nonglandular trichomes, increased spider mite resistance. For instance, spider mite resistance was highly correlated with a high density of glandular type IV trichome in several tomato wild relatives (Maluf et al., 2007; Onyambus et al., 2011; Rakha et al., 2017; Saeidi et al., 2007). In this study, type IV trichomes were not involved in spider mite resistance; however, type VII trichomes

were found in accessions of *S. macrocarpon*. Type VII is a short glandular trichome, with a single stalk cell and a berry-shaped glandular head composed of 7 to 10 cells. In tobacco, type VII trichomes have been shown to secrete proteins called phylloplanins, which have antifungal activities (Shepherd et al., 2005). The absence of type IV and type VII trichomes on the leaf surface could explain the severe damage observed on *S. aethiopicum* accessions. Two *S. aethiopicum* accessions (VI042749 and VI042753) were moderately resistant, but type IV and type VII trichomes were absent. In contrast, *S. aethiopicum* accession VI050406 was highly susceptible, but it had a high density of type VII trichomes. This implies that resistance to spider mites by *S. aethiopicum* is probably based on a mechanism different than that of trichomes. Although we did not study the chemical composition of glandular trichomes, it is possible that type VII glandular trichomes derived from *S. macrocarpon* produce specific compounds that can be toxic, repellent, and trap spider mites, but this needs to be confirmed. McDowell et al. (2011) found that glandular trichomes in several *Solanum* species contain highly diverse sets of acyl sugars, fatty acids, alkaloids, and terpenoids that might contribute to plant defense.

Identification of a resistant source is the first step toward development of pest-resistant cultivars. Our screening showed relatively high spider mite resistance in two accessions of *S. macrocarpon*, and moderate resistance was identified in other *S. macrocarpon* accessions and in two accessions of *S. aethiopicum*. Such accessions may be exploited in breeding programs to develop spider mite–resistant cultivars, not only in these African eggplant species but also in the more common eggplant. To our knowledge, this is the first report of the evaluation of a large number of *S. aethiopicum* accessions for spider mite resistance.

Literature Cited

Acquadro, A., L. Barchi, P. Gramazio, E. Portis, S. Vilanova, C. Comino, M. Plazas, J. Prohens, and S. Lanteri. 2017. Coding SNPs analysis highlights genetic relationships and evolution pattern in eggplant complexes. PLoS One 12:e0180774.

Adedeji, O., O.Y. Ajuwon, and O.O. Babawale. 2007. Foliar epidermal studies, organographic distribution and taxonomic importance of trichomes in the family Solanaceae. Intl. J. Bot. 3:276–282.

Adeniji, O. and A. Aloyce. 2012. Farmer's knowledge of horticultural traits and participatory selection of African eggplant varieties (*Solanum aethiopicum*) in Tanzania. Tropicultura 30:185–191.

Bletsosa, F., D. Roupakias, M. Tsaktsira, and A. Scaltsoyjannes. 2004. Production and characterization of interspecific hybrids between three eggplant (*Solanum melongena* L.) cultivars and *Solanum macrocarpon* L. Scientia Hort. 101: 11–21.

Bostanian, N.J., M. Trudeau, and J. Lasnier. 2003. Management of the two-spotted spider mite, *Tetranychus urticae* [Acari: Tetranychidae] in eggplant fields. Phytoprotection 84:1–8.

Bukenya, Z.R. and J.F. Carasco. 1994. Biosystematic study of *Solanum macrocarpon S. dasyphyllum* complex in Uganda and relations with *S. linnaeanum*. J. East Afr. Agr. For. 59:187–204.

Cazaux, M., M. Navarro, K.A. Bruinsma, V. Zhurov, T. Negrave, T. Van Leeuwen, V. Grbic, and M. Grbic. 2014. Application of two-spotted spider mite *Tetranychus urticae* for plant-pest interaction pests and natural enemies. Agr. For. Entomol. 7:265–276.

Collonnier, C., K. Mulya, I. Fock, I. Mariska, A. Servaes, F. Vedel, S. Siljak-Yakovlev, V. Souvannavong, G. Ducreux, and D. Sihachakr. 2001. Source of resistance against *Ralstonia solanacearum* in fertile somatic hybrids of eggplant (*Solanum melongena* L.) with *Solanum aethiopicum* L. Plant Sci. 160:301–313.

Daunay, M.C. and P. Hazra. 2012. Eggplant, p. 257–322. In: K. Peter and P. Hazra (eds.). Handbook of vegetables. Studium Press, Houston, TX.

Daunay, M.C., R.N. Lester, and H. Laterrot. 1991. The use of wild species for the genetic improvement of brinjal-eggplant (*Solanum melongena*) and tomato (*Lycopersicon esculentum*), p. 389–413. In: J.C. Hawkes, R.N. Lester, M. Nee, and N. Estrada (eds.). Solanaceae III, taxonomy, chemistry, evolution. Royal Botanic Gardens Kew and Linnean Soc., London, UK.

Glas, J.J., B.C. Schimmel, J.M. Alba, R. Escobar-Bravo, R.C. Schuurink, and M.R. Kant. 2012. Plant Glandular Trichomes as Targets for Breeding or Engineering of Resistance to Herbivores. Intl. J. Mol. Sci. 13:17077–17103.

Global Biodiversity Information Facility. 2017. 20 Jan. 2017. <http://www.gbif.org>.

Gowda, P.H.R., K.T. Shivashankar, and S.H. Joshi. 1990. Interspecific hybridization between *Solanum melongena* and *Solanum macrocarpon*: study of the F1 hybrid plants. Euphytica 48: 59–61.

Hasanuzzaman, A.M., M.N. Islam, Y. Zhang, C.Y. Zhang, and T.X. Liu. 2016. Leaf morphological characters can be a factor for intra-varietal preference of whitefly *Bemisia tabaci* (Hemiptera:Aleyrodidae) among eggplant varieties. PLoS One 11(4):E0153880.

Hébert, Y. 1985. Comparative resistance of nine species of the genes *Solanum* to bacterial wilt (*Psedomonas solanacearum*) and the nematode *Meloidogyne incognita*. Implications for the breeding of aubergine (*S. melongena*) in the humid tropical zone. Agronomie 5:27–32.

Khan, M.M.R., M. Hasnunnahar, and S. Isshiki. 2013. Production of amphidiploids of the hybrids between *Solanum macrocarpon* and eggplant. HortScience 48:422–424.

Khanamani, M., Y. Fathipour, H. Hajiqanbar, and A. Sedaratian. 2014. Two-spotted spider mite reared on resistant eggplant affects consumption rate and life table parameters of its predator, *Typhlodromus bagdasarjani* (Acari: Phytoseiidae). Exp. Appl. Acarol. 63:241–252.

Knapp, S., M.S. Vorontsova, and J. Prohens. 2013. Wild relatives of the eggplant (*Solanum melongena* L.: Solanaceae): New understanding of species names in a complex group. PLoS One 8:e57039.

Lester, R.N. 1986. Taxonomy of scarlet eggplants, *Solanum aethiopicum* L. Acta Hort. 182:125–132.

Lester, R.N. and M.C. Daunay. 2003. Diversity of African vegetable *Solanum* species and its implications for a better understanding of plant domestication. Schr. Genet. Ressour. 22:137–152.

Lester, R.N. and L. Niakan. 1986. Origin and domestication of the scarlet eggplant, *Solanum*

aethiopicum, from *S. anguivi* in Africa, p. 433–456. In: W.G. D'Arcy (ed.). Solanaceae: Biology and Systematics. Columbia University Press, New York, NY.

Luckwill, L.C. 1943. The genus Lycopersicon: A historical, biological and taxonomy survey of the wild and cultivated tomatoes. Aberdeen Univ. Stud. 120:1–44.

Maluf, W.R., I.F. Inoue, R.P.D. Ferreira, L.A.A. Gomes, E.M. Castro, and M.G. Cardoso. 2007. Higher glandular trichome density in tomato leaflets and repellence to spider mites. Pesqui. Agropecu. Bras. 42:1227–1235.

Mărgineanu, A.M., I. Erdelyi-Molnár, and E. Rakosy-Tican. 2014. Trichome types analysis and their density in parental species *Solanum tuberosum* and *Solanum chacoense* and their derived somatic hybrids. Scientific Annals of Alexandru Ioan Cuza University. New Series, Section 2. Vegetal Biology. 60:33–42.

Maundu, P., E. Achigan-Dako, and Y. Morimoto. 2009. Biodiversity of African Vegetables, p. 65–104. In: C.M. Shackleton, M.W. Pasquini, and A.W. Drescher (eds.). African indigenous vegetables in urban agriculture. London and Sterling, London, UK.

McDowell, E.T., J. Kapteyn, A. Schmidt, C. Li, J.H. Kang, A. Descour, F. Shi, M. Larson, and A.L. Schilmiller. 2011. Comparative functional genomic analysis of *Solanum* glandular trichome types. Plant Physiol. 155:524–539.

Mitchell, C., R.M. Brennan, J. Graham, and A.J. Karley. 2016. Plant defense against herbivorous pests: Exploiting resistance and tolerance traits for sustainable crop protection. Front. Plant Sci. 7:1132.

Nyadanu, D. and S.T. Lowor. 2015. Promoting competitiveness of neglected and underutilized crop species: Comparative analysis of nutritional composition of indigenous and exotic leafy and fruit vegetables in Ghana. Genet. Resources Crop Evol. 62:131–140.

Oboh, G., M.M. Ekperigin, and M.I. Kazeem. 2005. Nutritional and haemolytic properties of eggplants (*Solanum macrocarpon*) leaves. J. Food Compos. Anal. 18:153–160.

Onyambus, G.K., R.O. Maranga, L.M. Gitonga, and M. Knapp. 2011. Host plant resistance among tomato accessions to the spider mite *Tetranychus evansi* in Kenya. Exp. Appl. Acarol. 54:385–393.

Plazas, M., I. Andujar, S. Vilanova, P. Gramazio, F.J. Herraiz, and J. Prohens. 2014a. Conventional and phenomics characterization provides insight into the diversity and relationships of hypervariable scarlet (*Solanum aethiopicum* L.) and gboma (*S. macrocarpon* L.) eggplant complexes. Front. Plant Sci. 5:318.

Plazas, M., J. Prohens, A.N. Cunat, S. Vilanova, P. Gramazio, F.J. Herraiz, and I. Andujar. 2014b. Reducing capacity, chlorogenic acid content and biological activity in a collection of scarlet (*Solanum aethiopicum*) and gboma (*S. macrocarpon*) eggplants. Intl. J. Mol. Sci. 15:17221–17241.

Polignano, G., P. Uggenti, V. Bisignano, and C. Della Gatta. 2010. Genetic divergence analysis in eggplant (*Solanum melongena* L.) and allied species. Genet. Resources Crop Evol. 57:171–181.

Prohens, J., M. Plazas, M.D. Raigon, J.M. Segu-Simarro, J.R. Stommel, and S. Vilanova. 2012. Characterization of interspecific hybrids and first backcross generations from crosses between two cultivated eggplants (*Solanum melongena* and *S. aethiopicum* Kumba group) and implications for eggplant breeding. Euphytica 186:517–538.

Rakha, M., N. Bouba, S. Ramasamy, J. Regnard, and P. Hanson. 2017. Evaluation of wild tomato accessions (*Solanum* spp.) for resistance to two-spotted spider mite (*Tetranychus urticae* Koch) based on trichome type and acylsugar content. Genet. Resources Crop Evol. 64:1011–1022.

Rizza, F., G. Mennella, C. Collonnier, D. Sihachakr, V. Kashyap, M. Rajam, M. Prestera, and G. Rotino. 2002. Androgenic dihaploids from somatic hybrids between *Solanum melongena* and *S. aethiopicum* gilo as a source of resistance to *Fusarium oxysporum* f. sp. *melongenae*. Plant Cell Rpt. 11:1022–1032.

Rotino, G.L., E. Perri, N. Acciarri, F. Sunseri, and S. Arpaia. 1997. Development of eggplant varietal resistance to insects and diseases via plant breeding. Adv. Hort. Sci. 11:193–201.

Rotino, G.L., T. Sala, and L. Toppino. 2014. Eggplant, p. 381–409. In: A. Pratap and J. Kumar (eds.). Alien gene transfer in crop plants. Volume 2. Springer, New York, NY.

Saeidi, Z., B. Mallik, and R.S. Kulkarni. 2007. Inheritance of glandular trichomes and two-spotted spider mite resistance in cross *Lycopersicon esculentum* 'Nandi' and L. pennellii 'LA2963'. Euphytica 154:231–238.

San José, R., M. Plazas, M.C. Sánchez-Mata, M. Cámara, and J. Prohens. 2016. Diversity in composition of scarlet (*S. aethiopicum*) and gboma (*S. macrocarpon*) eggplants and of interspecific hybrids between S. aethiopicum and common eggplant (*S. melongena*). Genet. Resources Crop Evol. 45:130–140.

San José, R., M.C. Sánchez, M.M. Cámara, and J. Prohens. 2013. Composition of eggplant cultivars of the occidental type and implications for their improvement of nutritional and functional quality. Intl. J. Food Sci. Technol. 48:2490–2499.

Schilmiller, A.L., R.L. Last, and E. Pichersky. 2008. Harnessing plant trichome biochemistry for the production of useful compounds. Plant J. 54:702–711.

Schippers, R.R. 2000. African Indigenous Vegetables: An Overview of the Cultivated Species. Natural Resources Inst./ACP-EU Tech. Ctr. Agr. Rural Cooperation, Chatham, UK.

Shepherd, R.W., W.T. Bass, R.L. Houtz, and G.J. Wagner. 2005. Phylloplanins of tobacco are defensive proteins deployed on aerial surfaces by short glandular trichomes. Plant Cell 17:1851–1861.

Simmons, A.T. and G.M. Gurr. 2005. Trichomes of *Lycopersicon* species and their hybrids: Effects on studies. J. Vis. Expt. 89:51738.

Srinivasan, R. 2009. Insect and mite pests on eggplant: A field guide for identification and management. AVRDC Publication. 64: 09–729.

Steinite, I. and G. Ievinsh. 2003. Possible role of trichomes in resistance of strawberry cultivars against spider mite. Acta Univ. Latviensis 662:59–65.

Stephenson, C., M. De Moraes, and M.C. Mescher. 2018. Leaf trichomes affect caterpillar feeding in an instar-specific manner. Commun. Integr. Biol.,, doi: 10.1080/19420889.2018.1486653.

Sunseri, F., G.B. Polignano, V. Alba, C. Lotti, V. Bisignano, G. Mennella, A.D. Alessandro, M. Bacchi, P. Riccardi, M.C. Fiore, and L. Ricciardi. 2010. Genetic diversity and characterization of African eggplant germplasm collection. Afr. J. Plant Sci. 4:231–241.

Taher, D., S.Ø. Solberg, J. Prohens, Y. Chou, M. Rakha, and T. Wu. 2017. World Vegetable Center eggplant collection: Origin, composition, seed dissemination and utilization in breeding. Front. Plant Sci. 8:1484.

Tian, D., J. Tooker, M. Peiffer, S.H. Chung, and G.W. Felton. 2012. Role of trichomes in defense against herbivores: Comparison of herbivore response to woolly and hairless trichome mutants in tomato (*Solanum lycopersicum*). Planta 236:1053–1066.

Toppino, L., G. Valè, and G.L. Rotino. 2008. Inheritance of *Fusarium* wilt resistance introgressed from *Solanum aethiopicum Gilo* and *Aculeatum* groups into cultivated eggplant (*S. melongena*) and development of associated PCR-based markers. Mol. Breed. 22:237–250.