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Host range of the invasive tomato pest *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) on solanaceous crops and weeds in Tanzania

Jason D. Smith¹, Thomas Dubois², Raphael Mallogo², Efrem-Fred Njau³, Steven Tua², and Ramasamy Srinivasan^{4,*}

Abstract

The tomato leafminer, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), a devastating pest of tomato, invaded Tanzania in 2014. There is now a pressing need to determine the extent of *T. absoluta* infestations in tomato, other solanaceous crops, and wild plants of Tanzania, to support research and to develop pest management programs. In Sep and Oct 2015, we visited 15 randomly selected villages in 4 leading tomato-producing districts (Arumeru, Lushoto, Kilolo, and Mvomero) and sampled fields representing 9 solanaceous crops and weeds. *Tuta absoluta* was present in all 4 districts. Overall, in tomato (*Solanum lycopersicum* L.) *T. absoluta* established 1.0 ± 1.3 (mean \pm standard deviation) mines per leaf and damaged $15 \pm 15\%$ of fruits; in eggplant (aubergine) (*Solanum melongena* L.) it established 0.3 ± 0.7 mines per leaf and damaged $0 \pm 0\%$ of fruits; in potato (*Solanum tuberosum* L.) *T. absoluta* established 0.17 ± 0.1 mines per leaf; and in 2 African nightshades (*Solanum nigrum* L. and *Solanum americanum* Mill.) *T. absoluta* established 0.02 ± 0.03 mines per leaf (fruits of the latter 2 were not sampled). Pepper (*Capsicum annuum* L.) and African eggplant (*Solanum aethiopicum* L.) were not affected by *T. absoluta*. We found 3 solanaceous weeds in the vicinity of *T. absoluta*-infested fields in Arumeru District: *Solanum incanum* L., *Datura stramonium* L., and *Nicandara physalodes* (L.) Gaertn. None of these species were infested by *T. absoluta*; however, the latter 2 were infested by *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), which has habits and larvae that resemble those of *T. absoluta*.

Key Words: Leafminer; exotic pest; IPM; East Africa; eggplant; *Phthorimaea operculella*

Resumen

El minador del tomate, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), una plaga devastadora de tomate, invadió Tanzania en el 2014. Actualmente existe una necesidad apremiante de determinar la extensión de la infestación de *T. absoluta* en tomate y otros cultivos de solanáceas y plantas silvestres de Tanzania para apoyar la investigación y el desarrollo de programas de manejo de plagas. En sep y oct del 2015, visitamos 15 aldeas seleccionadas al azar en 4 distritos productores de tomate (Arumeru, Lushoto, Kilolo, y Mvomero) y muestreamos campos que representan 9 cultivos de solanáceas y malezas. *Tuta absoluta* estuvo presente en los 4 distritos. En general, en tomate (*Solanum lycopersicum* L.), *T. absoluta* estableció 1.0 ± 1.3 (media \pm desviación estándar) minas por hoja y dañó $15 \pm 15\%$ de las frutas; en berenjena (*Solanum melongena* L.) estableció 0.3 ± 0.7 minas por hoja y dañó $0 \pm 0\%$ de las frutas; en papa (*Solanum tuberosum* L.) estableció 0.17 ± 0.1 minas por hoja; y en 2 especies de tomatillo de diablo africano (*Solanum nigrum* L. y *Solanum americanum* Mill.) estableció 0.02 ± 0.03 minas por hoja (no se tomaron muestras de los frutos de los últimos 2). El chile dulce (*Capsicum annuum* L.) y la berenjena africana (*Solanum aethiopicum* L.) no se vieron afectadas por *T. absoluta*. Encontramos 3 malezas solanáceas cerca de los campos infestados de *T. absoluta* en el distrito de Arumeru: *Solanum incanum* L., *Datura stramonium* L. y *Nicandara physalodes* (L.) Scop. Ninguna de estas especies fue infestada por *T. absoluta*; sin embargo, estos últimos 2 fueron infestados por *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), que tiene hábitos y larvas que se asemejan a *T. absoluta*.

Palabras Clave: Minador de hojas; plaga exótica; MIP; Africa Oriental; berenjena; *Phthorimaea operculella*

Tuta absoluta Meyrick (Lepidoptera: Gelechiidae), the South American tomato leafminer, is an insect pest that causes major losses to tomato (*Solanum lycopersicum* L.; Solanaceae) production worldwide. Up until the 2000s, its effects were limited to its native range in South America. Within that range, *T. absoluta* proved difficult to control by chemical means because not only do their larvae gain shelter from pesticides by mining inside tomato leaves, stems, and fruits

(Tropea Garzia et al. 2012), but *T. absoluta* populations developed resistance to a range of pesticide classes (Ferracini et al. 2012; Guedes & Picanço 2012). Pesticide resistance, coupled with a high rate of reproduction (up to 11 generations per yr), facilitate *T. absoluta* outbreaks that can destroy up to 100% of infested tomato crops (EPPO 2005; Desneux et al. 2011). *Tuta absoluta* attained global prominence as an invasive pest in 2006 when it was introduced into Spain (Tropea

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Garzia et al. 2012). It has since invaded other countries in Europe, the Mediterranean, northern Africa (Desneux et al. 2011; Mohamed et al. 2012), and South Asia (Kalleswaraswamy et al. 2015; Shashank et al. 2015; Bajracharya et al. 2016; Hossain et al. 2016). *Tuta absoluta* also crossed the Sahara Desert and is now seen as a serious threat to tomato production in sub-saharan Africa (Brévault et al. 2014), where preliminary reports suggest it has already reached South Africa, invading Tanzania and several other countries on the way (Chidege et al. 2016; Campos et al. 2017).

The presence of *Tuta absoluta* in Tanzania, which was first documented by the Tropical Pesticides Research Institute in 2014 (Chidege et al. 2016), stands as a major threat to tomato production, which annually exceeds the weight of Tanzania's other horticultural products combined (Minja et al. 2011). Although the extent of *T. absoluta* damage in Tanzania has not been rigorously estimated, it is understood that poorly managed *T. absoluta* infestations lead to devastating reductions of tomato yields (Desneux et al. 2010; Guedes & Picanço 2012). Indeed, the severity of the infestation in Tanzania attracted significant media attention (Ihucha 2015, 2016). Research is needed to assess the scope of the problem across Tanzania's major tomato growing regions and thereby inform local and international agencies seeking to respond with funding, research, and grower education.

Research also is needed to determine the host range of *T. absoluta* in Tanzania. Although *T. absoluta* prefers tomato as its host (EPPO 2005), it also attacks a number of other of solanaceous crops including eggplant (*Solanum melongena* L., also called aubergine), potato (*Solanum tuberosum* L.), tobacco (*Nicotiana tabacum* L.), and African eggplant (*Solanum aethiopicum* L.) (EPPO 2005; Brévault et al. 2014; Mohamed et al. 2015). *Tuta absoluta* also has been found on a range of wild solanaceous plants (e.g., *Solanum* spp. and *Datura* spp.), which indicates that weed sanitation may be an important tactic for managing pest populations (EPPO 2005; Mohamed et al. 2015). Furthermore, 1 of the commonly cited wild hosts, *Solanum nigrum* L., is a cultivated vegetable (African nightshade) in Tanzania and may be at risk. It is important to note that different *T. absoluta* populations may vary in host usage. For example, a study in Argentina found that *T. absoluta* caterpillars could not survive on eggplant, whereas a study in Sudan reported that they could survive on it (Pereyra & Sánchez 2006; Mohamed et al. 2015). It is possible that invasive populations of *T. absoluta* are adapting to novel hosts (Abbes et al. 2012; Mohamed et al. 2015), because besides Solanaceae, *T. absoluta* has been reported to feed on plants from the families Amaranthaceae, Asteraceae, Brassicaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, and Poaceae (Mohamed et al. 2015; CABI 2017). Thus, it is important to determine in which hosts *T. absoluta* is able to develop in each region that it invades.

In this study, we report on a survey conducted in 2015 to determine the host range and infestation rates of *T. absoluta* on solanaceous crops and common weeds in Tanzania. The survey was conducted in major tomato producing regions of Tanzania.

Materials and Methods

SELECTION OF SURVEY SITES

Four leading tomato growing districts of Tanzania were identified in consultation with the Tanzanian Horticultural Association: Arumeru District of Arusha Region, Lushoto District of Tanga Region, Kilolo District of Iringa Region, and Mvomero District of Morogoro Region

(Fig. 1). The District Agricultural Officers from each of these districts were contacted to obtain lists of 10 to 20 villages where tomato and at least 2 other solanaceous crops were being cultivated. The lists of villages were randomly ranked and the lowest-ranking villages (numbers 1, 2, and 3) were pre-selected as survey sites. The Agricultural Extension Agents from each location were contacted to arrange visits. In cases where the extension agent was not available, the next-lowest ranked village was substituted. Also, where geographic spacing of the 3 randomly selected villages was less than 10 km apart, 1 of the villages was exchanged for the next lowest ranking village. However, in one instance, in the Arumeru District, 2 villages that we surveyed were closer than expected (3.4 km apart).

The aforementioned sites were surveyed between 9 and 30 Sep 2015. Because none of the villages that we initially surveyed in Arumeru were growing potato, 3 additional Arumeru villages were visited to survey in potato in mid-Oct 2015. The survey locations, as well as crops and weeds at each location, are summarized in Table 1. Our sampling activities targeted the dry season before the short Nov/Dec rainy season.

Survey maps were produced with the statistical software R in conjunction with software packages ggmap, mapproj, rgdal, and ggplot2 (Wickham 2009; Bivand et al. 2012; Kahle & Wickham 2013; R Core Team 2014; Bivand & Lewin-Koh 2015). District outlines were extracted from administrative maps from DIVA-GIS (Hijmans et al. 2012).

SAMPLING METHODS

Within each randomly selected village, we sampled 1 field per available solanaceous crop. Fields were pre-selected by the Agricultural Extension Officer and typically represented the nearest fields to our meeting location. Each crop field was sampled in a zigzag pattern at 10 points that included interior plants as well as plants on the field margins; however, the extreme margins (2 m border) were not sampled. At each sample point we counted the total leaves and total *T. absoluta* mines from 1 individual plant so as to determine the number of mines per leaf. Additionally, at each point the 10 nearest fruits (if available) were sampled for any signs of *T. absoluta* damage, for a total of 100 fruits per field. To confirm *T. absoluta* as the agent of observed fruit damage, we looked for the characteristic pin-hole damage caused by *T. absoluta* caterpillars in tomato, or we dissected the fruit with a knife (other fruits). *Tuta absoluta* caterpillars were identified in the field according to 3 criteria: characteristic leaf mines, body form and size as described in USDA (2011), and a distinctive dark prothoracic band as described in Roditakis et al. (2010).

Overall, the survey included the following crops: tomato, African eggplant, eggplant (aubergine), pepper (*Capsicum annuum* L.), African nightshades (*Solanum americanum* Mill. and *Solanum nigrum* L.), and potato. We also investigated whether weeds harbor *T. absoluta* larvae by sampling weedy solanaceous species around *T. absoluta*-infested tomato fields in Arumeru District. Because weed distribution was patchy rather than uniform throughout the fields, we haphazardly selected 10 plants from inside and around tomato fields. Species surveyed included *Datura stramonium* L. var *inermis* (Jacq.), *Solanum incanum* L., and *Nicandra physalodes* (L.) Gaertn. No other solanaceous weeds were observed in the vicinity of tomato fields in the Arumeru District (the district in which target weeds were identified for this survey).

Representative weed specimens are archived in the National Herbarium of Tanzania. Caterpillars from *T. absoluta*-like mines in weed leaves were collected alive and reared to adulthood in plastic containers in the laboratory. Caterpillars from *S. incanum* did not survive

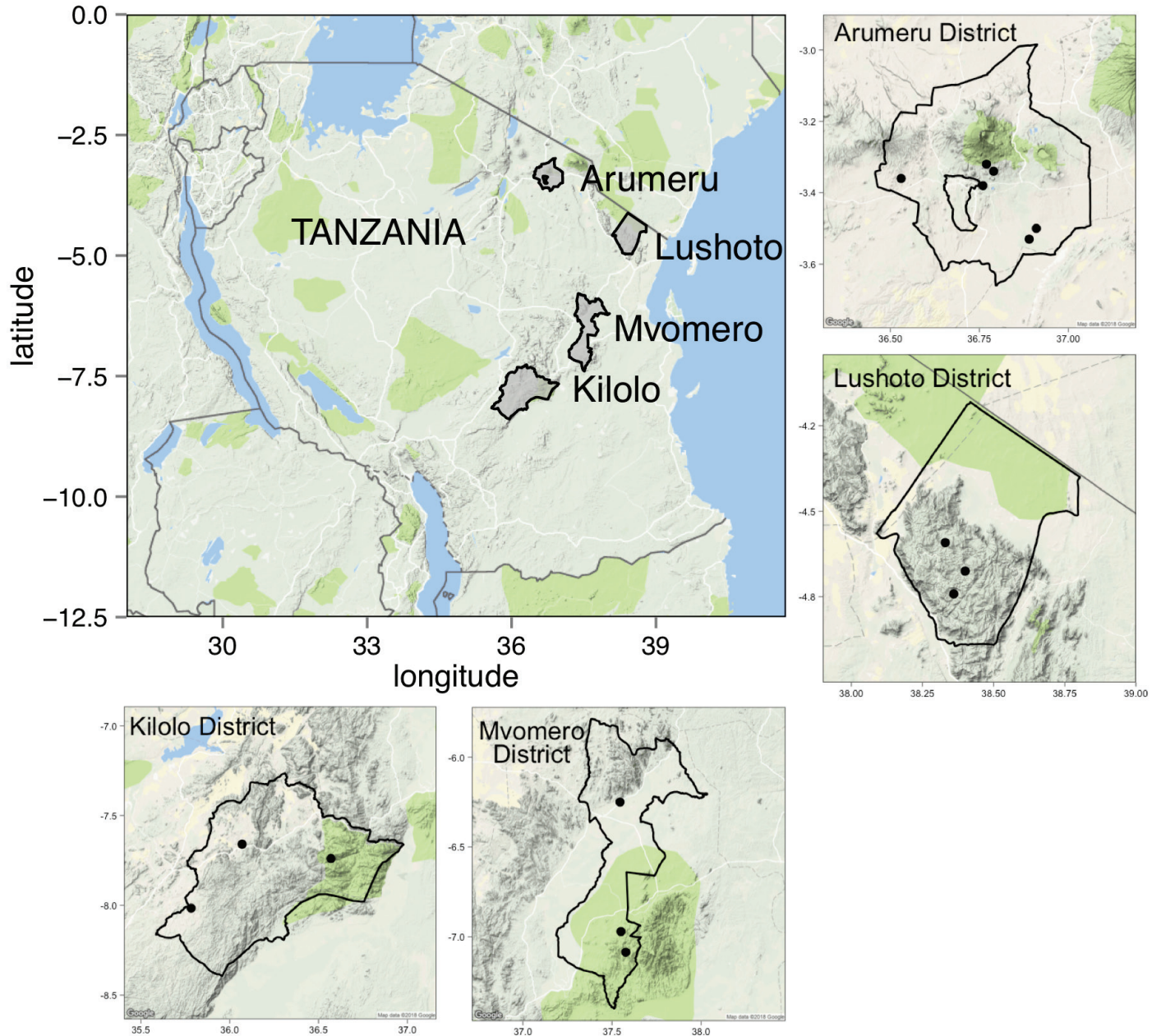


Fig. 1. Map of locations surveyed to determine host range and infestation level of *Tuta absoluta* in solanaceous crops and weeds in 2015. Four districts were targeted, each within the major tomato-producing regions of Tanzania. Within each district, 3 villages (indicated by black circles) were randomly selected for the survey (see Table 1).

on *S. incanum* leaves nor on tomato leaves and, thus, could not be identified. Caterpillars from *D. stramonium* and *N. physalodes* survived well on their respective host leaves. Emerging adults were sent to Dr. Sangmi Li (Arizona State University) for identification and archived in the Arizona State University Hasbrouck Insect Collection.

FARMER SURVEY

When available, growers from each location were asked whether they recognized *T. absoluta* (either by name or by photo), and what crops, if any, they thought that *T. absoluta* affected. They also were asked what interventions they had taken for *T. absoluta* (if any). Only 3 to 5 growers per district were surveyed because others were unavailable to comment.

Results

GEOGRAPHIC RANGE OF *TUTA ABSOLUTA* IN TANZANIA

Tuta absoluta was present in each of the districts that we surveyed and was the cause of measurable foliar damage in every tomato field that we visited (Fig. 2; Tables 2 and 3).

HOST RANGE AND INFESTATION RATES OF *TUTA ABSOLUTA*

Among the crops and weeds that we surveyed, tomato, eggplant (aubergine), African nightshades, and potato all exhibited *T. absoluta* mines, but African eggplant and pepper did not (Fig. 3A; Table 2). Only tomato sustained damage to the fruit from *T. absoluta* caterpill-

Table 1. Survey locations and crops sampled at each site in Tanzania. Each “X” represents an individual field. Not all crops were available in all villages.

Village	Latitude	Longitude	African Eggplant	African Nightshades	Eggplant (Aubergine)	Pepper	Potato	Tomato
Arumeru District								
Msitu wa Mbogo	3.53°S	36.89°E		X	X	X		X
Ndoombo	3.32°S	36.77°E					X	
Seela	3.34°S	36.79°E					X	
Shangarai	3.38°S	36.76°E		X	X	X		X
Sura	3.36°S	36.53°E					X	
Valeska	3.50°S	36.91°E	X	X		X		X
Kilolo District								
Ikokoto	7.74°S	36.57°E	X	X		X		X
Kimamba	7.66°S	36.07°E		X		X		X
Utengule	8.02°S	35.78°E			X	X		X
Lushoto District								
Boheloi	4.79°S	38.36°E	X	X	X	X	X	X
Chumbageni	4.71°S	38.40°E	X			X	X	X
Mlesa	4.61°S	38.33°E	X	X	X	X		X
Mvomero District								
Kipera	6.97°S	37.55°E			X	X		X
Mkindo	6.25°S	37.55°E	X			X		X
Nyandira	7.09°S	37.58°E	X			X	X	X

Species names: African eggplant (*Solanum aethiopicum*), African nightshades (*Solanum nigrum* and *Solanum americanum*), eggplant (aubergine) (*Solanum melongena*), pepper (*Cap-sicum annuum*), potato (*Solanum tuberosum*), and tomato (*Solanum lycopersicum*).

lars (Fig. 3B; Table 3). In tomato fields, mine density ranged from 0.1 to 4.4 mines per leaf, and the percentage of fruits damaged by *T. absoluta* ranged from 0 to 41%. In eggplant fields, *T. absoluta* damage varied from 0 to 2.7 mines per leaf, but fruits were not affected by *T. absoluta*. In potato fields *T. absoluta* damage ranged from 0 to 0.3 mines per leaf. In African nightshades, *T. absoluta* damage ranged from 0 to only 0.08 mines per leaf. Average foliage and fruit damage levels for each crop and district are presented in Tables 2 and 3. No *T. absoluta* mines were detected in tissues or fruits of pepper plants or African eggplants.

Although we observed leaf mines in *D. stramonium* and *N. physalodes* that resembled *T. absoluta* feeding galleries, caterpillars reared from these mines to adulthood proved not to be *T. absoluta*, but *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), the potato tuberworm. We also observed feeding galleries in *S. incanum* leaves that superficially resembled *T. absoluta* galleries, although in these samples the caterpillars appeared to have consumed the lower leaf surface (which is usually not consumed by *T. absoluta*), leaving only the dense trichome layer of the plant to serve as the lower boundary of the mine. Caterpillars from *S. incanum* mines that we attempted to rear in the laboratory died before pupating, but we concluded that they likely were not *T. absoluta* because they refused to eat tomato leaves and they lacked the distinctive black band behind the head that is characteristic of *T. absoluta*.

GROWER AWARENESS OF *TUTA ABSOLUTA*

A majority of growers (15 out of 19) had heard of *T. absoluta* prior to our survey, and 16 out of 19 recognized photos of the moth whether or not they knew its name. Although 15 of the growers knew that *T. absoluta* could affect tomato crops, only 1 suspected that it also affects eggplant and nightshades, and none of the farmers answered that *T. absoluta* affects potato. The only pest management strategy that these farmers knowingly employed against *T. absoluta* was spraying conventional pesticides.

Discussion

This survey confirms the recent report of *T. absoluta* in Tanzania (Chidege et al. 2016), and establishes that *T. absoluta* has invaded each of the major tomato producing regions of Tanzania: Arusha, Tanga, Morogoro, and Iringa. The presence of *T. absoluta* in Tanzania poses a serious threat to tomato production. Although most growers are keeping fruit damage well below 50% with the assistance of conventional pesticides, net yield losses are actually greater than the observed fruit damage because foliage damage also reduces tomato yields by limiting photosynthetic capacity of the plants. This challenge for growers is likely to intensify given the propensity of *T. absoluta* to evolve resistance to conventional pesticides (Guedes & Picanço 2012). In general, evolution of pesticide resistance may be delayed through spray rotation (Silva et al. 2011) and integration with other tactics as part of an integrated pest management or IPM strategy, but the farmers we surveyed were relying on conventional pesticides as their sole management tactic, and to our knowledge pesticide rotation is not a common practice in Tanzania or other countries in the region. Although the farmer survey sample size is admittedly small at only 19 (because our surveillance methods did not require growers to be present during surveys), it suggests that most tomato growers in Tanzania's leading tomato production regions recognize *T. absoluta* as a tomato pest, but they do not approach management with an IPM paradigm. Overall, at least 15% of tomatoes are damaged, and the true value is likely to be higher because our survey included tomatoes that would be on the vine and exposed to *T. absoluta* for additional weeks.

Although *T. absoluta* targeted tomato as a host more than other solanaceous crops (Fig. 3), tomato is not the only crop susceptible to *T. absoluta* infestations. Eggplant (aubergine), potato, and African nightshades also frequently sustained foliar damage from this pest in our study (Fig. 3). These findings concur with reports from Senegal, Sudan, and Tunisia regarding the susceptibility of these crops to *T. absoluta* (Desneux et al. 2010; Brévault et al. 2014; Mohamed et al. 2015; Ab-

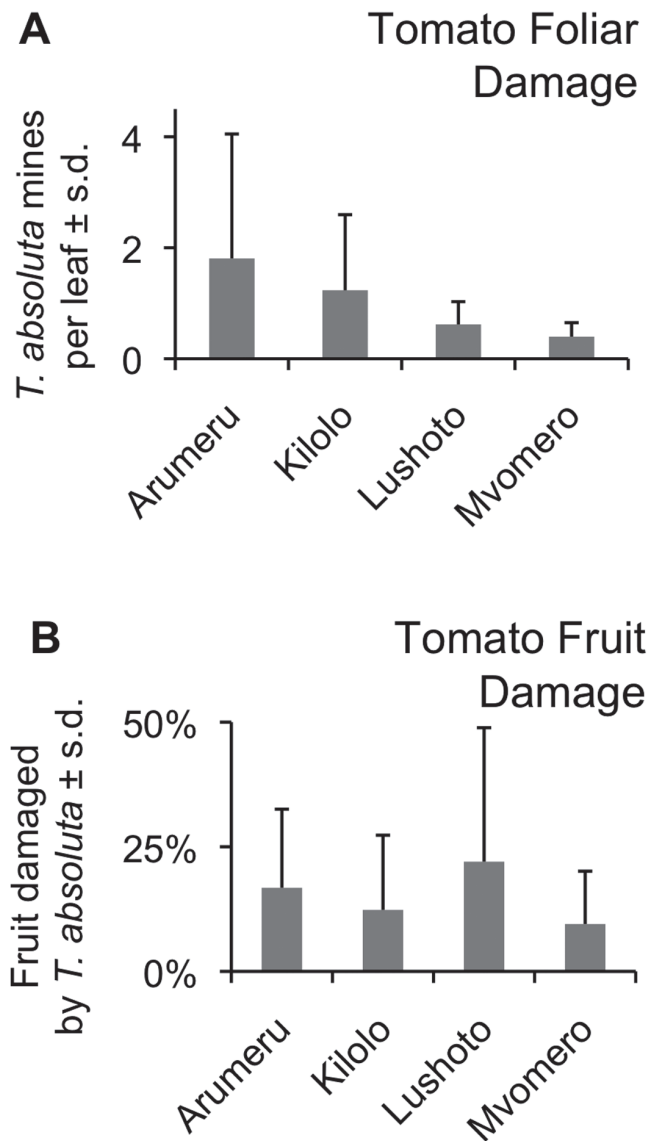


Fig. 2. Tomato (*Solanum lycopersicum*) foliar and fruit damage by *Tuta absoluta* in 4 districts of Tanzania. Damage was assessed in fields from 3 randomly selected villages per district by counting the number of *T. absoluta* mines per leaf (A) and the percentage of fruits that were damaged by *T. absoluta* (B) in 10 locations within each field.

bes et al. 2016). But unlike Mohamed et al. (2015), we did not observe any damage to eggplant (aubergine) fruits. This suggests that reductions to eggplant yields in Tanzania are thus far indirect, although the possibility of direct fruit damage by *T. absoluta* in the future cannot be ruled out. By contrast, damage to edible parts of African nightshade was direct, because nightshades are grown for their leaves. Whereas nightshades (*S. nigrum*) are regarded merely as weeds in other parts of the global distribution of *T. absoluta* (Desneux et al. 2010), they are important vegetable crops in East Africa, which heightens the local significance of this pest-host association. Only a small fraction, less than 1%, of nightshade leaves were infested in the fields that we surveyed. However, one of the authors of the current study (S. T.) has observed *T. absoluta* causing much greater harm to nightshade crops in Manyara Region (data not shown). These differences in infestation rates may



Fig. 3. *Tuta absoluta*-related damage in solanaceous crops and weeds in Tanzania. Damage values are averaged across all survey locations (see Table 1). Damage was quantified as the number of *T. absoluta* mines per leaf (A) and percentage of *T. absoluta*-damaged fruits (B) in 10 locations within each sampled field. Six to 12 fields were sampled per crop, and 1 to 3 fields per weed species (see Table 2). Tomato, *Solanum lycopersicum*; eggplant or aubergine, *Solanum melongena*; African (Afr.) eggplant, *Solanum aethiopicum*; African (Afr.) nightshades, *Solanum nigrum* and *Solanum americanum*; pepper, *Capsicum annum*; and 3 weed species, *Datura stramonium*, *Nicandra physalodes*, and *Solanum incanum*.

indicate useful variation in the susceptibility of cultivated varieties of nightshades that could be exploited to minimize future losses. Alternatively, the differences in infestation rates may be due to the relative distribution or absence of other major host plants of *T. absoluta*.

Two crops that were not affected by *T. absoluta* are pepper and African eggplant. These crops are sometimes omitted from lists of *T. absoluta* host plants (e.g., EPPO 2005; Desneux et al. 2010). However, recent reports indicate that *T. absoluta* infested pepper in Turkey (Bayram et al. 2015) and African eggplant in Senegal (Brévault et al. 2014). Despite these reports, our survey indicates that these crops are not currently affected by *T. absoluta* in Tanzania.

Table 2. *Tuta absoluta* mines per leaf in 9 solanaceous species in 4 districts of Tanzania (mean \pm SD between fields; number of fields shown in parentheses). Ten plants per field were sampled in a zigzag pattern.

	District				Overall
	Arumeru	Kilolo	Lushoto	Mvomero	
Crops					
African eggplant	0.00 (1)	0.00 (1)	0.00 \pm 0.00 (3)	0.00 \pm 0.00 (2)	0.00 \pm 0.00 (7)
African nightshades	0.00 \pm 0 (3)	0.04 \pm 0.06 (2)	0.02 \pm 0.03 (2)	(0)	0.02 \pm 0.03 (7)
Eggplant (aubergine)	0.03 \pm 0.02 (2)	0.00 (1)	0.03 \pm 0.04 (2)	1.70 (1)	0.30 \pm 0.69 (6)
Pepper	0.00 \pm 0.00 (3)	0.00 \pm 0.00 (3)	0.00 \pm 0.00 (3)	0.00 \pm 0.00 (3)	0.00 \pm 0.00 (12)
Potato	0.21 \pm 0.09 (9)	(0)	0.12 \pm 0.10 (2)	0.00 (1)	0.17 \pm 0.10 (12)
Tomato	1.81 \pm 2.24 (3)	1.23 \pm 1.36 (3)	0.62 \pm 0.41 (3)	0.40 \pm 0.25 (3)	1.01 \pm 1.28 (12)
Weeds					
<i>Datura stramonium</i>	0.00 \pm 0.00 (2)	(0)	0.00 (1)	(0)	0.00 \pm 0.00 (3)
<i>Nicandra physalodes</i>	0.00 (1)	(0)	(0)	(0)	0.00 (1)
<i>Solanum incanum</i>	0.00 (1)	(0)	(0)	(0)	0.00 (1)

Crop species names: African eggplant (*Solanum aethiopicum*), African nightshades (*Solanum nigrum* and *Solanum americanum*), eggplant (aubergine) (*Solanum melongena*), pepper (*Cap-sicum annuum*), potato (*Solanum tuberosum*), and tomato (*Solanum lycopersicum*).

Table 3. Percentage of fruits damaged by *Tuta absoluta* in 4 districts of Tanzania (mean \pm SD between fields; number of fields shown in parentheses). In each field, 100 fruits in total were sampled from 10 locations in a zigzag pattern. No fruits were sampled from potato (because they are cultivated for tubers, not fruits).

Crop	District				Overall
	Arumeru	Kilolo	Lushoto	Mvomero	
African Eggplant	0.0% (1)	(0)	0.0 \pm 0.0% (2)	0.0 \pm 0.0% (2)	0.0 \pm 0.0% (5)
African Nightshades	0.0 \pm 0.0% (2)	(0)	0.0 \pm 0.0% (2)	(0)	0.0 \pm 0.0% (4)
Eggplant (aubergine)	0.0% (1)	0.0% (1)	0.0% (1)	(0)	0.0 \pm 0.0% (3)
Pepper	0.0 \pm 0.0% (3)	0.0 \pm 0.0% (3)	0.0 \pm 0.0% (2)	0.0 \pm 0.0% (3)	0.0 \pm 0.0% (11)
Potato	(0)	(0)	(0)	(0)	(0)
Tomato	16.8 \pm 15.8% (3)	12.3 \pm 15.0% (3)	22.0 \pm 26.9% (2)	9.5 \pm 10.6% (2)	15.0 \pm 14.8% (10)

Species names: African eggplant (*Solanum aethiopicum*), African nightshades (*Solanum nigrum* and *Solanum americanum*), eggplant (aubergine) (*Solanum melongena*), pepper (*Cap-sicum annuum*), potato (*Solanum tuberosum*), and tomato (*Solanum lycopersicum*).

In addition to crop plants, we examined whether wild solanaceous plants in and around tomato fields in Arumeru might be serving as alternate hosts for *T. absoluta*. Although we identified 3 weeds bearing *T. absoluta*-like mines inhabited by lepidopteran larvae (*S. incanum*, *D. stramonium*, and *N. physalodes*), our follow-up work established that none of the caterpillars were *T. absoluta*. These data can be regarded as evidence that *T. absoluta* is not using common solanaceous weeds as hosts; however, it should be considered preliminary because only 3 sites were formally surveyed for *D. stramonium*, and only 1 site each for *S. incanum* and *N. physalodes* (Table 2). That said, we informally looked for *T. absoluta* mines in these weeds throughout the entire survey and did not find a single *T. absoluta*-infested weed, which implies that *T. absoluta* is passing by these plants in favor of tomato and, to a lesser extent, eggplant, potato, and nightshades. However, this does not rule out the possibility that *T. absoluta* might use non-preferred hosts in the absence of its preferred hosts, because our survey centered on areas that predominantly produce tomato.

Our encounter with *P. operculella* caterpillars in *D. stramonium* and *N. physalodes* when we were looking for *T. absoluta* is not surprising because these related lepidopterans look similar and use similar hosts (USDA 2011). Yet this experience underscores the importance of confirming larval identity and host compatibility through laboratory studies that complement field surveys. Taking these steps would enhance the usefulness of reports claiming many new host species for *T. absoluta* (Bayram et al. 2015; Mohamed et

al. 2015). Recent examples of such laboratory studies confirmed that eggplant (aubergine) and *S. nigrum* are viable hosts for *T. absoluta*, whereas *D. stramonium* and *Datura ferox* L. (Solanaceae) are not compatible hosts (Mohamed et al. 2015; Abbes et al. 2016). This later finding was consistent with the absence of *T. absoluta* on *D. stramonium* in our study.

Phthorimaea operculella, first detected in Tanzania in the late 1980s by pheromone trapping, is an important pest of potatoes in East Africa (Parker & Hunt 1989). Our findings indicate that *P. operculella* uses *D. stramonium* and *N. physalodes* as alternate host plants. These findings have been observed independently in India and Rhodesia, respectively (Das & Raman 1994). Thus, although our data do not support the practice of removing *D. stramonium* and *N. physalodes* for *T. absoluta* control, sanitation of these weeds still should be recommended in potato IPM programs.

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