African Entomology 2022, 30: e12056 (5 pages)
https://doi.org/10.17159/2254-8854/2022/a12056
RESEARCH ARTICLE

ISSN (online) 2224-8854

Identification of alternative hosts of the tomato leafminer *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) in West Africa

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Tuta absoluta (Meyrick, 1917) (Lepidoptera: Gelechiidae) reached West Africa in 2012 and has since become a major tomato pest. Various alternative strategies for pest control have been identified worldwide, including crop rotation, to deprive the insect of its food. However, this method can only be implemented if a good knowledge of the local host plants of the leafminer have been identified. Here, we have assessed the capacity of *Tuta absoluta* to develop on 27 common vegetable crops in West Africa, representing the Poaceae, Apiaceae, Convolvulaceae, Amaranthaceae, Malvaceae, Lamiaceae, Cucurbitaceae, Fabaceae, Brassicaceae, Asteraceae, Solanaceae, and Amaryllidaceae. The tomato leafminer was only able to develop and complete its life cycle on crops within the genus *Solanum*. Among the 27 plant species tested, *Solanum lycopersicum* L. (tomato) was identified as the best host, allowing for rapid development (22.2 ± 1.4 days) and a high survival rate (84%). *Solanum tuberosum* L. (Irish potato) (24.4 ± 0.8 days; survival rate 40%), *Solanum aethiopicum* L. (African eggplant) (24.3 ± 0.6 days; survival rate 52%) and *Solanum melongena* L. (eggplant) (25.9 ± 1.8 days; survival rate 24%) were three other possible hosts. Larval development occurred on onion (*Allium cepa* L.), but not pupation. A strategy that includes a prolonged absence of the genus *Solanum* in a production area would be associated with a considerable reduction in leafminer population size.

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DATES
Received: 23 August 2021
Accepted: 22 September 2021

KEYWORDS
development cycle
host plants
pest control
Solanum
vegetable crops

INTRODUCTION

The South American tomato leafminer *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) is an economic pest of tomato, which has been prevalent in South America since the 1960s (Biondi et al. 2018). The larvae feed on all aerial parts of the plant, destroying vegetative and reproductive organs, including fruits, and can cause production losses of up to 100% if no effective control methods are used (Desneux et al. 2010; Sawadogo et al. 2020a). After its discovery in Europe (Spain) in 2006 (Urbaneja et al. 2007), it has acquired the status of a global pest of tomato due to its discovery in several parts of the world (Biondi et al. 2018). It reached North Africa in 2008, West Africa in 2012, and the Caribbean in 2018 (Abbes et al. 2012; Pfeiffer et al. 2013; Sylla et al. 2017; Son et al. 2017; USDA-APHIS 2011; Verheggen & Fontus 2019). The invasiveness of the species could be attributed to its high reproductive capacity (i.e. a multivoltine species that can lay more than 240 eggs per female) (Fernandez & Montagne 1990; Germain et al. 2009), its rate of expansion (800 km per year) (Biondi et al. 2018), ability to easily locate its hosts (Bawin et al. 2017) , and above all its resistance to several chemical insecticides (Guedes et al. 2019; Han et al. 2019; Sawadogo et al. 2020b).

Various strategies for control of *Tuta absoluta* have been implemented worldwide, including tolerant cultivars, beneficial species, entomopathogens, biopesticides, pheromones, and crop rotation (Abd El-Ghany et al. 2018; Cagnotti et al. 2021; Ferracini et al. 2019; Gharekhani & Salek-Ebrahimi 2014; Jallow et al. 2020; Caparros Megido et al. 2013a; Ndereyimana et al. 2019; Ouardi et al. 2012). The objective of crop rotation is to deprive the insect of its food by alternating tomato production with other vegetable crops. Such an approach is successfully implemented in some tomato production areas in the USA (Portakaldali et al. 2013). However, this method can only be implemented if a good knowledge of the local host plants of the tomato leafminer have been identified (Bawin et al. 2016; Cherif & Verheggen, 2019).

The main host plant of the tomato leafminer is tomato (*Solanum lycopersicum* L.), but it has been known to feed on other solanaceous plants, such as Irish potato (*Solanum tuberosum* L.), eggplant (*Solanum melongena* L.), Peruvian pepino (*Solanum muricatum* Aiton), and black nightshade (*Solanum nigrum* L.). The insect can also feed on other plant families, including the Amaranthaceae, Euphorbiaceae, Cucurbitaceae, Geraniaceae, Fabaceae, Asteraceae, and Malvaceae, where it can complete at least part of its cycle (Abbes et al. 2016; Cherif & Verheggen 2019; Mohamed et al. 2015; Sylla et al. 2019; Portakaldali et al. 2013; Vargas 1970).

Sawadogo et al. (2020a) identified 27 crops commonly used in rotation or association with tomato. We, therefore, decided to evaluate the ability of the tomato leafminer to develop on these plants species, paying attention to larval and pupal development, as well as survival rates at all stages of the life cycle.

MATERIAL AND METHODS

Insects

Three hundred larvae were collected in February 2020 in an open field of tomato located in the village of Goué (12°35′45″ N, 01°24′00″ W), province of Oubritenga, in Burkina Faso. We then built a tomato leafminer mass rearing facility within the Research and Training Centre of the Nazi Boni University at Bobo Dioulasso (11°09′53″ N, 04°18′54″ W). The insects were carefully contained in cages 80 cm long, 40 cm wide and 40 cm high and fed on Rossol tomato plants. During rearing the temperature was 28 ± 3 °C, the relative humidity 50 ± 15%, and the photoperiod equally split between dark and light (i.e. 12 h dark:12 h light per 24 h).

Plant material

Twenty-seven plant species were used in this trial (Table 1). They were cultivated in a greenhouse in jars containing soil that had been sterilised by heating at 60 °C overnight.

Experimental setup

Tomato leafminer eggs were collected from the rearing cages and five eggs deposited on a soft leaf of an approximately 1-month-old plant of each species. The leaf was then placed on moistened blotting paper contained in a Petri dish (8.9 cm diameter). The dish was then closed and sealed with parafilm. For each plant species, 25 eggs were used for the test (five replicates, with five eggs per replicate). After hatching, the larvae were fed exclusively on the leaves of the species on which they had emerged. Fresh leaves were provided daily and the boxes emptied of old leaves and excrement. Blotting paper was also moistened on-demand until pupation. After emergence, the adults were kept in the same plastic Petri dishes and always moistened, but no food provided, to evaluate their lifespan.

When L1 larvae could not develop, we collected L2 and L3 larvae from the *Tuta absoluta* rearing cages to check their ability to use the tested plant species as food and pursue their life cycle. Observations were made each morning and evening with a binocular magnifying glass to record the dates of hatching, pupation, emergence, and death of the adult.

Data analysis

After checking the normality of the data, we calculated the descriptive statistics for the data and used non-parametric Kruskal–Wallis tests to compare the duration of the different developmental stages of the pest on the different crops. The two-by-two comparison of the rankings of the averages was done using the post hoc Dunn's Multiple Comparison Test (at a 5% level of significance). These different analyses were carried out with the software XLSTAT and IBM SPSS statistics 25.

RESULTS

No plant species prevented the hatching of leafminer eggs. Nevertheless, we found differences in incubation times on the different plants ($K = 256.45$, $P < 0.0001$), which varied from 3.0 ± 0.3 days on *Capsicum chinense* Jacq. to 4.1 ± 0.4 days on *Vigna unguiculata* (L.) Walp..

Table 1. List of the plant species used in the study

Family	Species	Varieties	Common names
Solanaceae	*Solanum lycopersicum* L.	Tropimech	Tomato
	Solanum tuberosum L.	Daifla	Irish potato
	Solanum melongena L.	F1 Kalenda	Eggplant
	Solanum aethiopicum L.	Meketan	African eggplant, Chinese scarlet eggplant
	Capsicum chinense Jacq.	Jaune du Burkina	Bonnet pepper, Hot pepper
	Capsicum annuum L.	Yolo wonder	Sweet pepper
Poaceae	*Zea mays* L.	FBC6	Indian corn, Maize
	Oryza sativa L.	FKR62N	Asian rice
	Sorghum bicolor (L.) Moench	Kapelga	Great millet, Sorghum
Amaranthaceae	*Amaranthus* L. sp.	Vert de Loumbila	Amaranth
	Amaranthus L. sp.	Sauvage	Amaranth
	Spinacia oleracea L.	Local	Spinach
Malvaceae	*Abelmoschus esculentus* (L.) Moench	Indiana	Gumbo, Okra
	Hibiscus sabdariffa L.	R 121	Indian-sorrel, Sorrel
Cucurbitaceae	*Cucumis sativus* L.	Shalini F1	Cucumber
	Cucurbita pepo L.	Medina +F1	Marrow, Summer squash
	Citrullus lanatus (Thunb.) Matsum. & Nakai	Kaolack	Afghan-melon, Watermelon
Fabaceae	*Phaseolus vulgaris* L.	Alyze	Common bean, Green bean
	Vigna unguiculata (L.) Walp.	Komcalle	Asparagus bean, Cowpea
	Vigna subterranea (L.) Verdc.	Konkoumzalem	Bambara bean, Potato peas
	Arachis hypogaea L.	Fleur 11	Earthnut, Peanut
Apiaceae	*Daucus carota* L.	Thema	Carrot
Asteraceae	*Lactuca sativa* L.	Tahoma	Lettuce
Brassicaceae	*Brassica oleracea* L.	F1 KK Cross	Cabbage
Convolvulaceae	*Ipomoea batatas* (L.) Lam.	Nayoumondo-2	Sweet potato
Lamiaceae	*Mentha* L. spp.	Local	Mint
Amaryllidaceae	*Allium cepa* L.	Ares	Onion

Outside the *Solanum* genus, *Tuta absoluta* larvae were not able to develop and complete their life cycle (Table 2). For the genus *Solanum*, there were intrageneric differences in survival rates, with survival rates on *Solanum lycopersicum* (84%) greater than on *Solanum aethiopicum* L. (40%) and *Solanum tuberosum* (52%) respectively. *Solanum melongena* allowed complete development of *Tuta absoluta*, but with a lower survival rate (24%).

On other genera (i.e. not *Solanum*) larvae survived up to three days: from 1.3 ± 0.5 days on *Cucumis sativus* L. to 2.8 ± 0.3 days on *Capsicum annuum* L.. The larval lifespans were much higher on *Solanum* species ($K = 435.64$, $P < 0.0001$), than other species. For *Solanum* species, larvae had a shorter lifespan ($K = 34.54$, $P < 0.0001$) on *Solanum lycopersicum* (11.4 ± 0.3 days) than on the other three species, whose lifespans varied from 12.3 ± 0.5 on *Solanum melongena* to 12.5 ± 0.5 days on *Solanum tuberosum*.

As for the L2 and L3 larvae collected in the tomato leafminer rearing cages and deposited on the leaves of the different species, all of them died in less than three days, except those deposited on *Allium cepa* L., where they were able to feed for seven days without reaching the pupal stage.

The duration of the chrysalis stage was affected by the host plant ($K = 25.75$, $P < 0.0001$), with the duration of the stage shorter on *Solanum lycopersicum* (6.8 ± 1.0 days) than on the other three species of *Solanum* (i.e. from 7.9 ± 0.9 days to 9.7 ± 1.4 days). Adults fed on *Solanum lycopersicum* (10.0 ± 4.7 days) lived longer ($K = 8.61$, $P = 0.03$) than those fed on the other three species (i.e. from 6.5 ± 3.9 to 7.0 ± 4.1 days).

The complete life cycle was consequently affected by the host plant ($K = 32.32$, $P < 0.0001$) and was shorter on *Solanum lycopersicum* (22.2 ± 1.4 days), than on the other three *Solanum* species (i.e. from 24.3 ± 0.6 to 25.9 ± 1.8 days).

DISCUSSION

Only the four commonly cultivated *Solanum* species can host *Tuta absoluta*, allowing the pest to complete its life cycle, with a high survival rate. These results confirm some of those of previous works (Brévault et al. 2014; Caparros Megido et al. 2013b; Negi et al. 2018; Pereyra & Sanchez 2006; Sylla et al. 2018) . We found that species belonging to the genus Capsicum (*Capsicum annuum* and *Capsicum chinense*), despite belonging to the Solanaceae, are not suitable host plants for this pest. These results contradict those obtained by Portakaldali et al. (2013) who found that *Capsicum annuum* was a host plant for the tomato leafminer in Turkey. We confirm the results of previous work, which found that *Tuta absoluta* was not able to complete its life cycle on plant species outside the Solanaceae. The larvae may be unable to mine and feed (due to the cellular structure of the tissues, and robustness of the epidermis), but other factors may also explain their low survivability, including poor organoleptic qualities of tissues, the presence of a toxin, and physical barriers formed by rough trichomes, which could injure the larvae when they move in search of better areas to mine (Awmack & Leather 2002; Krechemer & Foerster 2017; Pereyra & Sanchez 2006).

We found a shorter duration of larval development on

Table 2. Development capacities of *Tuta absoluta* on the different crop species

Crops	Hatching rate (%)	Survival rate (%)	Incubation time	Larval lifespan	Pupal lifespan	Adult lifespan	Life cycles
Solanum lycopersicum	100^{e}	84^{d}	4.0 ± 0.6^{efg}	11.4 ± 0.^{3}g	6.8 ± 1.0^{a}	10.0 ± 4.7^{b}	22.2 ± 1.4^{a}
Solanum tuberosum	88^{bcde}	40^{c}	4.0 ± 0.2^{e}	12.5 ± 0.^{5}g	7.9 ± 0.9^{b}	7.0 ± 4.1^{a}	24.4 ± 0.8^{b}
Solanum melongena	80^{abcd}	24^{b}	3.7 ± 0.6^{cd}	12.3 ± 0.5^{g}	9.7 ± 1.4^{b}	6.9 ± 3.4^{a}	25.9 ± 1.8^{b}
Solanum aethiopicum	96de	52^{c}	4.0 ± 0.2^{e}	12.4 ± 0.6^{g}	7.9 ± 0.9^{b}	6.5 ± 3.9^{a}	24.3 ± 0.6^{b}
Capsicum annuum	96de	0^{a}	3.7 ± 0.3^{cd}	2.8 ± 0.3^{f}	–	–	–
Capsicum chinense	100^{e}	0^{a}	3.0 ± 0.3^{a}	1.9 ± 0.2^{cd}	–	–	–
Zea mays	80^{abcd}	0^{a}	3.4 ± 0.3^{bc}	2.2 ± 0.2^{de}	–	–	–
Oryza sativa	68^{a}	0^{a}	3.4 ± 0.4^{abc}	1.9 ± 0.2^{d}	–	–	–
Sorghum bicolor	72^{ab}	0^{a}	4.0 ± 0.2^{e}	1.5 ± 0.5^{a}	–	–	–
Daucus carota	92^{cde}	0^{a}	4.0 ± 0.2^{de}	1.4 ± 0.5^{a}	–	–	–
Ipomoea batatas	96de	0^{a}	3.3 ± 0.4^{ab}	2.1 ± 0.2^{d}	–	–	–
Amaranthus sp.	80^{abcd}	0^{a}	4.0 ± 0.2^{de}	1.4 ± 0.5^{a}	–	–	–
Amaranthus sp.	88^{bcde}	0^{a}	4.0 ± 0.2^{e}	1.4 ± 0.5^{a}	–	–	–
Spinacia oleracea	92^{cde}	0^{a}	4.0 ± 0.2^{e}	1.3 ± 0.5^{a}	–	–	–
Abelmoschus esculentus	76^{abc}	0^{a}	3.6 ± 0.3^{c}	2.0 ± 0.2^{d}	–	–	–
Hibiscus sabdariffa	96de	0^{a}	4.0 ± 0.4^{fg}	2.8 ± 0.3^{f}	–	–	–
Mentha spp.	80^{abcd}	0^{a}	3.6 ± 0.2^{bc}	2.7 ± 0.3^{ef}	–	–	–
Cucumis sativus	92^{cde}	0^{a}	4.0 ± 0.2^{e}	1.3 ± 0.^{5}a	–	–	–
Cucurbita pepo	88^{bcde}	0^{a}	4.0 ± 0.2^{e}	1.5 ± 0.5^{a}	–	–	–
Citrullus lanatus	84^{abcde}	0^{a}	4.0 ± 0.2^{e}	1.3 ± 0.5^{a}	–	–	–
Phaseolus vulgaris	88^{bcde}	0^{a}	4.1 ± 0.2^{ef}	1.7 ± 0.4^{abc}	–	–	–
Vigna unguiculata	92^{cde}	0^{a}	4.1 ± 0.^{4}g	2.9 ± 0.2^{f}	–	–	–
Vigna subterranea	92^{cde}	0^{a}	4.0 ± 0.2^{e}	2.2 ± 0.6^{d}	–	–	–
Arachis hypogaea	96de	0^{a}	4.0 ± 0.2^{e}	1.7 ± 0.4^{ab}	–	–	–
Brassica oleracea	96de	0^{a}	4.0 ± 0.2^{e}	2.4 ± 1.5^{bcd}	–	–	–
Lactuca sativa	88^{bcde}	0^{a}	3.6 ± 0.3^{bc}	2.8 ± 0.3^{f}	–	–	–
Allium cepa	76^{abc}	0^{a}	3.7 ± 0.6^{c}	2.1 ± 0.2^{de}	–	–	–
K	46.02	380.50	256.45	435.64	25.75	8.61	32.32
$P > F$	0.009	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.03	< 0.0001

Variables sharing the same letter are not significantly different from each other (threshold = 5%, according to the post hoc Dunn's Multiple Comparison Test) tomato than on the other three *Solanum* species tested, which confirms the finding of Negi et al. (2018), who found duration of the larval stage on tomato was shorter than on potato, or eggplant. This difference within the same genus could be due to the difference in genetic material (species or even varieties) used. Indeed, even within the same species, genetic variability leads to differences in palatability, nutritional and organoleptic quality as well as the ability to produce toxins to counter pest attacks (Awmack & Leather 2002; Bawin et al. 2015; Krechemer & Foerster 2017). Onion, on which L2 and L3 larvae were able to maintain themselves for seven days without being able to move to pupation, is a poor host. The nutritional value is low, or its leaves contain toxic substances whose activity is detrimental in the medium term. Species such as *Nicotiana tabacum* L., *Vicia faba* L., and *Malva sylvestris* L., are also able to support partial development of the tomato leafminer (Abdul-Ridha et al. 2012; Bawin et al. 2016; Cherif & Verheggen 2019).

Our study did not take into account non-crop species but it appears that several species belonging to the Solanaceae family, namely *Atropa belladonna* L., *Datura stramonium* L., *Datura ferox* L, *Lycium barbarum L.*, *Nicotiana glauca* Graham, *Solanum dulcamara* L., *Solanum nigrum*, *Solanum elaeagnifolium* Cav., and *Lycopersicum puberulum* Phil., are potential hosts of the tomato leafminer (Bawin et al. 2016, 2015; García & Espul 1982). In particular, studies conducted by Idris et al. (2020) and Campos et al. (2021), show that the black nightshade *Solanum nigrum* allows *Tuta absoluta* to complete its life cycle. In comparison to tomato, the leafminer has slightly lower fecundity and longevity on *Solanum nigrum*. Particular attention should be paid to this plant, especially as it is a perennial and widely distributed plant in Africa.

In a context where (1) vegetable production is market-oriented, (2) production is increasingly subject to economically important pests, (3) the massive use of pesticides increases production costs and considerably reduces producers' earnings, and (4) more and more producers on production sites are organized in groups, associations or cooperatives, it is time to think about pest management on the scale of the production site or drainage basin (MAAH 2019; Sawadogo et al. 2020a). This could become a reality where producers within a group of this nature unanimously choose the crops they will produce according to market characteristics and pests. For tomato leafminer management, where the four *Solanum* crops studied are among the main marketed vegetable crops in the country, they could be rotated yearly with onion, cabbage (the two most important vegetable crops in terms of production) or okra, which represent a very large market share in all regions of the country (MAAH 2019). Even if these crops are rotated, special attention should also be given to the monitoring of weeds and perennials that act as shelters for the leafminers (e.g. *Solanum nigrum*), in order to avoid even minimal maintenance of the leafminer population during intercropping with a non-host species.

ACKNOWLEDGMENTS

This research was funded by the Academy of Research and Higher Education-Commission Development Cooperation (ARES-CDD), as part of the PRD-ProDuIRe project. The authors declare that they have no conflict of interest.

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