Physiological Entomology (2020), DOI: 10.1111/phen.12332

Insecticide susceptibility level and control failure likelihood estimation of Sub-Saharan African populations of tomato leafminer: Evidence from Burkina Faso

MATHIEU W. SAWADOGO[1,2], IRÉNÉE SOMDA[2], SOULEYMANE NACRO[3], ANNE LEGRÈVE[4] and FRANÇOIS J. VERHEGGEN[1]

[1]Gembloux Agro-Bio Tech, TERRA, University of Liege, Gembloux, Belgium, [2]Institut du Développement Rural, Université Nazi Boni, Bobo-Dioulasso, Burkina Faso, [3]Plant production, Institut de l'Environnement et de Recherches Agricoles, Ouagadougou, Burkina Faso and [4]Earth and Life Institute, Catholic University of Louvain, Leuven, Belgium

Abstract. The South American tomato pinworm, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is a leafminer species currently considered as one of the major pests of fresh tomatoes around the world. The species settled in north Africa in 2007, before being observed in the entire continent. Widespread insecticide use has led to the emergence of resistant populations in South America and Europe, but no large-scale insecticide resistance assessment has been performed in Sub-Saharan Africa so far. In this study, we collected *T. absoluta* larvae from locations widely distributed in Burkina Faso, where the pest was first detected in 2016. Acute toxicity of the all available molecules in Burkina Faso was evaluated in the laboratory on F1 individuals, including acetamiprid, abamectin, spinosad, cypermethrin, chlorpyrifos, λ-cyhalothrin, deltamethrin, and *Bacillus thuringiensis*. No LC50 differences among *T. absoluta* populations were highlighted, except for *Bacillus thuringiensis*. Insects were still highly susceptible to abamectin [LC50 < 0.4 mg/L; Control failure likelihood (CFL) = −25%], spinosad (LC50 < 0.6 mg/L; CFL = 25%) and chlorpyrifos-ethyl (LC50 between 254 and 458 mg/L; CFL = −15%), but were less susceptible to acetamiprid (CFL ranging from 72% to 91%), cypermethrin (CFL = 80%), λ-cyhalothrin (CFL =79%), and deltamethrin (CFL ranging from 51% to 66%), with LC50 values for these insecticides ranging between 100 and 525 mg/L. Pending a proper communication strategy, we hope this work could help producers avoiding the most inefficient active substances.

Key words. abamectin, acetamiprid, acute toxicity, *bacillus thuringiensis*, chlorpyrifos, pyrethroids, spinosad.

Introduction

The South American tomato pinworm *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is a leafminer species currently considered to be one of the major pests of tomato (L.) (Biondi et al., 2018). Like other Gelechiidae, all *T. absoluta* larval stages feed on the mesophyll of aerial parts of plants, including stems, apexes, flowers, fruits, and leaves (Abbas et al., 1993; Pouey et al., 1994; Miranda et al., 1998). At high density, the pest causes significant yield losses due to leaf and fruit damages (Desneux et al., 2010).

From its area of origin, a Chilean population of this pest was introduced in Spain in 2006 (Urbaneja et al., 2007; Guillemaud et al., 2015; Biondi et al., 2018), then spread over the Mediterranean littoral (Desneux et al., 2010, 2011), including North Africa in 2007, and arrived in West Africa in 2012, probably first in Senegal (Pfeiffer et al., 2013; Mansour et al., 2018). In

Correspondence: François J. Verheggen, Gembloux Agro-Bio Tech, TERRA, University of Liege, Avenue de la Faculté d'Agronomie 2B, B-5030 Gembloux, Belgium. Tel.: +32 81622662. Email: fverheggen@uliege.be

2016, it was reported for the first time in Burkina Faso (Son et al., 2017a), a country where tomato cultivation plays a very important socio-economic role (MAH, 2001) with an estimated 12 635 tonnes in 2017 (FAOSTAT, 2019). Unfortunately, very few insecticide formulations are registered for the control of this new pest, leading tomato producers to use any available substances to attempt to reduce yield loss. During preliminary surveys performed by the authors, many of them have testified their inefficiency, with the result that many producers ended up abandoning their fields at the mercy of *T. absoluta*. The plausible explanation for these treatment failures is that the introduced pest has developed resistance mechanisms (Guedes & Siqueira, 2012).

Indeed, several studies performed over the world show that certain *T. absoluta* populations are resistant to several molecules, including abamectin, alpha-cypermethrin, azadirachtin, bifenthrin, cartap, chlorantraniliprole, chlofenapyr, chlorpyrifos, cyantraniliprole, cypermethrin, deltamethrin, triazophos, diazinon, diflubenzuron, emamectin benzoate, flubendiamide, indoxacarb, metaflumizon, methamidophos, permethrin, spinetoram, spinosad, tau-fluvalinate, teflubenzuron, thiamethoxam, triflumuron, pyridalyl, *Bacillus thuringensis*, and λ cyhalothrin. *T. absoluta* would mainly use two types of mechanisms to develop resistance to pesticides. The first one involves detoxifying enzymes, including esterases and monooxygenases, dependent on cytochrome P450 (Siqueira et al., 2000, 2001; Reyes et al., 2012; Campos et al., 2015a, b; Karaağaç, 2015; Silva et al., 2015; Barati et al., 2018; Zibaee et al., 2018). The second mechanism involves mutations in the pest genome (Haddi et al., 2012, 2017; Silva et al., 2015, 2016a; Berger et al., 2016; Douris et al., 2017; Roditakis et al., 2017a, b; Zibaee et al., 2018; Grant et al., 2019; Moradi et al., 2019). These resistance mechanisms were previously shown to lead treatment failures in the field (Silva et al., 2011, 2015; Haddi et al., 2012, 2017; Roditakis et al., 2013a, b, 2018), resulting in the farmers to overuse pesticides by increasing doses and frequencies of applications, and subsequently harm human, animal, and environmental health (Mirhosseini et al., 2019; Moradi et al., 2019).

We, therefore, decided to conduct this study to evaluate the sensitivity of four populations of *T. absoluta* collected in the open-field cultivations to the main molecules commercialized in Burkina Faso, in the hope we could recommend avoiding the use of particularly inefficient active substances.

Materials and methods

Insects

We collected *T. absoluta* individuals from four populations in Burkina Faso (Fig. 1). Growers complained about the ineffectiveness of pesticides against this pest at all four locations. Insects were collected from cultivated tomato plants as larvae (200–300 individuals/population), and were brought to the laboratory at the Training and Research Center of the University Nazi Boni (UNB) in Bobo Dioulasso (Fig. 1). The populations of Ouahigouya and Lombila were collected between October 16 and 18, 2018 and those of Goue and Pindga between January 10 and 13, 2019. The larvae were fed with pesticide-free tomato cv. Mongal leaves, in 80 × 40 × 40 cages with a relative humidity of 50 ± 15% and with a controlled temperature of 28 ± 3 °C, and a photoperiod of 12 h of light 12 h of darkness. The insecticide assays were carried out with F1 populations.

Insecticides

No insecticides are specifically registered for the control of *T. absoluta* in the 13 countries that make up the Sahelian Pesticides Committee (SPC) (see list of approved pesticides at http://insah.cilss.int/index.php/csp/). To achieve this experiment, we selected eight single active ingredient insecticides registered for tomato production and available on the market: the neonicotinoids acetamiprid 25 g L^{-1} (emulsifiable concentrate - EC) (Titan 25 EC, Arysta Lifescience, recommended dose RD = 1.5 L ha^{-1}), avermectins/milbemycins abamectin 18 g L^{-1} EC (Abalone 18 EC, Arysta Lifescience, RD = 1 L ha^{-1}), spinosyns spinosad 0.24 g L^{-1} CB (Success appât 0.24 CB Dow Agrosciences Export S.A.S, RD = 1 L ha^{-1}), organophosphate chlorpyrifos 480 g L^{-1} EC (Pyrical 480 EC, Arysta Lifescience, RD = 1 L ha^{-1}), *Bacillus thuringiensis* var. Kurstaki 16 000 UI/mg (Bio K 16, Savana, RD = 1.5 kg ha^{-1}) and pyrethroids cypermethrin 50 g L^{-1} EC (Cypercal 50 EC, Arysta Lifescience, RD = 1 L ha^{-1}), λ-cyhalothrin 25 g L^{-1} EC (Lambda power, Zhejiang Chemical I/E Crop, RD = 0.8 L ha^{-1}), and deltamethrin 25 g L^{-1} EC (Tamega, Savana, RD = 0.5 L ha^{-1}).

Insecticide assays

The bioassay was conducted in accordance with the *T. absoluta*-specific IRAC method n°22 (detailed on www.irac-online.org). In brief, L2 larvae of a population of *T. absoluta* were fed fresh young tomato leaves previously soaked for 3 s in a given concentration of a commercial product containing Triton X100 wetting agent (0.2 g/L) and dried for 30 min. A control treatment without insecticide (distilled water + Triton X100) is used to record natural mortalities. Leaflets were then placed in a Petri dish containing moisten filter paper and sealed with parafilm. Five or six larvae were introduced in each Petri dish, stored at a temperature of 28 ± 3 °C and a relative humidity of 50 ± 15%, as described in Roditakis et al. (2013a, b) and Michaelides et al. (2019). A total of 32 larvae per insecticide concentration were tested: three Petri dishes containing five larvae and two Petri dishes containing six larvae were used. A minimum of six different concentrations were tested per insecticide product. Mortality rates were assessed 72 h after the larvae were introduced in the Petri dishes. Larvae were considered dead if they were unable to make coordinated movement from gentle stimulus with a fine pointed forceps.

Statistical analyses

As suggested by the above- mentioned IRAC method, mortality percentages generated in dose–response bioassays were

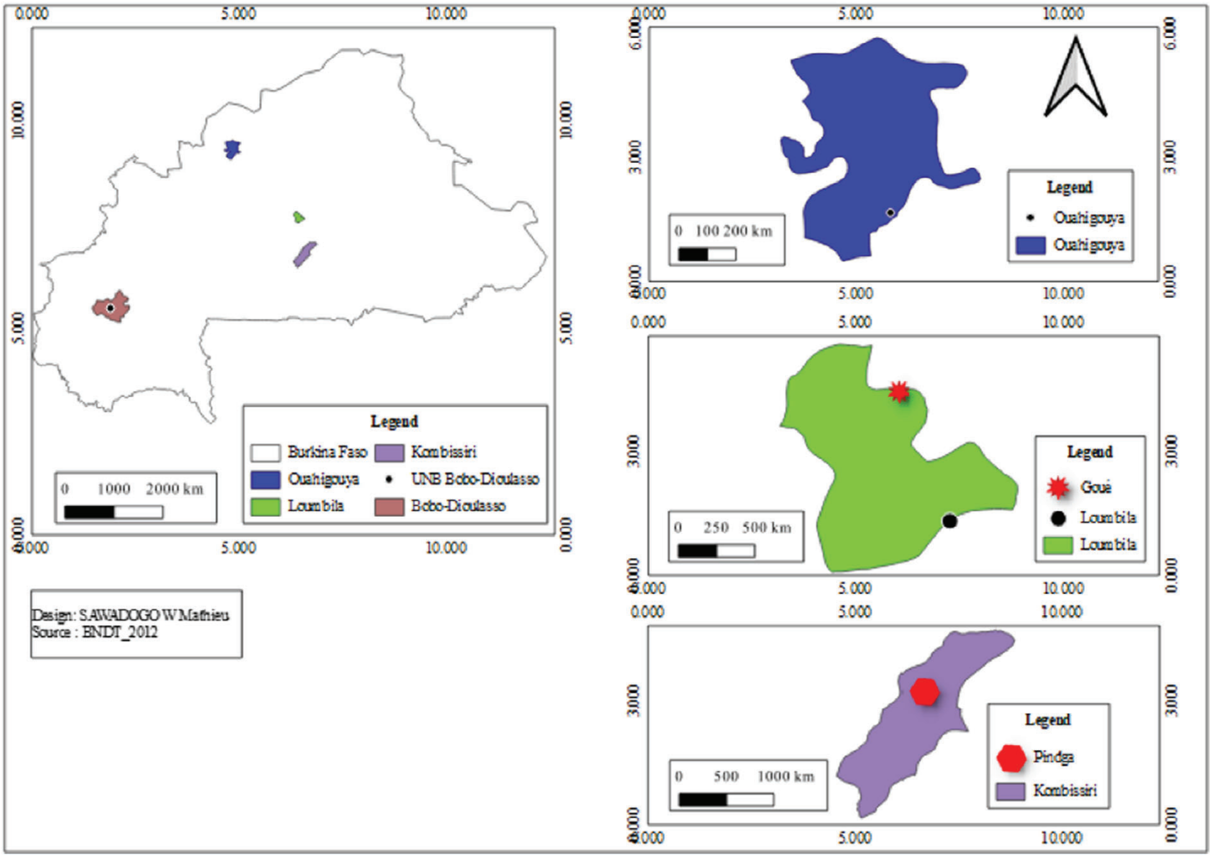

Fig. 1. Location of the four collected *T. absoluta* populations

calculated using Abbott's formula (Abbot, 1925) to take into account mortality observed in untreated control. Using Statgraphics 18 software, mortality percentages were then subjected to a Probit Analysis (commonly used in toxicology to determine the relative toxicity of chemicals to living organisms) following Finney et al. (1964) to obtain lethal concentration (LC) estimates for each insect population tested. The control failure likelihood (CFL) was calculated according to the method described by Guedes (2017): CFL = 100 − [achieved mortality (%) × 100]/expected mortality (80% for SPC). The resistance ratio (RR) is the quotient of the LC50 value of different populations on the value of the population with the smallest LC50 value.

Results

Table 1 lists all results of the Probit Analysis. For all tested molecules, the theoretical values did not differ significantly from the observed values (low $\chi 2$ values; *P*-values >0.05). The Probit model was, therefore, considered suitable for all following analyses.

There was no significant difference between *acetamiprid* LC50 values for the 4 populations. LC50 are 485.6, 455.8, 363.5, and 340.5 mg/L for the populations of Goué, Pindga, Ouahigouya, and Loumbila, respectively. Very high control failure likelihood ranging from 72% to 91% have been observed. The slopes of the concentration/mortality curves ranged from 0.003 to 0.006, showing similar responses for all populations. Low slope values mean that to increase slightly larval mortality, a large increase in insecticide concentration is required, suggesting a high level of resistance to this molecule.

Abamectin LC50 values were similar for all four populations: 0.33, 0.26, 0.26, and 0.22 mg/L for the populations of Goué, Pindga, Loumbila, and Ouahigouya, respectively. Small differences were observed among slope values suggesting a certain homogeneity for all tested populations to abamectin. There is no risk of treatment failure with this molecule.

LC50 values associated with *chlorpyrifos-ethyl* from all *T. absoluta* populations do not differ significantly from each other. LC50s ranged from 254.5 to 458.6 mg/L, which is lower than 0.38% of the recommended dose, suggesting that the four populations are sensitive to this molecule with limited risk of treatment failure.

Spinosad LC50 values were all statistically similar, and were 0.55, 0.44, 0.39, and 0.33 mg/L for the populations of Goué, Loumbila, Pindga, and Ouahigouya, respectively. Slight slope variation (1.01–3.49) also indicates a homogeneous response of all four populations. At the dose recommended by the manufacturer very limited treatment failure should be observed.

Table 1. Susceptibility of different *T. absoluta* populations from Burkina Faso to the most commonly used insecticides in the country

Insecticide	Population	N	LC50 (mg/L)	Confidence Level (95%)	LC80 (mg/L)	Confidence Level (95%)	Slope ± SE	$\chi 2$	Control Failure Likelihood (CFL)	RR
Acetamiprid	Pindga	192	455.8	355.0–710.5	727.0	546.9–1224.2	0.003 ± 0.001	1.26	85	1.33
	Goué	192	485.6	337.9–1151.4	829.0	558.6–2256.3	0.003 ± 0.001	0.86	79	1.42
	Loumbila	192	340.5	254.8–522.6	610.6	459.8–1134.3	0.003 ± 0.001	0.07	72	1
	Ouahigouya	192	363.5	305.7–411.5	507.7	451.5–632.0	0.006 ± 0.002	0.02	91	1.06
Abamectin	Pindga	192	0.26	0.11–0.38	0.68	0.53–0.96	1.83 ± 0.46	5.47	−25	1.18
	Goué	192	0.33	0.25–0.42	0.53	0.43–0.70	3.17 ± 0.71	3.53	−25	1.5
	Loumbila	256	0.26	0.14–0.36	0.60	0.49–0.79	2.50 ± 0.44	3.21	−25	1.18
	Ouahigouya	448	0.22	0.11–0.32	0.60	0.51–0.75	2.58 ± 0.50	1.97	−25	1
Chlorpyrifos-ethyl	Pindga	192	458.6	359.3–697.7	895.5	670.4–1678.2	0.002 ± 0.001	0.26	−15	1.8
	Goué	192	396.8	311.7–488.9	682.0	565.1–986.2	0.003 ± 0.001	1.79	−24	1.55
	Loumbila	192	384.0	305.3–457.3	635.1	544.91–811.7	0.004 ± 0.001	2.51	−24	1.5
	Ouahigouya	192	254.5	213.9–305.2	369.6	316.5–461.3	0.008 ± 0.002	2.75	−25	1
Spinosad	Pindga	192	0.39	0.34–0.58	1.29	1.00–1.84	2.84 ± 0.57	3.19	−25	1.33
	Goué	192	0.55	0.46–0.64	0.80	0.70–0.92	3.49 ± 0.12	6.97	−25	1.25
	Loumbila	192	0.44	0.03–0.64	0.75	0.60–1.00	1.01 ± 0.22	1.17	−25	1.18
	Ouahigouya	192	0.33	0.14–0.56	0.89	0.64–1.68	1.52 ± 0.51	1.54	−25	1
Bacillus thuringiensis subsp. *kurstaki*	Pindga	192	7.0	5.6–8.0	10.6	9.47–12.56	0.23 ± 0.01	0.22	−25	1
	Goué	192	18.9	12.4–26.7	37.1	28.9–51.9	0.05 ± 0.01	2.88	−24	2.7
	Loumbila	192	8.4	7.3–9.6	12.5	11.1–14.7	0.21 ± 0.01	0.95	−25	1.2
	Ouahigouya	192	68.6	46.0–95.1	135.9	106.1–206.3	0.013 ± 0.005	3.33	30	9.81
Cypermethrin	Goué	192	523.3	407.3–891.0	881.8	649.1–1743.4	0.003 ± 0.001	2.79	80	1
λ-Cyhalothrin	Goué	192	411.4	304.4–1207.0	733.2	505.8–3131.9	0.003 ± 0.002	0.12	79	1
Deltamethrin	Goué	192	178.2	121.0–223.1	339.8	292.9–404.9	0.005 ± 0.001	4.91	66	1.53
	Ouahigouya	192	116.1	13.3–220.5	291.1	200.9–1364.5	0.005 ± 0.001	1.6	51	1

N = number of tested larvae; LD = Lethal dose; SE = standard error of slope; $\chi 2$: Chi-square testing linearity of dose–mortality response; resistance ratio (RR) is the quotient of the LC50 value of different populations on the value of the population with the smallest LC50 value.
LC are expressed in mg/L except for *Bacillus thuringiensis* were million unit/L are used.

Cypermethrin (LC50 = 523.3 mg/L) and *λ-cyhalothrin* (LC50 = 411.4 mg/L) could only be tested against *T. absoluta* from Goué, whereas *deltamethrin* was evaluated against insects from Goué (LC50 = 178.2 mg/L) and Ouahigouya (LC50 = 116.1 mg/L) only. Control failure probabilities of 80%, 79%, and between 51% and 66% were measured for cypermethrin, λ-cyhalothrin, and deltamethrin, respectively. For these three active molecules, the calculated slopes are similar (0.003–0.005) suggesting that a large increase of insecticide concentration is required to reach a small increase in larval mortality.

Bacillus thuringiensis LC50 values ranged from $6.99.10^6$ IU/L (Pindga population) to $68.58.10^6$ IU/L (Ouahigouya population). For the populations of Pindga, Goué and Loumbila, there is a very limited risk of control failure, which is not the case for the population of Ouahigouya where there is a 30% chance of treatment failure. The calculated slopes and resistance ratios suggest that the population of Ouahigouya is expressing a higher level of resistance that the other three populations.

Discussion

The first African countries to declare the presence of *T. absoluta* were Tunisia, Algeria and Morocco, during the 2007–2008 tomato growing season (Mansour et al., 2018). Then, the pest has quickly invaded other Mediterranean countries including Egypt and Libya in 2009. Using a CLIMEX model, Tonnang et al. (2015) portrayed Sub-Saharan Africa as a region of high risk of invasion and establishment of *Tuta absoluta*. And these predictions were quickly confirmed, as *T. absoluta* has established in Nigeria (2015), South Africa (2016), and Mozambic (2016), just to name a few (Mansour et al., 2018). In Burkina Faso, the pest was first reported in 2016 but local farmers state that the pest was established several years earlier (Son et al., 2017a). The spread of *T. absoluta* to Burkina Faso could be the consequence of adults' natural dissemination, or import from neighboring affected countries of vegetables carrying larvae or eggs (Verheggen & Fontus, 2019). Based on the results of this study, we raise the hypothesis that all populations found in Burkina Faso originate from a single African area (Guedes & Siqueira, 2012). Indeed, we compared the insecticide resistance of four populations collected at distant locations of Burkina Faso and we could not identify significant differences among these populations in terms susceptibility to the different tested insecticide formulations (Resistance rations RR ranged typically between 1 and 2). However, the specific data obtained from the *B. thuringiensis* treatments do not support fully that hypothesis, but rather suggest that the population of Ouahigouya could have a different origin (The calculated RR of the Ouahigouya population is 9.81). Moreover, the chemical insecticides to which the insects were resistant to are commonly used to control *T. absoluta* in Sub-Saharan Africa (Mansour et al., 2018).

The LC_{50} values are typically used to compare susceptibility of target populations, whereas calculated slopes inform us about the amount of active ingredients needed to increase the biocidal efficacy. Based on the generated values of LC50 and slopes, we can identify three groups of active substances:

(1) With high LC50 values (ranging from 100 to 600 mg/L) and low slope values (<0.01), acetamiprid, deltamethrin, λ-cyhalothrin, and cypermethrin belong to the first group of insecticides against which *T. absoluta* show some levels of resistance with a control failure likelihood between 51% and 91%. This is coherent with the low level of efficacy reported by the local producers during our insect collection. Earlier evidences of the inefficiency of some of these chemicals were reported around the globe, and since 1980 in Bolivia (Moore, 1983).

(2) The insecticides of our second group, comprising chlorpyriphos, spinosad, and abamectin, are considered efficient to control *T. absoluta* populations from Burkina Faso without significant risk of control failure. Spinosad and abamectin show low LC50 values (<0.60 mg/L) and high slope values (>1.0). Similar LC50 values were obtained for abamectin in Turkey and Brazil (Siqueira et al., 2001; Silva et al., 2011, 2016b; Konuş, 2014; Barati et al., 2018) and for spinosad in Iran, Greece, Spain, Brazil, and Turkey (Campos et al., 2015a; Yalçin et al., 2015; Silva et al., 2016a; Roditakis et al., 2017a, 2018; Barati et al., 2018). The relatively lower expression of resistance against abamectin could be explained by the fact that this product is used at lower doses in the field, is typically used to control mites and is more rapidly degraded in the environment with low bioaccumulation (Clark et al., 1995). However, based on a rapid survey we performed during our samplings, farmers now started using extensively these products to control the leafminers, with repeated treatments and unrecommended elevated doses. It would not be surprising to see in close future the emergence of resistance, as observed in Europe (Roditakis et al., 2013a, b; Yalçin et al., 2015). Regarding chlorpyrifos-ethyl, observed LC50 are similar to those obtained in Greece and Brazil where the populations were considered sensible (Roditakis et al., 2013a, b; Campos et al., 2014; Haddi et al., 2017).

(3) Finally, the microbiological insecticide *Bacillus thuringiensis* showed contrasted results among the surveyed populations, with LC50 ranging from 7 (Pindga population) to 69 UI/l (Ouahigouya population). Low slopes values were also observed for the populations expressing higher LC50 values (Ouahigouya and Goué) with a Control failure likelihood equal to 30% for the population of Ouahigouya, suggesting that these populations express higher levels of resistance against this biological product. The likely explanation for this resistance is that after the discovery of *T. absoluta* in 2016 in Ouahigouya, Bt pesticides were recommended to growers in that locality. This molecule has been used so abusively that there has even been a rupture and an increase in the price of the product on the market. The microbial-based insecticide *B. thuringiensis* was reported efficient in the North of the African continent, especially in Egypt and Tunisia (Kaouthar et al., 2011; El-Aassar et al., 2015). The same range of LC50 values were associated with Bt-sensitive populations in Iran and Brazil (Silva et al., 2011; Barati et al., 2018). But multiple insect species, including *T. absoluta*, have developed a resistance to *B. thuringiensis*, especially Lepidopterans, thanks to a mutation in the membrane transporter ABCC2 (Moore, 1983; Baxter et al., 2011).

Previous reports highlighted the need to reinforce preventive measures of control at the borders of the country, to limit the importation and exportation of contaminated fruits and plants (Son et al., 2017b). But the widespread of established populations of the tomato leafminer in Sub-Saharan African countries make the few existing preventive measures obsolete. It now seems much more important to protect the incomes of local farmers by proposing integrated pest management strategies adapted to local socio-economic and technical conditions. Alternatives to the chemical and biological substances tested in the present study exist and showed efficiency in Africa and outside (Jactel et al., 2019). Biological insecticides should be favoured and included in the IPM program: Spinosad was found effective in the present study, and neem extracts were previously shown effective in controlling *T. absoluta* in Egyptian open-field tomatoes (Khidr et al., 2013). Alternative control measures include pheromone-based mass trapping, insect-proof nets, and the conservation and release of indigenous biological control agents (Caparros Megido et al., 2013a, b, 2014; Mansour et al., 2018). Among them, numerous *Nesidiocoris tenuis* were observed in the tomato fields during the present study. The opportunity to mass produce and release them should be considered. Finally, one should identify the host reservoir of the leafminer, probably used to survive during crop rotation (Cherif & Verheggen, 2019).

Acknowledgements

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 conflicts of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Abbas, M.S.T., Aboo-Zeid, N.A. & Megahed, M.M. (1993) On the natural enemies of the potato tuber moth *Phthorimaea operculella* in Egypt. *Egyptian Journal of Agricultural Research*, **71**, 943–950.

Abbot, W.S. (1925) A method of computing the effectiveness of an insecticide. *Journal of Economic Entomology*, **18**, 265–266.

Barati, R., Hejazi, M.J. & Mohammadi, S.A. (2018) Insecticide susceptibility in *Tuta absoluta* (Lepidoptera: Gelechiidae) and metabolic characterization of resistance to diazinon. *Journal of Economic Entomology*, **20**, 1–7.

Baxter, S.W., Badenes-Pérez, F.R., Morrison, A. *et al.* (2011) Parallel evolution of *Bacillus thuringiensis* toxin resistance in lepidoptera. *Genetics*, **189**, 675–679.

Berger, M., Puinean, A.M., Randall, E. *et al.* (2016) Insecticide resistance mediated by an exon skipping event. *Molecular Ecology*, **25**, 5692–5704.

Biondi, A., Guedes, R.N.C., Wan, F. & Desneux, N. (2018) Ecology, worldwide spread, and management of the invasive South American tomato pinworm, *Tuta absoluta*: past, present, and future. *Annual Review of Entomology*, **63**, 239–258.

Campos, M.R., Rodrigues, A.R.S., Silva, W.M. *et al.* (2014) Spinosad and the tomato borer *Tuta absoluta*: a bioinsecticide, an invasive pest threat, and high insecticide resistance. *PLoS One*, **9**, 1–12.

Campos, M.R., Silva, T.B.M., Silva, W.M. *et al.* (2015a) Spinosyn resistance in the tomato borer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Journal of Pest Science*, **88**, 405–412.

Campos, M.R., Silva, T.B.M., Silva, W.M. *et al.* (2015b) Susceptibility of *Tuta absoluta* (Lepidoptera: Gelechiidae) Brazilian populations to ryanodine receptor modulators. *Pest Management Science*, **71**, 537–544.

Caparros Megido, R., Brostaux, Y., Haubruge, E. & Verheggen F.J. (2013a) Propensity of the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), to develop on four potato plant varieties. *American Journal of Potato Research*, **90**, 255–260.

Caparros Megido, R., Haubruge, E. & Verheggen, F. J. (2013b). Pheromone-based management strategies to control the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae). A review. *Biotechnology, Agronomy, Society and Environment*, **17**, 475–482.

Caparros Megido, R., De Backer, L., Ettaïb, R. *et al.* (2014) Role of larval host plant experience and solanaceous plant volatile emissions in *Tuta absoluta* (Lepidoptera: Gelechiidae) host finding behavior. *Arthropod-Plant Interactions*, **8**, 293–304.

Cherif, A. & Verheggen, F. (2019) A review of *Tuta absoluta* (Lepidoptera: Gelechiidae) host plants and their impact on management strategies. *Biotechnology, Agronomy, Society and Environment*, **23**, 270–278.

Clark, J.M., Scott, J.G., Campos, F. & Bloomquist, J.R. (1995) Resistance to avermectins: extent, mechanisms, and management implications. *Annual Review of Entomology*, **40**, 1–30.

Desneux, N., Wajnberg, E., Wyckhuys, K.A.G., *et al.* (2010) Biological invasion of European tomato crops by *Tuta absoluta*: ecology, geographic expansion and prospects for biological control. *Journal of Pest Science*, **83**, 197–215.

Desneux, N., Luna, M.G., Guillemaud, T. & Urbaneja, A. (2011) The invasive South American tomato pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: the new threat to tomato world production. *Journal of Pest Science*, **84**, 403–408.

Douris, V., Papapostolou, K.M., Ilias, A. *et al.* (2017) Investigation of the contribution of RyR target-site mutations in diamide resistance by CRISPR/Cas9 genome modification in Drosophila. *Insect Biochemistry and Molecular Biology*, **87**, 127–135.

El-Aassar, M.R., Soliman, M.H.A. & Abd Elaal, A.A. (2015) Efficiency of sex pheromone traps and some bio and chemical insecticides against tomato borer larvae, *Tuta absoluta* (Meyrick) and estimate the damages of leaves and fruit tomato plant. *Annals of Agricultural Sciences*, **60**, 153–156.

FAOSTAT. (2019) *Tomato Production Situation in Burkina Faso* [WWW document]. URL http://www.fao.org/faostat/fr/#data/QC [accessed on 23 may 2019].

Finney, D.J. (1964) *Probit Analysis*. Cambridge University Press, Cambridge, UK.

Grant, C., Jacobson, R., Ilias, A. *et al.* (2019) The evolution of multiple-insecticide resistance in UKpopulations of tomato leafminer, *Tuta absoluta*. *Pest Management Science*, **75**, 2079–2085.

Guedes, R.N.C. (2017) Insecticide resistance, control failure likelihood and the first law of geography. *Pest Management Science*, **73**, 479–484.

Guedes, R.N.C. & Siqueira, H.A.A. (2012) The tomato borer *Tuta absoluta*: insecticide resistance and control failure. *CAB Reviews* **7**: 1–7.

Guillemaud, T., Blin, A., LeGoff, I. *et al.* (2015) The tomato borer, *Tuta absoluta*, invading the Mediterranean Basin, originates from a single introduction from Central Chile. *Scientific Reports*, **14**, 1–5.

Haddi, K., Berger, M., Bielza, P. *et al.* (2012) Identification of mutations associated with pyrethroid resistance in the voltage-gated sodium channel of the tomato leaf miner (*Tuta absoluta*). *Insect Biochemistry and Molecular Biology*, **42**, 506–513.

Haddi, K., Berger, M., Bielza, P. *et al.* (2017) Mutation in the ace-1 gene of the tomato leaf miner (*Tuta absoluta*) associated with organophosphates resistance. *Journal of Applied Entomology*, **141**, 612–619.

Jactel, H., Verheggen, F., Thiéry, D., *et al.* (2019) Alternatives to neonicotinoids. *Environment International*, **129**, 423–429.

Kaouthar, L.G., Manel, S., Mouna, M. & Ridha, B. (2011) Lutte intégrée contre la mineuse de la tomate, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) en Tunisie. *Entomologie faunistique*, **63**, 125–132.

Karaağaç, U.S. (2015) Enzyme activities and analysis of susceptibility levels in Turkish *Tuta absoluta* populations to chlorantraniliprole and metaflumizone insecticides. *Phytoparasitica*, **43**, 693–700.

Khidr, A.A., Gaffar, S.A., Nada, M.S. *et al.* (2013) New approaches for controlling tomato leafminer, *Tuta absoluta* (Meyrick) in tomato fields in Egypt. *Egyptian Journal of Agricultural Research*, **91**, 335–348.

Konuş, M. (2014) Analysing resistance of different *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) strains to abamectin insecticide. *Turkish Journal of Biochemistry*, **39**, 291–297.

MAH. (2001) *Recensement General de L'agriculture: Rapport Générale du Module Maraîchage. Ministère de l'Agriculture et de l'Hydraulique du Burkina Faso* [WWW document]. URL http://cns.bf/IMG/pdf/rga_maraichage_derniere_version.pdf [accessed on 22 may 2019].

Mansour, R., Brévault, T., Chailleux, A. *et al.* (2018) Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomologia Generalis*, **38**, 83–112.

Michaelides, G., Seraphides, N., Pitsillou, M. & Sfenthourakis, S. (2019) Susceptibility of Cypriot Tuta absoluta populations to four targeted insecticides and control failure likelihood. *Journal of Applied Entomology*, **143**, 508–517.

Miranda, M.M.M., Picanço, M., Zanuncio, J.C. & Guedes, R.N.C. (1998) Ecological Life Table of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Biocontrol Science and Technology*, **8**, 597–606.

Mirhosseini, M.A., Fathipour, Y., Holst, N. *et al.* (2019) An egg parasitoid interferes with biological control of tomato leafminer by augmentation of *Nesidiocoris tenuis* (Hemiptera*: Miridae*). *Biological Control*, **133**, 34–40.

Moore, J.E. (1983) Control of tomato leafminer (*Scrobipalpula absoluta*) in Bolivia. *Tropical Pest Management*, **29**, 231–238.

Moradi, S., Khani, S., Ansari, M. & Shahlaei, M. (2019) Atomistic details on the mechanism of organophosphates resistance in insects:

Insights from homology modeling, docking and molecular dynamic simulation. *Journal of Molecular Liquids*, **276**, 59–66.

Pfeiffer, D.G., Muniappan, R., Sall, D. *et al.* (2013) First record of *Tuta absoluta* (Lepidoptera: Gelechiidae) in Senegal. *Florida Entomologist*, **96**, 661–662.

Pouey, G.F., Chirinos, D.T. & Rivero, G. (1994) Notas sobre *Keiferia lycopersicella* (Walsingham), (Lepidoptera: Gelechiidae), en Venezuela. *Boletín de entomología venezolana*, **9**, 203–206.

Reyes, M., Rocha, K., Alarcón, L. *et al.* (2012) Metabolic mechanisms involved in the resistance of field populations of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) to spinosad. *Pesticide Biochemistry and Physiology*,**102**, 45–50.

Roditakis, E., Skarmoutsou, C. & Staurakaki, M. (2013a) Toxicity of insecticides to populations of tomato borer *Tuta absoluta* (Meyrick) from Greece. *Pest Management Science*, **69**, 834–840.

Roditakis, E., Skarmoutsou, C., Staurakaki, M. *et al.* (2013b) Determination of baseline susceptibility of European populations of *Tuta absoluta* (Meyrick) to indoxacarb and chlorantraniliprole using a novel dip bioassay method. *Pest Management Science*, **69**, 217–227.

Roditakis, E., Mavridis, K., Riga, M. *et al.* (2017a) Identification and detection of indoxacarb resistance mutations in the para sodium channel of the tomato leafminer, *Tuta absoluta*. *Pest Management Science*, **73**, 1679–1688.

Roditakis, E., Steinbach, D., Moritz, G. *et al.* (2017b) Ryanodine receptor point mutations confer diamide insecticide resistance in tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae). *Insect Biochemistry and Molecular Biology*, **80**, 11–20.

Roditakis, E., Vasakis, E., García-Vidal, L. *et al.* (2018) A four-year survey on insecticide resistance and likelihood of chemical control failure for tomato leaf miner *Tuta absoluta* in the European/Asian region. *Journal of Pest Science*, **91**, 421–435.

Silva, G.A., Picanço, M.C., Bacci, L. *et al.* (2011) Control failure likelihood and spatial dependence of insecticide resistance in the tomato pinworm, *Tuta absoluta*. *Pest Management Science*, **67**, 913–920.

Silva, W.M., Berger, M., Bass, C. *et al.* (2015) Status of pyrethroid resistance and mechanisms in Brazilian populations of *Tuta* absoluta. *Pesticide Biochemistry and Physiology*, **122**, 8–14.

Silva, W.M., Berger, M., Bass, C. *et al.* (2016a) Mutation (G275E) of the nicotinic acetylcholine receptor α6 subunit is associated with high levels of resistance to spinosyns in *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Pesticide Biochemistry and Physiology*, **131**, 1–8.

Silva, T.B.M., Silva, W.M., Campos, M.R. *et al.* (2016b) Susceptibility levels of *Tuta absoluta* (Meyrick) (Lepidoptera: *Gelechiidae*) to minor classes of insecticides in Brazil. *Crop Protection*, **79**, 80–86.

Siqueira, H.A.A., Guedes, R.N.C., Picanco, M.C. (2000) Cartap resistance and synergism in populations of *Tuta absoluta* (Lepidoptera: Gelechiidae). *Journal of Applied Entomology*, **124**, 233–238.

Siqueira, H,A,A., Guedes, R.N.C., Fragoso, D.B. & Magalhaes, L.C. (2001) Abamectin resistance and synergism in Brazilian populations of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *International Journal of Pest Management*, **47**, 247–251.

Son, D., Bonzi, S., Somda, I. *et al.* (2017a) First record of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) in Burkina Faso. *African Entomology*, **25**, 259–263.

Son, D., Somda, I., Legreve, A. & Schiffers, B. (2017b) Pratiques phytosanitaires des producteurs de tomates du Burkina Faso et risques pour la santé et l'environnement. *Cahiers Agricultures*, **26**, 1–6.

Tonnang, H.E., Mohamed, S.F., Khamis, F. & Ekesi S (2015) Identification and risk assessment for worldwide invasion and spread of *Tuta absoluta* with a focus on Sub-Saharan Africa: implications for phytosanitary measures and management. *PloS One* **10**: e0135283.

Urbaneja, A., Vercher, R., Navarro, V. *et al.* (2007) La polilla del tomate, *Tuta absoluta*. *Phytoma Espana*, **194**, 16–23.

Verheggen, F. & Fontus, R.B. (2019) First record of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Haiti. *Entomologia Generalis*, **38**, 349–353.

Yalçin, M., Mermer, S., Kozaci, L.D. & Turgut C (2015) Insecticide resistance in two populations of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) from Turkey. *Türkiye Entomoloji Dergisi*, **39**, 137–145.

Zibaee, I., Mahmood, K., Esmaeily, M. *et al.* (2018) Organophosphate and pyrethroid resistances in the tomato leaf miner *Tuta absoluta* (Lepidoptera: Gelechiidae) from Iran. *Journal of Applied Entomology*, **142**, 181–191.

Accepted 29 July 2020