



Geographic variation of host preference by the invasive tomato leaf miner *Tuta absoluta*: implications for host range expansion

Serigne Sylla^{1,2} · Thierry Brévault^{2,3,4} · Lucie S. Monticelli⁵ · Karamoko Diarra¹ · Nicolas Desneux⁵

Received: 8 March 2018 / Revised: 7 February 2019 / Accepted: 18 February 2019 / Published online: 5 March 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Host range evolution is a central issue for pest management, particularly for invasive species of agricultural importance. The invasive tomato leaf miner, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), a key pest of tomato in Europe and recently in sub-Saharan Africa, is a good model organism to better understand underlying processes. We studied oviposition acceptance (proportion of females accepting a given plant as host for laying egg), oviposition preference (number of eggs laid by females on a given host plant) and performance (offspring development estimated as survival from egg to adult) of two *T. absoluta* populations originating from France (FRA) and Senegal (SEN) on six solanaceous plants (tomato, eggplant, Ethiopian eggplant, potato, sweet pepper and pepper). The ovipositional behavioral pattern differed between the two populations; the SEN population showed higher oviposition acceptance on Ethiopian eggplant and sweet pepper than the FRA population. In addition, SEN population showed higher oviposition preference toward sweet pepper and potato than the FRA population. By contrast, the FRA population showed higher preference toward tomato and eggplant than the SEN population. The two populations of *T. absoluta* performed best on tomato (the preferred host plant) and showed similar decreasing trend in performance when comparing the two populations on the various other host plants. For both populations, performance on solanaceous plant species was closely related to ovipositional response of females to these plants. The differences observed between the two populations may indicate an ongoing differentiation in the host range of *T. absoluta* in the two invaded areas, possibly due to the abundance of these alternative host crops in Senegal at a period when tomato crops are scarce.

Keywords Preference–performance · Host use · Adaptation · Solanaceae · Invasive species

Key message

- Preference–performance traits of French and Senegalese *Tuta absoluta* populations (FRA and SEN, respectively) were evaluated on six solanaceous plants.

- Both *T. absoluta* populations preferred and performed best on tomato.
- SEN showed higher acceptance than FRA for Ethiopian pepper and showed higher preference than FRA for potato.
- Survival from egg to adult on the various plants did not differ between the two populations.
- The results suggest ongoing differentiation in the host range of *T. absoluta* across invaded areas.

Communicated by M. Traugott.

✉ Serigne Sylla
syllaserigne2@gmail.com

¹ Faculté des Sciences et Techniques, Université Cheikh Anta Diop (UCAD), Dakar, Senegal
² BIOPASS, CIRAD-IRD-ISRA-UCAD, Dakar, Senegal
³ CIRAD, UPR AIDA, 34398 Montpellier, France
⁴ AIDA, Univ Montpellier, CIRAD, Montpellier, France
⁵ INRA (French National Institute for Agricultural Research), Université Côte d'Azur, CNRS, UMR 1355-7254, Institut Sophia Agrobiotech, 06903 Sophia Antipolis, France

Introduction

Phytophagous insects account for a large part of terrestrial biodiversity (Strong et al. 1984). Understanding the mechanisms underlying their diversity has been a central topic in ecology and evolutionary biology (Ehrlich and Raven 1964; Futuyma and Moreno 1988; Jaenike 1990; Mitter and Farrell 1991; Futuyma and Agrawal 2009). Some species show

geographic variations in the use of host plants, which may be a recent or ongoing evolutionary process (Singer et al. 1992; Bigger and Fox 1997; Thompson 1999; Funk and Bernays 2001; Nylín et al. 2009; Kohyama et al. 2012). Such changes in host use pattern of herbivorous insects may occur when populations experience new plant species, and adaptation to new host plants can involve changes in life history traits such as adult oviposition behavior, larval feeding behavior and/or digestive physiology (Dethier 1954; Bush 1975; Feeny et al. 1985). Oligophagous species can colonize new hosts in areas where their original or preferred hosts are absent or much less abundant. The availability of new hosts can therefore facilitate the continued expansion of such species in regions beyond the geographic scope of native hosts. For example, the common brimstone, *Gonepteryx rhamni* L. (Lepidoptera, Pieridae), one of the few butterflies with host-limited spatial distribution, was able to expand its British distribution following the introduction of extra host plants in North Wales (Gutiérrez and Thomas 2001).

Herbivorous insects specialization has been viewed as the result of an optimization process of a host plant use, potentially limiting larval performance on other hosts (Futuyma and Moreno 1988). The ‘trade-off’ hypothesis for food specialization postulates that increased performance on a given resource comes at the cost of decreased performance on other resources (Jaenike 1990; Noriyuki and Osawa 2012). The ‘trade-off’ hypothesis is tightly linked to the ‘preference–performance’ stating that females will tend to oviposit on hosts on which their offspring perform the best, particularly when offspring are poorly mobile (Gripenberg et al. 2010). Accordingly, females should prefer hosts that are most suitable for larval development and accept less suitable plant species when the preferred host is either absent or not found (Jaenike 1978; Thompson 1988; Scheirs and Bruyn 2001; Awmack and Leather 2002). In oligophagous insects, relation between female preference and larval performance should be very tight as larvae can survive only in a small number of host plants. However, some studies indicate that females of some insect species do not select exclusively plants or habitats that are optimal for larval growth (Wiklund 1975; Rausher 1979; Friberg et al. 2008), and can lay eggs on plants that are unsuitable for offspring development (Chew 1975; 1981). Assessing the relationship between adult oviposition preference and larval performance is thus of utmost importance to better understand host specificity and host shifts, particularly for invasive insect species (Futuyma and Agrawal 2009).

The tomato leaf miner, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), native to South America, has become a key invasive pest of tomato (Desneux et al. 2010; Campos et al. 2017). It was first observed outside South America in Eastern Spain in 2006 and 2 years later in North Africa, where damage in greenhouses and open fields reached

80–100% (Desneux et al. 2011; Biondi et al. 2018). The pest was then detected in most sub-Saharan African countries (Adamou et al. 2016; Son et al. 2017; Visser et al. 2017, and see Mansour et al. 2018 for a review), including Senegal (Pfeiffer et al. 2013; Brévault et al. 2014; Sylla et al. 2017). It has also been reported in the Middle East (Campos et al. 2017) and more recently in India (Sankarganesh et al. 2017) threatening now China tomato crops (Xian et al. 2017; Han et al. 2018). In a recent study, Guillemaud et al. (2015) provided strong evidence that a single introduction from Chile to Spain has occurred, followed by a geographic expansion in the Afro-Eurasia supercontinent. The same study indicated an almost complete absence of genetic structuring in the invaded areas from southern Spain to Israel and from Israel to Morocco. Many cultivated host plants, primarily from the family Solanaceae, have been reported for *T. absoluta* (Table 1). However, oviposition preference or larval performance on such host plants has been partially assessed, particularly in recently invaded areas. Besides cultivated Solanaceae, *T. absoluta* was reported to lay eggs and develop on wild solanaceous plants such as *Solanum nigrum* L. (black nightshade), *Atropa belladonna* L. and *Datura stramonium* L. (Desneux et al. 2010; Bawin et al. 2015; Abbes et al. 2016).

In the present study, we assessed the oviposition acceptance–preference and developmental performance of immature stages on various host plants of two populations of *T. absoluta* originating from Europe (France) and sub-Saharan Africa (Senegal). We hypothesized that any significant difference between the two populations in oviposition acceptance–preference or larval performance on a series of host plants might indicate possible ongoing differentiation of their respective host range. Based on the trade-off and preference–performance hypotheses, the objective was to verify to what extent (1) immature stages perform better on the most preferred host and (2) local availability of alternative host plants can alter the preference–performance relationship. Results are discussed in the light of possible genetic-based adaptation to resources available in the invaded areas and potential for host shift.

Materials and methods

Laboratory experiments

Two populations of *T. absoluta* were used for laboratory experiments. The French strain (FRA) originated from 65 individuals collected in 2009 on greenhouse tomato plants in the South of France, to which at least 50 tomato field-collected individuals were added yearly. The Senegal strain (SEN) originated from collections of > 200 larvae on tomato fields in the Niayes area of Senegal in January 2015. Both

Table 1 Host crops of the tomato leaf miner, *Tuta absoluta*, in native (South America) versus invaded areas (Europe and Africa)

| Area | Family | Host plant | Common name | Main reference | Importance ^a |
|--------------------------|--------------------------|--------------------------------|----------------------------|----------------------------|-------------------------|
| Native South America | Solanaceae | <i>Solanum lycopersicum</i> | Tomato | Vargas (1970) | +++ |
| | | <i>Solanum tuberosum</i> | Potato | Campos (1976) | ++ |
| | | <i>Solanum melongena</i> | Eggplant | Galarza (1984) | ++ |
| | | <i>Solanum sisymbriifolium</i> | Litchi tomato | Galarza (1984) | + |
| | | <i>Capsicum annuum</i> | Pepper | García and Espul (1982) | + |
| | | <i>Nicotiana tabacum</i> | Tobacco | Mallea et al. (1974) | + |
| | | <i>Nicotiana rustica</i> | Mapacho tobacco | Desneux et al. (2010) | + |
| | | <i>Nicandra physalodes</i> | Apple pf Peru | Desneux et al. (2010) | + |
| | | <i>Solanum dulcamara</i> | Bittersweet | Vargas (1970) | + |
| Invaded Europe | Solanaceae | <i>Solanum lycopersicum</i> | Tomato | Urbaneja et al. (2013) | +++ |
| | | <i>Solanum tuberosum</i> | Potato | Desneux et al. (2010) | +++ |
| | | <i>Solanum melongena</i> | Eggplant | Desneux et al. (2010) | ++ |
| | | <i>Solanum muricatum</i> | Pepino | Wyckhuys et al. (2013) | + |
| | | <i>Capsicum annuum</i> | Pepper | Portakaldali et al. (2013) | + |
| | | <i>Nicotiana tabacum</i> | Tobacco | Desneux et al. (2010) | + |
| | | <i>Physalis peruviana</i> | Cape gooseberry | Tropea Garzia (2009) | + |
| | Amaranthaceae | <i>Chenopodium album</i> | Lamb's quarters | Portakaldali et al. (2013) | + |
| | | <i>Beta vulgaris vulgaris</i> | Sugar beet | Portakaldali et al. (2013) | + |
| | Convolvulaceae | <i>Convolvulus arvensis</i> | Field Bindweed | Portakaldali et al. (2013) | + |
| <i>Calystegia sepium</i> | | Hedge Bindweed | Portakaldali et al. (2013) | + | |
| Fabaceae | <i>Phaseolus vulgari</i> | Common bean | Wyckhuys et al. (2013) | + | |
| Invaded Africa | Solanaceae | <i>Solanum lycopersicum</i> | Tomato | Kharroubi (2008) | +++ |
| | | <i>Solanum tuberosum</i> | Potato | Guenauoui (2008) | ++ |
| | | <i>Solanum melongena</i> | Eggplant | Guenauoui (2008) | ++ |
| | | <i>Solanum aethiopicum</i> | African eggplant | Brévault et al. (2014) | + |
| | | <i>Capsicum annuum</i> | Pepper | Ouardi et al. (2012) | + |

^aImportance describes the incidence of damage caused by *T. absoluta* on the various possible host plants, the magnitude of potential negative effects of infestation (+, ++ or +++) is relative to the optimal host (i.e. tomato being at maximum of negative impact: +++)

colonies were reared under laboratory conditions (photoperiod 16L:8D, 25 ± 2 °C, 65 ± 10% R.H.) in mesh cages (120 × 70 × 125 cm) containing four tomato potted plants and honey/water mix (10%) provided ad libitum.

Six main solanaceous plants commonly found in the main vegetable-cropping area in Senegal were selected to assess *T. absoluta* oviposition acceptance–preference and larval performance under laboratory conditions: tomato (*S. lycopersicum* cv. Xina, Tropicasem), potato (*S. tuberosum* cv. Alaska, Gopex), pepper (*C. frutescens* cv. Bombardier, Technisem), sweet pepper (*C. annuum* cv. Goliath F1, Technisem) and two eggplant species (*S. melongena* cv. Kalenda F1, Technisem and *S. aethiopicum* cv. Keur Mbir Ndao, Tropicasem). Plants were grown using small plastic pots filled with commercial compost.

Oviposition acceptance and Oviposition preference—Female oviposition acceptance and preference for the six selected solanaceous plants were individually assessed in no choice tests. Gravid females were considered mated as they were kept together in cohorts with males for a minimum of 5 days before being used in oviposition experiments. Tests were performed in cylindrical plastic cages (10 cm diameter and 20 cm height) containing one single plant (4 weeks). Eggs were counted on plants 24 h after release of females

into cages defining the oviposition acceptance as the proportion of females that laid at least one egg on the plant species tested and the oviposition preference as the number of eggs laid by females on the tested plants. Twelve replicates were performed for each plant species.

Juvenile Performance (egg to adult)—For each of the six selected solanaceous plants, three eggs per plant (on 10 plants) were individually placed on randomly selected leaves covered with a mesh bag. Then, egg hatching, larval development and adult emergence were checked daily. The offspring development was estimated as the proportion of surviving individuals from egg to adult, as well as the development time to reach adulthood. Laboratory experiments were conducted in climatic chambers at 25 ± 1 °C, 65 ± 10% R.H., and a photoperiod 16L:8D (hours).

Field survey

Monitoring of a set of 527 solanaceous field crops was carried out over two cropping seasons (from January to June) in 2014 and 2015 in the main vegetable-producing area in Senegal (Niayes). The objective was to assess the host plant range of *T. absoluta* and the proportion of infested plants. In each sampled field, 24 plants were randomly selected and

checked for the presence of *T. absoluta* mines (with or without larvae).

Statistical analyses

All statistical analyses were carried out using R version 3.2.3 (R. Core Team 2015). Oviposition acceptance (proportion of females that laid at least one egg on tested plants) or preference (number of eggs laid by females on tested plants) were compared on the six tested solanaceous plants as well as between the two populations (FRA and SEN) for each plant using a generalized linear model with a binomial distribution (link = logit) and a Poisson error distribution (link = log), respectively ('stats' package). A generalized linear model, respectively, with a binomial distribution (link = logit) and a Poisson error distribution (link = log) was used to analyze the effect of plant species on egg and larval performance (survival and development time from egg to adult). Multiple comparisons of mean values were performed with the least significant difference (Tukey) post hoc test ($P < 0.05$) using the 'multcomp' package. A MANOVA Wilk's test was used to compare the performance end points between the two populations per given host plant. Occurrence (proportion of infested fields) and incidence (proportion of infested plants) of *T. absoluta* as a function of monitored solanaceous field crops were analyzed using a generalized linear model with a binomial distribution (link = logit). The relationship between larval performance and oviposition acceptance–preference or field incidence was assessed using Spearman's correlation.

Results

Oviposition acceptance and oviposition preference

The oviposition acceptance of females from both the FRA and SEN populations varied depending on the plant species encountered ($\chi^2_5 = 48.3$, $P < 0.001$, $\chi^2_5 = 65.5$, $P < 0.001$, respectively) (Fig. 1a). The proportion of females from the FRA and SEN populations that laid at least one egg on the plant was the highest on *S. lycopersicum* (11/12 for both populations), whereas it was the lowest on *C. annuum* (0/12 and 3/12, respectively) and *C. frutescens* (0/12 for both populations). This proportion differed also depending on the population tested. The SEN population had a higher oviposition acceptance on *S. aethiopicum* and *C. annuum* than the FRA population ($\chi^2_1 = 4.64$, $P = 0.031$, $\chi^2_3 = 6.89$, $P = 0.032$, respectively), as well as in case of *S. tuberosum*, although it was only marginally significant ($\chi^2_1 = 2.72$, $P = 0.099$).

The oviposition preference of females from both the FRA and SEN populations varied depending on the plant species encountered ($\chi^2_5 = 814.76$, $P < 0.001$, $\chi^2_5 = 290.08$,

$P < 0.001$, respectively) (Fig. 1b). The number of eggs laid by the FRA and SEN females was the highest on *S. lycopersicum* (≈ 23 and 11, respectively), whereas it was the lowest on *C. annuum* (0 and ≈ 1 , respectively) and *C. frutescens* (no eggs deposited by the two parasitoid populations). This number differed also depending on the population tested. The FRA population laid a higher number of eggs than the SEN population in *S. lycopersicum* and *S. melongena* ($\chi^2_1 = 48.53$, $P < 0.001$, $\chi^2_1 = 33.88$, $P < 0.001$, respectively), whereas the SEN population laid a higher number of eggs than the FRA population in *S. tuberosum* and *C. annuum* ($\chi^2_1 = 14.01$, $P < 0.001$, $\chi^2_1 = 8.32$, $P = 0.004$, respectively).

Juvenile performance (egg to adult)

Proportion of eggs reaching the adult stage varied significantly depending on the plant species for the FRA ($\chi^2_5 = 187.07$, $P < 0.001$) and SEN ($\chi^2_5 = 179.09$, $P < 0.001$) populations (Table 2). Survival rate of the FRA population was higher on *S. lycopersicum* than that on *S. melongena* and *S. tuberosum*, themselves higher than on *S. aethiopicum*. Survival rate of SEN did not significantly differ on *S. lycopersicum* and *S. melongena*, but was higher on *S. lycopersicum* than on *S. tuberosum* and *S. aethiopicum* (Table 2). For both populations, there was low or no survival on *C. annuum* and *C. frutescens*, respectively. Survival from egg to adult did not differ significantly between populations, for one given host plant (MANOVA Wilk's test, $P > 0.05$).

Development time from egg to adult also differed significantly depending on the plant species for the FRA ($\chi^2_4 = 5.46$, $P < 0.01$) and SEN ($\chi^2_4 = 9.24$, $P < 0.001$) populations (Table 2). For both populations, it was the shortest when larvae fed on *S. lycopersicum*. Larvae from the SEN population developed faster than those of the FRA population when they fed on *S. lycopersicum* ($F = 27.0$, $P < 0.01$) and *S. tuberosum* ($F = 42.3$, $P < 0.01$). No difference between strains was observed on other tested plants.

Oviposition acceptance and performance (survival from egg to adult) were highly correlated for FRA ($r = 0.92$, $P < 0.01$) and SEN ($r = 0.99$, $P < 0.01$) (Fig. 2a). Oviposition preference and performance were also highly correlated for FRA ($r = 0.88$, $P < 0.01$) and SEN ($r = 0.91$, $P < 0.01$) (Fig. 2b).

Field survey

Most tomato fields (> 90% occurrence) showed symptoms of *T. absoluta* presence (Table 3). Damage caused by *T. absoluta* was lower ($\chi^2_{5,517} = 474.4$; $P < 0.001$), but also frequently observed (> 50% occurrence) on potato and eggplant fields and more sporadically in Ethiopian eggplant, sweet pepper and pepper fields (25% occurrence). The incidence of the pest was the highest in tomato fields,

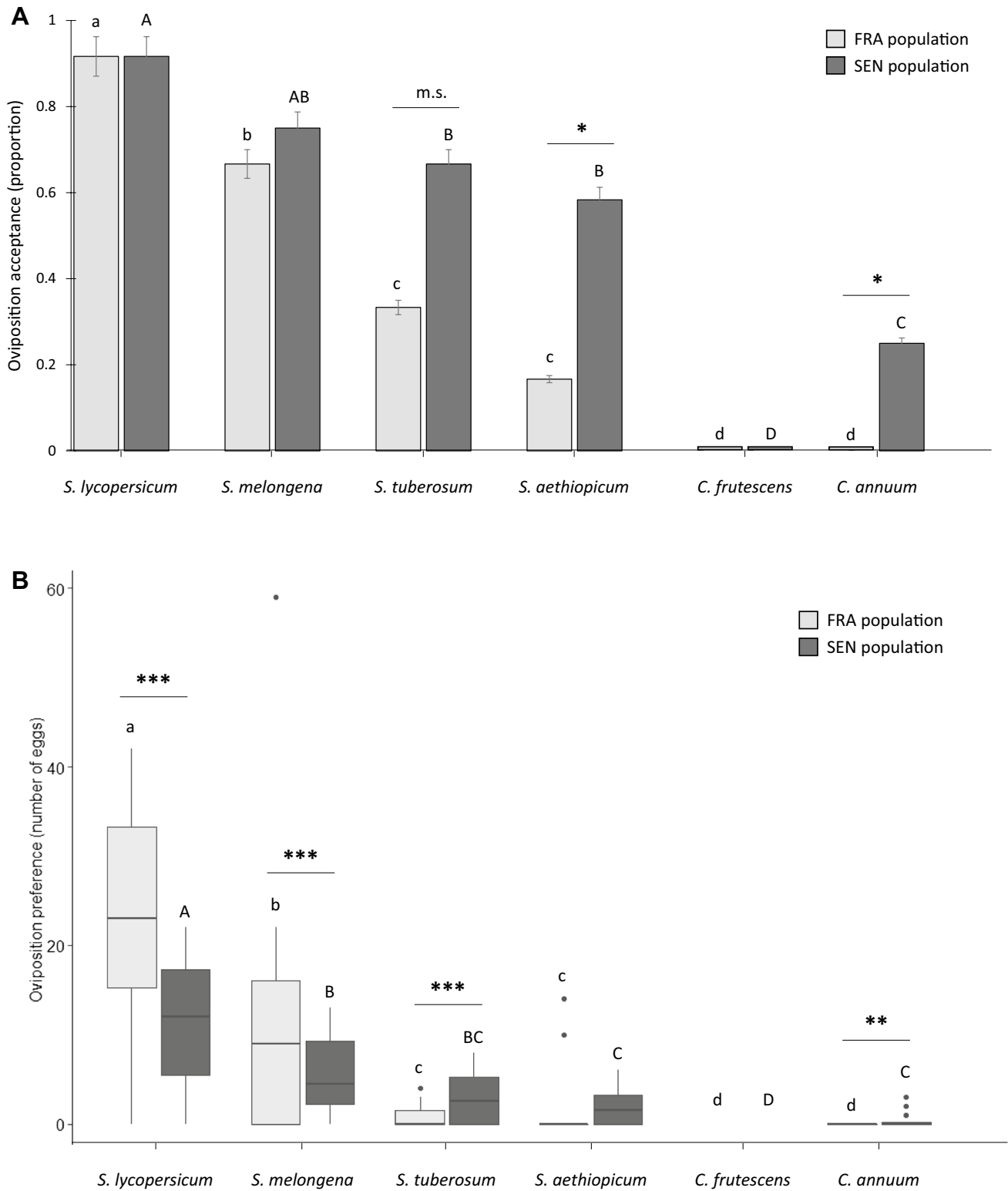


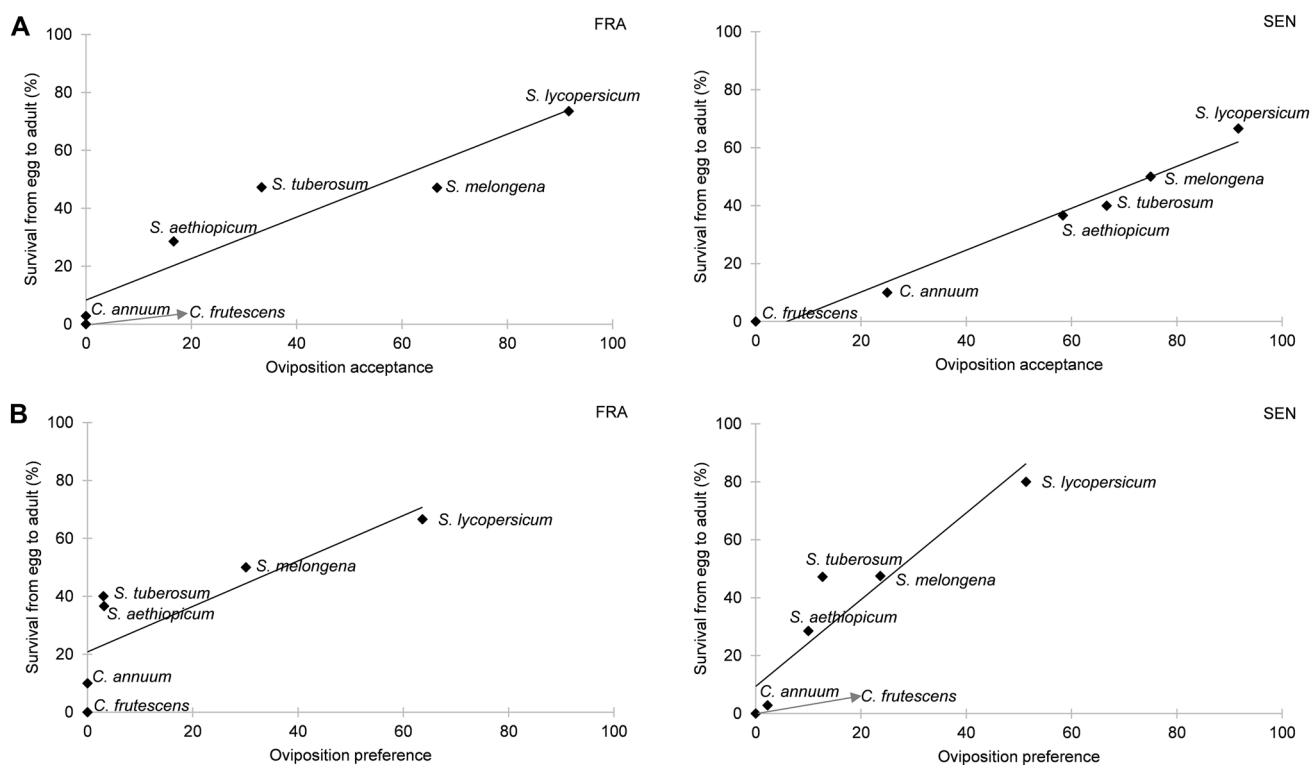
Fig. 1 **a** Oviposition acceptance (mean proportion of females that laid at least one egg on tested host plants \pm SEM) and **b** oviposition preference (number of eggs laid by females on tested plants \pm SEM) of *Tuta absoluta* females on six solanaceous plants. For one given population (FRA or SEN), bars followed by the same letter are not

significantly different from each other according to Tukey’s post hoc test ($P < 0.05$). Asterisks indicate significant difference between the two populations in oviposition acceptance or preference for a given plant, according to MANOVA Wilk’s test (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; m.s. means marginally significant $P < 0.10$)

Table 2 Mean (\pm SE) values of the performance (survival and development time from egg to adult) of two *Tuta absoluta* populations from Senegal (SEN) and France (FRA) on six solanaceous plants

| Plant species | FRA | | SEN | |
|-----------------------------|-------------------|-------------------------|--------------------|-------------------------|
| | Survival (%) | Development time (days) | Survival (%) | Development time (days) |
| <i>Solanum lycopersicum</i> | 73.5 \pm 7.57 a | 25.2 \pm 0.30 a* | 66.6 \pm 8.75 a | 21.2 \pm 0.54 a |
| <i>Solanum melongena</i> | 47.1 \pm 8.98 b | 30.6 \pm 0.42 c | 50.0 \pm 9.28 ab | 25.3 \pm 0.34 b |
| <i>Solanum tuberosum</i> | 47.2 \pm 8.43 b | 28.4 \pm 0.30 b* | 40.0 \pm 9.09 bc | 25.1 \pm 0.41 b |
| <i>Solanum aethiopicum</i> | 28.5 \pm 7.93 c | 28.7 \pm 0.47 b | 36.6 \pm 8.94 bc | 28.5 \pm 0.57 c |
| <i>Capsicum annuum</i> | 2.9 \pm 2.85 d | 31.0 \pm 0.50 c | 10.0 \pm 5.57 d | 34.0 \pm 0.73 d |
| <i>Capsicum frutescens</i> | 0.0 \pm 0.0 d | – | 0.0 \pm 0.0 e | – |

Within each column, values followed by the same letter are not significantly different from each other according to Tukey's post hoc test (at the $P < 0.05$ level). Asterisks indicate significant difference between the two populations in development time on a given plant, according to MANOVA Wilk's test ($*P < 0.05$)

**Fig. 2** Relationship between **a** oviposition acceptance of *Tuta absoluta* females and juvenile survival (egg to adult) on six solanaceous plants and **b** oviposition preference of *Tuta absoluta* females and survival from egg to adult on six solanaceous plants, for FRA and SEN populations

with an average of 54% infested plants ($\chi^2_{3,517} = 5723.3$; $P < 0.001$), far ahead of other solanaceous crops such as potato (24%) and eggplant (17%). Very few damage (< 10% infested plants) were observed in Ethiopian eggplant, sweet pepper or pepper fields. Damage occasionally reached (max proportion of infested plants in one given field) 100% infested plants in 15, 5, 4 and 1% of monitored fields for tomato, potato, eggplant, and sweet pepper, respectively. A positive relationship was observed between oviposition acceptance ($r = 0.94$, $P = 0.01$) or between

oviposition preference ($r = 0.91$, $P < 0.01$) and incidence in the field.

Discussion

We demonstrated differences in the oviposition acceptance–preference and development performance on the six tested solanaceous plants between the two populations of *T. absoluta* originating from Europe (France) and sub-Saharan

Table 3 Occurrence and incidence of the tomato leaf miner, *Tuta absoluta*, on solanaceous crops in the Niayes area in Senegal (2014–2015 survey)

| Crop | <i>N</i> | Occurrence (%) | Incidence (%) | Max incidence (%) |
|---------------------|----------|----------------|---------------|-------------------|
| Tomato | 226 | 90.4 <i>a</i> | 53.8 <i>a</i> | 100 |
| Eggplant | 123 | 61.0 <i>b</i> | 17.3 <i>c</i> | 100 |
| Potato | 40 | 70.0 <i>b</i> | 24.0 <i>b</i> | 100 |
| Ethiopian egg-plant | 45 | 35.6 <i>c</i> | 7.8 <i>d</i> | 90 |
| Sweet pepper | 69 | 20.3 <i>c</i> | 3.9 <i>e</i> | 100 |
| Pepper | 20 | 25.0 <i>c</i> | 2.8 <i>e</i> | 20 |

A total of 24 plants per field were observed. *N* number of observed fields. Occurrence: percentage of fields with at least one infested plant. Incidence: percentage of plants with at least one damaged leaf (at least one mine). For one given column, values followed by the same letter are not significantly different from each other according to Tukey's post hoc test ($P < 0.05$)

Africa (Senegal). Such differences may indicate possible ongoing differentiation of their respective host range. For both populations, there was a strong relationship between oviposition acceptance (preference) and successful development (performance) of *T. absoluta* immature stages; the best performance of juveniles was on the most preferred host, tomato. The population collected in the most recently invaded area, i.e., Senegal, did not specialize on this preferred host plant, likely due to local availability of various alternative host plants associated with a spatial and/or temporal lack of the preferred host.

Both populations displayed the same general pattern of oviposition acceptance–preference among the six solanaceous tested plants, ranking from highly accepted-preferred for tomato as the major host plant, moderately for eggplant, followed by potato and Ethiopian eggplant, to less accepted-preferred for sweet pepper and pepper. The pattern of female oviposition response to *Solanum* versus *Capsicum* genus is likely linked to phylogenetic distance (Nylin et al. 2014). There were still differences occurring between SEN and FRA populations regarding preference traits, e.g., SEN population showing higher oviposition preference toward sweet pepper and potato than the FRA population. These differences in acceptance and/or preference between FRA and SEN populations may indicate an ongoing differentiation in host range of *T. absoluta* between the two invaded areas. In most of the phytophagous insects, the plant on which larvae will feed on often depends on the mother's oviposition preference (Thompson 1988; Gripenberg et al. 2010; Gómez Jiménez et al. 2014). As a result, oviposition behavior is a critical factor for the development of the larvae, and the first component was exposed to selection. Specialist insects can quickly expand their host range if a new host plant is

taxonomically, chemically or morphologically close to its natural host (Lawton and Strong 1981; Dalin et al. 2006). Cases of geographic differentiation of host use among populations of invasive species have been reported, for example, for the ragweed leaf beetle, *Ophraella communa* LeSage (Coleoptera: Chrysomelidae) in Japan (Fukano et al. 2016). In its native range, *O. communa* mostly feeds on *Ambrosia artemisiifolia* and it does not utilize *A. trifida* as a host plant even though these plants are sympatrically distributed. However, the beetle began to attack also the novel host *A. trifida* soon after its introduction into Japan, indicating the ongoing host range expansion of *O. communa* in Japan.

The populations displayed the same general pattern of performance on the six solanaceous tested plants. Both populations performed best on tomato, in terms of survival and development time. In herbivorous insects, high survival rates and shorter development times are considered to be indicators of host plant suitability (Greenberg et al. 2002; Awmack and Leather 2002). Both populations can develop on other cultivated Solanaceae including eggplant, potato and Ethiopian eggplant. This suggests that the invasive pest has high potential to use secondary host plants, which can allow *T. absoluta* populations to persist in habitats where the major host plant is scarce (Tonnang et al. 2015). Our results confirmed and also showed high ability of *T. absoluta* population to develop on potato crops (Caparros Megido et al. 2013). Conversely, we showed that both populations are poorly adapted to develop on sweet pepper and pepper as was observed in the previous study (Biondi et al. 2018). The only reliably identified observations of *T. absoluta* attacking sweet pepper have been reported, but no indications have been found that *T. absoluta* is able to complete its lifecycle on this plant (Guenauoui et al. 2010).

The preference–performance hypothesis predicts that female insects maximize their fitness by using host plants which are associated with high larval performance (Jaenike 1990; Desneux et al. 2009). For both populations, performance (survival from egg to adult) on solanaceous plant species was closely related to ovipositional response of females to these plants. Both populations of *T. absoluta* performed best on the preferred host plant, tomato. On one hand, it is possible that the SEN population already experienced ongoing adaptation to locally available host plants such as Ethiopian eggplant and potato, associated with spatial or temporal lack of tomato. FRA population might have remained highly specialized in the absence of alternative hosts and repeated cycles on tomato in greenhouses. However, the adaption to novel hosts does not appear to result in decreased performance on the preferred host (Hoeksema and Forde 2008). In addition, *T. absoluta* may need time to develop further its host range due to the strong association with its host plants during its life cycle, like most endophytes (Strong et al. 1984; Gaston 1992).

The two-year survey of six commonly cultivated solanaceous crops in Senegal showed the highest incidence of *T. absoluta* on tomato, with potential severe damages (Brévault et al. 2014). In addition, pest damage was also frequently observed on eggplant and potato fields and more sporadically in Ethiopian eggplant, whereas very low incidence (< 10% infested plants) was observed on sweet pepper or pepper fields (Diatte et al. 2018). This host use pattern observed from the field matched with response of the SEN population to the same host plants in the laboratory, both in terms of oviposition acceptance–preference and development. Results from the field indicate that *T. absoluta* has great potential to cause important damage to other plants from the family Solanaceae. Many solanaceous species have been considered as host plants, but empirical data on their suitability and carrying capacity (source vs. sink) as well as modulating factors, such as, for example, bottom-up effect (e.g., Han et al. 2014; Blazheyski et al. 2018), are still lacking to make better predictions on the pest population dynamics and geographic expansion.

Author contributions

SS, TB, KD and ND made substantial contributions to conception and design of experiments. SS conducted field and laboratory experiments. SS, LSM and TB analyzed the data. SS, LSM, TB and ND wrote the manuscript. All authors read and approved the manuscript.

Acknowledgements We express our sincere gratitude to IRD (PEERS-BIOBIO), Divecosys (Action incitative CIRAD), IFS (International Foundation for Science, Sweden) and IPM Innovation Lab funded by USAID Cooperative Agreement No. AID-OAA-L-15-00001 for financial support. We also thank O. Ndoye (Fédération des Producteurs Maraîchers de la zone des Niayes) and Oumar Seydi (Master student) for technical assistance with field samplings and laboratory experiment.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Abbes K, Harbi A, Elimem M et al (2016) Bioassay of three solanaceous weeds as alternative hosts for the invasive tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae) and insights on their carryover potential. *Afr Entomol* 24:334–342

Adamou H, Adamou B, Garba M et al (2016) Confirmation of the presence of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Niger (West Africa). *Int J Environ Sci Technol* 5:4481–4486

Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47:817–844

Bawin T, Dujeu D, De Backer L et al (2015) Could alternative solanaceous hosts act as refuges for the tomato leafminer, *Tuta absoluta*? *Arthropod Plant Interact* 9:425–435

Bigger DS, Fox LR (1997) High-density populations of diamondback moth have broader host-plant diets. *Oecologia* 112:179–186

Biondi A, Guedes RNC, Wan FH, Desneux N (2018) Ecology, worldwide spread and management of the invasive South American tomato pinworm, *Tuta absoluta*: past, present and future. *Annu Rev Entomol* 63:239–258

Blazheyski S, Kalaitzaki AP, Tsagkarakis AE (2018) Impact of nitrogen and potassium fertilization regimes on the biology of the tomato leaf miner *Tuta absoluta*. *Entomol Gen* 37:157–174

Brévault T, Sylla S, Diatte M et al (2014) *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae): a new threat to tomato production in sub-Saharan Africa. *Afr Entomol* 22:441–444

Bush GL (1975) Sympatric speciation in phytophagous parasitic insects. In: *Evolutionary strategies of parasitic insects and mites*. Springer, pp 187–206

Campos RG (1976) Control químico del “minador de hojas y tallos de la papa” (*Scrobipalpus absoluta* Meyrick) en el valle del Cañete. *Rev Peru Entomol* 19:102–106

Campos MR, Adiga A, Guedes RNC, Biondi A, Desneux N (2017) From the Western Palearctic region to beyond: *Tuta absoluta* ten years after its Europe invasion. *J Pest Sci* 90:787–796

Caparros Megido R, Brostaux Y, Haubruge E, Verheggen FJ (2013) Propensity of the Tomato Leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), to develop on four potato plant varieties. *Am J Potato Res* 90:255–260

Chew FS (1975) Coevolution of pierid butterflies and their cruciferous food plants. I. The relative quality of available resources. *Oecologia* 20:117–127

Chew FS (1981) Coexistence and local extinction in two Pierid butterflies. *Am Nat* 118:655–672

Dalin P, Kindvall O, Björkman C (2006) Predator foraging strategy influences prey population dynamics: arthropods preying on a gregarious leaf beetle. *Anim Behav* 72:1025–1034

Desneux N, Barta RJ, Hoelmer KA, Hopper KR, Heimpel GE (2009) Multifaceted determinants of host specificity in an aphid parasitoid. *Oecologia* 160:387–398

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

Desneux N, Luna MG, 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. *J Pest Sci* 84:403–408

Dethier VG (1954) Evolution of feeding preferences in phytophagous insects. *Soc Study Evol* 8:33–54

Diatte M, Brévault T, Sylla S, Tendeng E, Sall-Sy D, Diarra K (2018) Arthropod pest complex and associated damage in field-grown tomato in Senegal. *Int J Trop Insect Sci* 38:243–253

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. *Evolution* 18:586–608

Feeny P, Blau WS, Kareiva PM (1985) Larval growth and survivorship of the black swallowtail butterfly in Central New York. *Ecol Monogr* 55:167–187

Friberg M, Olofsson M, Berger D et al (2008) Habitat choice precedes host plant choice niche separation in a species pair of a generalist and a specialist butterfly. *Oikos* 117:1337–1344

Fukano Y, Doi H, Thomas CE et al (2016) Contemporary evolution of host plant range expansion in an introduced herbivorous beetle *Ophraella communa*. *J Evol Biol* 29:757–765

Funk DJ, Bernays EA (2001) Geographic variation in host specificity reveals host range evolution in *Uroleucon ambrosiae* aphids. *Ecology* 82:726–739

- Futuyma DJ, Agrawal AA (2009) Macroevolution and the biological diversity of plants and herbivores. *Proc Natl Acad Sci* 106:18054–18061
- Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. *Annu Rev Ecol Syst* 19:207–233
- Galarza J (1984) Laboratory assessment of some solanaceous plants as possible food-plants of the tomato moth *Scrobipalpus absoluta* (Meyr.) (Lepidoptera: Gelechiidae). *Idia* 421/424:30–32
- García MF, Espul JC (1982) Bioecología de la polilla del tomate (*Scrobipalpus absoluta*) en Mendoza, República Argentina
- Gaston KJ (1992) Taxonomy of taxonomists. *Nature* 356:281–282
- Gómez Jiménez MI, Sarmiento CE, Díaz MF et al (2014) Oviposition, larval preference, and larval performance in two polyphagous species: does the larva know best? *Entomol Exp Appl* 153:24–33
- Greenberg SM, Sappington TW, Sétamou M, Liu T-X (2002) Beet armyworm (Lepidoptera: Noctuidae) host plant preferences for oviposition. *Environ Entomol* 31:142–148
- Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationships in phytophagous insects. *Ecol Lett* 13:383–393
- Guenauoui Y (2008) Nouveau ravageur de la tomate en Algérie : Première observation de *Tuta absoluta*, mineuse de la tomate invasive, dans la région de Mostaganem, au printemps 2008. *Phytoma- Déf Végétaux* 617:18–19
- Guenauoui Y, Bensaad F, Ouezzi K (2010) Primeras experiencias en el manejo de la polilla del tomate, *Tuta absoluta* (Meyrick) (Lep: Gelechiidae) en la área noroeste del país: estudios preliminares de control biológico mediante el uso de enemigos naturales nativos. *Phytoma Esp Rev Prof Sanid Veg* 117:112–113
- Guillemaud T, Blin A, Le Goff I et al (2015) The tomato borer, *Tuta absoluta*, invading the Mediterranean Basin, originates from a single introduction from Central Chile. *Sci Rep* 5:8371
- Gutiérrez D, Thomas CD (2001) Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni*. *Ecol Entomol* 25:165–170
- Han P, Lavoit AV, Le Bot J, Amiens-Desneux E, Desneux N (2014) Nitrogen and water availability to tomato plants triggers bottom-up effects on the leafminer *Tuta absoluta*. *Sci Rep* 4:4455
- Han P, Zhang YN, Lu ZZ et al (2018) Are we ready for the invasion of *Tuta absoluta*? Unanswered key questions for elaborating an Integrated Pest Management package in Xinjiang, China. *Entomol Gen* 38:113–125
- Hoeksema JD, Forde SE (2008) A meta-analysis of factors affecting local adaptation between interacting species. *Am Nat* 171:275–290
- Jaenike J (1978) On optimal oviposition behavior in phytophagous insects. *Theor Popul Biol* 14:350–356
- Jaenike J (1990) Host specialisation in phytophagous insects. *Annu Rev Ecol Syst* 21:243–273
- Kharroubi A (2008) Agriculture: *Tuta absoluta* threatens the Moroccan tomato
- Kohyama TI, Matsumoto K, Katakura H (2012) Geographic variation of host use in the leaf beetle *Agelasa nigriceps* suggests host range expansion: host range evolution in *Agelasa nigriceps*. *Entomol Exp Appl* 142:165–174
- Lawton JH, Strong DR (1981) Community patterns and competition in folivorous insects. *Am Nat* 118:317–338
- Mallea AR, Mácola GS, García JG et al (1974) *Nicotiana tabacum* L. var. *virginica*, nuevo hospedero de *Scrobipalpus absoluta* (Meyrick) Povolny (Gelechiidae-Lepidoptera). *Rev Fac Cs Agrar* 18:13–15
- Mansour R, Brévault T, Chailleux A et al (2018) Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomol Gen* 38:83–112
- Mitter C, Farrell B (1991) Macroevolutionary aspects of insect-plant relationships. *Insect Plant Interact* 3:35–78
- Noriyuki S, Osawa N (2012) Intrinsic prey suitability in specialist and generalist *Harmonia ladybirds*: a test of the trade-off hypothesis for food specialization. *Entomol Exp Appl* 144:279–285
- Nylin S, Nygren GH, Söderlind L, Stefanescu C (2009) Geographical variation in host plant utilization in the comma butterfly: the roles of time constraints and plant phenology. *Evol Ecol* 23:807–825
- Nylin S, Slove J, Janz N (2014) Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. *Evolution* 68:105–124
- Ouardi K, Chouibani M, Rahel MA, El Akel M (2012) Stratégie Nationale de lutte contre la mineuse de la tomate *Tuta absoluta* Meyrick. *EPP Bull* 42:281–290
- Pfeiffer DG, Muniappan R, Sall D et al (2013) First record of *Tuta absoluta* (Lepidoptera: Gelechiidae) in Senegal. *Fla Entomol* 96:661–662
- Portakaldali M, Öztemiz S, Kütük H (2013) A new host plant for *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Turkey. *J Entomol Res Soc* 15:21–24
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, p 2013
- Rauscher MD (1979) Larval habitat suitability and oviposition preference in three related Butterflies. *Ecol Soc Am* 60:503–511
- Sankarganesh E, Firake DM, Sharma B, Verma VK, Behere GT (2017) Invasion of the South American Tomato Pinworm, *Tuta absoluta*, in northeastern India: a new challenge and biosecurity concerns. *Entomol Gen* 26:335–345
- Scheirs J, Bruyn LD (2001) Integrating optimal foraging and optimal oviposition theory in plant-insect research. *Oikos* 96:187–191
- Singer MC, Ng D, Vasco D, Thomas CD (1992) Rapidly evolving associations among oviposition preferences fail to constrain evolution of insect diet. *Am Nat* 139:9–20
- Son D, Bonzi S, Somda I et al (2017) First record of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) in Burkina Faso. *Afr Entomol* 25:259–263
- Strong DRJ, Lawton JJH, Southwood R (1984) Insects on plants: community patterns and mechanisms Harvard, vol 41. Blackwell Scientific Publications, Hoboken, p 1137
- Sylla S, Brévault T, Bocar Bal A et al (2017) Rapid spread of the tomato leafminer, *Tuta absoluta* (Lepidoptera, Gelechiidae), an invasive pest in sub-Saharan Africa. *Entomol Gen* 36:269–283
- Thompson JN (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomol Exp Appl* 47:3–14
- Thompson SN (1999) Nutrition and culture of entomophagous insects. *Annu Rev Entomol* 44:561–592. <https://doi.org/10.1146/annurev.ento.44.1.561>
- Tonnang HEZ, Mohamed SF, 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. <https://doi.org/10.1371/journal.pone.0135283>
- Tropea Garzia G (2009) *Physalis peruviana* L. (Solanaceae), a host plant of *Tuta absoluta* in Italy. *IOBC wprs Bull* 49:231–232
- Urbaneja A, Desneux N, Gabarra R et al (2013). Biology, ecology and management of the tomato borer, *Tuta absoluta*. In: Peña JE (ed) Potential invasive pests of agricultural crops, CABI series. pp 98–125. <https://doi.org/10.1079/9781845938291.0098>
- Vargas H (1970) Observaciones sobre la biología y enemigos naturales de la polilla del tomate, *Gnorimoschema absoluta* (Meyrick). (Lep. Gelechiidae). *Idesia* 1:75–110
- Visser D, Uys VM, Nieuwenhuis RJ, Pieterse W (2017) First records of the tomato leaf miner *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) in South Africa. *Bioinvasions Rec* 6:301–305
- Wiklund C (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* 18:185–197

- Wyckhuys K, Bordat D, Desneux N, Fuentes Quintero LS (2013) *Tuta absoluta* (Meyrick): un ravageur invasif des cultures maraîchères pour l'Afrique sub-saharienne. In: Nouveaux Ravageurs & Maladies Invasives, Guide 2. Comité de Liaison Europe-Afrique-Caraïbes-Pacifique. Pesticide Initiative Programme (COLEACP-PIP), Brussels, Belgium
- Xian XQ, Han P, Wang S, Zhang GF, Liu WX, Desneux N, Wan FH (2017) The potential invasion risk and preventive measures

against the tomato leafminer *Tuta absoluta* in China. Entomol Gen 36:319–333

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.