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1 ***Tuta absoluta* (Lepidoptera: Gelechiidae) success on common solanaceous**
2 **species from California tomato production areas**

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10

11 **Abstract**

12 *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is a devastating pest of tomato that
13 has invaded many regions of the world. To date, it has not been detected in North
14 America, but the pest reached Costa Rica in 2014, and seriously threatens the southern,
15 southwestern, and western United States including California. Although the primary host
16 of *T. absoluta* is tomato, several other species of Solanaceae may serve as alternative
17 hosts. In our study, we aimed to assess the potential risk that other solanaceous crops
18 and wild species that are often present in and around California tomato fields could serve
19 as hosts. To accomplish this, we conducted greenhouse and laboratory studies to
20 determine if two common cultivars of fresh market tomato, two common cultivars of
21 tomatillo, and the wild plants, *Solanum nigrum* L., *S. sarrachoides* (Sendtner) and *Datura*
22 *stramonium* L., are suitable hosts for reproduction and development of the pest.
23 According to our results, *D. stramonium* and tomatillo were unable to sustain *T. absoluta*
24 larval development in either greenhouse or laboratory studies, and therefore, they are
25 not likely to contribute to *T. absoluta* establishment during an invasion. On the contrary,
26 the two other solanaceous weeds, *S. nigrum* and *S. sarrachoides*, share a similar
27 potential as tomato to be reproductive and developmental hosts of *T. absoluta*, and might
28 play an important role in the establishment of the pest in California.

29

30 **Resumen**

31 *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) es una plaga devastadora del tomate
32 que ha invadido muchas regiones del mundo. Hasta la fecha, no se ha detectado en

33 América del Norte, pero la plaga llegó a Costa Rica en 2014 y amenaza seriamente el
34 sur, suroeste y oeste de los Estados Unidos, incluida California. Aunque el huésped
35 principal de *T. absoluta* es el tomate, hay otras especies de solanáceas que pueden
36 servir como huéspedes alternativos. El objetivo de nuestro estudio fue evaluar el riesgo
37 de que otros cultivos y especies silvestres pertenecientes a la familia de las solanáceas,
38 que a menudo están presentes en los campos de tomate de California y sus alrededores,
39 puedan servir como hospedadores. Para ello, en estudios de invernadero y de
40 laboratorio determinamos si dos cultivares comunes de tomate para mercado fresco,
41 dos cultivares comunes de tomatillo y las plantas silvestres *Solanum nigrum* L., *S.*
42 *sarrachoides* (Sendtner) y *Datura stramonium* L. son hospedadores adecuados para la
43 reproducción y el desarrollo de la plaga. De acuerdo con nuestros resultados, *D.*
44 *stramonium* y tomatillo no permitieron el desarrollo larvario de *T. absoluta* y, por lo tanto,
45 no es probable que contribuyan al establecimiento de *T. absoluta* en caso de una
46 invasión. Por el contrario, las otras dos plantas adventicias, *S. nigrum* y *S. sarrachoides*,
47 presentan un potencial similar al tomate como huéspedes para el desarrollo y
48 reproducción de *T. absoluta*, y podrían desempeñar un papel importante en el
49 establecimiento de la plaga en California.

50

51 **Keywords:** South American tomato leafminer, *Solanum lycopersicum*, jimsonweed,
52 nightshade, *Physalis ixocarpa*, tomatillo

53

54 **Introduction**

55 The South American tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera:
56 Gelechiidae) is a devastating pest of tomato. After mating, the *T. absoluta* female lays
57 its eggs individually in the upper part of the plant. All four larval instars feed on the leaf
58 by mining the mesophyll limiting the photosynthetic capacity of the plant. At high density,
59 other plant organs such as buds, sepals, stems and fruits may also be damaged. Mature
60 larvae may drop to the soil or find a hidden place within the plant vegetation to pupate.
61 (Biondi et al. 2018). The pest is thought to be native to the western part of South America.
62 It was reported only from South America until its 2006 detection in Spain (Urbaneja et al.
63 2007, Desneux et al. 2010). Since then *T. absoluta* has rapidly spread throughout the
64 Mediterranean basin and across Europe, Africa and Asia (Biondi et al. 2018). In the
65 Americas, the pest has expanded its range northward to Panama in 2010-2011 and to
66 Costa Rica in 2014-2015 (CABI 2018). The threat of *T. absoluta* reaching the tomato
67 production areas of the United States, including California, has prompted the

68 development of surveillance protocols and potential quarantine measures by the North
69 American Plant Protection Organization (Muruvanda et al. 2012). California produces
70 13,638 ha of fresh tomatoes and 104,409 ha of processing tomatoes with a total farmgate
71 value of \$1.3 billion USD (CDFA 2017).

72 Although pest invasions have always occurred, vastly expanded global trade has
73 intensified the problem (Pimentel et al. 2001). After an initial invasion, crop damage is
74 usually high and insecticide applications increase, in turn, causing disruption of
75 established integrated pest management (IPM) programs. This has been the typical
76 pattern observed following previous *T. absoluta* introductions, and it can be assumed to
77 be the case in North America as well. Although the success of an insect pest invasion
78 depends on many ecological factors, one of the most critical is the ability to find
79 alternative hosts for feeding, reproduction and development when the preferred host,
80 tomato, is not present.

81 At least 25 species of Solanaceae in the genera *Atropa*, *Capsicum*, *Datura*,
82 *Lycium*, *Lycopersicum*, *Nicotiana*, *Physalis* and *Solanum* have been observed or
83 experimentally evaluated for suitability as hosts of *T. absoluta* (Desneux et al. 2010,
84 Portakaldali et al. 2013, Bawin et al. 2015, 2016, Mohamed et al. 2015, Abbes et al.
85 2016, Smith et al. 2018, Sylla et al. 2019). However, the results of the alternative host
86 studies have not always been consistent. For example, although Desneux et al. (2010)
87 mentioned *Datura stramonium* L. and *D. ferox* L. as potential hosts for *T. absoluta*, Abbes
88 et al. (2016) observed no development of the pest on these two species. Further, plant
89 species belonging to the families Amaranthaceae, Convolvulaceae, Malvaceae and
90 Fabaceae have been reported as hosts in two studies (Desneux et al. 2010, Biondi et al.
91 2018), while in another testing of six species belonging to these families Bawin et al.
92 (2016) found none suitable for larval development. Despite these inconsistencies the
93 studies suggest that while tomato is the preferred host for *T. absoluta* development,
94 several other plant species may serve as alternative hosts. In addition to their role in
95 establishment, the recognition of alternative hosts that may serve as reservoirs for *T.*
96 *absoluta* must also be considered when attempting to detect its presence in a new
97 region.

98 The objective of our research was to determine if various Solanaceae species
99 that are often present in and around California tomato fields could serve as hosts,
100 thereby contributing to a successful invasion by this species. Greenhouse studies were
101 conducted to determine the suitability of each host plant species for reproduction and

102 development of *T. absoluta*, while laboratory studies were used to determine the effect,
103 if any, on adult survival, fecundity, adult host preference, and pre-imaginal development.

104

105 **Materials and Methods**

106 **Plant and Insect Sources**

107 The experiments were conducted at the facilities of the Institut de Recerca i Tecnologia
108 Agroalimentàries (IRTA), Cabrils (Barcelona) Spain, using Solanaceae species
109 commonly found in California including tomato (*Solanum lycopersicum* L.), tomatillo
110 (*Physalis ixocarpa* Brot.), jimsonweed (*D. stramonium*), black nightshade (*Solanum*
111 *nigrum* L.) and hairy nightshade (*Solanum sarrachoides* (Sendtner)) grown from seed.
112 Tomato and tomatillo were represented in the study with two cultivars each. For tomato,
113 the cultivars were “Patio Princess” (W. Atlee Burpee and Company, Warminster, PA), a
114 cultivar used by home gardeners, and “Qualit 23” (Lockhart Seeds Inc., Stockton, CA),
115 a common commercial cultivar. For tomatillo, the cultivars were “Purple” (W. Atlee
116 Burpee and Company, Warminster, PA), a cultivar used by home gardeners, and “Toma
117 Verde” (Lockhart Seeds Inc., Stockton, CA), a cultivar used in commercial production.
118 Jimsonweed, black nightshade, and hairy nightshade seeds were collected by hand near
119 Davis, CA, USA. The *T. absoluta* used in the experiments were derived from a
120 permanent colony maintained in Bugdorm cages (MegaView Science Education
121 Services Co., Ltd., Taichung, Taiwan) inside a growth chamber at 25 °C, 70% RH, and
122 16:8 (L:D) on tomato plants (cv. Roma V.F. Eurogarden) at IRTA (coordinates 41° 30'N;
123 2° 22' E). The colony was initiated in 2007 with individuals collected in nearby tomato
124 fields in Maresme County and annually refreshed with field individuals.

125

126 **Greenhouse experiment**

127 The suitability of each host plant species for *T. absoluta* growth and development was
128 investigated in a greenhouse study during April and May 2017. On April 19, a pair of *T.*
129 *absoluta* (male and female) adults were released on an individual plant of each species
130 or cultivar contained in a sleeve cage. Twelve plants of each species and/or cultivar were
131 used (n = 84). There were 7.1 ± 0.19 (mean ± SD) leaves per plant. The sleeve cages
132 were constructed of transparent micro-perforated film tied around the pot and secured at
133 the upper part to prevent escape. The adults were held in the cage for two days and
134 allowed to feed and reproduce. The adults were then removed, and the plants were
135 checked regularly for the presence of feeding galleries indicating that larvae were

136 present on the plant. Greenhouse temperature and RH were measured hourly with a
137 data-logger 175-H2 (Testo SE & Co. KGaA, Lenzkirch, Germany). The mean
138 temperature and RH was 23.2 °C (max = 41.9 °C; min = 10.0 °C) and 66.7% (max =
139 99.9%; min = 24.8%), respectively.

140 When most of the galleries were empty (May 18), each plant was rated for larval
141 feeding damage as 0 = no visible galleries, 1 = galleries present in some leaves, 2 =
142 galleries present in most leaves, and 3 = galleries present in all leaves. After rating, the
143 plants were cut just above ground level, and the above-ground part of each plant was
144 transferred into a separate transparent plastic cage (4.5L) covered with a cloth to provide
145 aeration. Each pot with the substrate was enclosed again in the sleeve cage. Both pots
146 and aerated cages were moved to a growth chamber at 25 °C, 70% RH, and 16:8 (L:D)
147 and checked regularly. The number of adults emerging from the plant material in the
148 aerated cages (above-ground plant parts) and from the pots (substrate) was recorded.
149 The sex of the emerging adults was determined.

150

151 **Laboratory experiments**

152 These experiments were conducted in growth chambers at 25 °C, 70% RH, and 16:8
153 (L:D) photoperiod.

154

155 **Adult Survival and Fecundity**

156 To investigate *T. absoluta* adult survivorship and fecundity, one female and one male,
157 less than 24 h-old, were placed in a 2L transparent plastic container (22 cm x 15.5 cm x
158 8 cm) with a mesh-covered 9 cm-diameter hole in the lid for aeration. The base of the
159 cage was lined with a moistened paper towel, and one leaf of each host plant (one leaflet
160 in the case of tomato) was placed on top of the paper. The petiole of the leaf or leaflet
161 was wrapped in a moist paper toweling to prevent desiccation. A test tube with a 10%
162 sucrose solution stoppered with cotton wool was attached to the wall of each tube to
163 provide additional food and water for the adults. Cages were checked daily and adult
164 survival recorded. Leaves and leaflets were changed three times a week and number of
165 *T. absoluta* eggs on each leaf or leaflet was recorded.

166

167 **Host Preference for Oviposition**

168 A choice experiment was conducted to determine the oviposition preference among the
169 two cultivars of tomato, *S. nigrum* and *S. sarrachoides*. A 4.5L transparent plastic cage

170 similar to that previously described was used. One leaf of *S. nigrum* and *S. sarrachoides*
171 and one leaflet of both tomato cultivars were placed inside each container. A pair of
172 *T. absoluta* adults was caged for 48 h, and the number of eggs on each plant
173 species/cultivar recorded.

174

175 Pre-imaginal Development

176 Pre-imaginal development was measured using the methodology proposed by Bawin et
177 al. (2015). Twenty-five eggs (less than 24 h-old) were taken from each host plant and
178 placed individually on top of a leaf or leaflet of the same host plant in a 9 cm diameter
179 Petri dish. The dish was lined with a moistened paper towel and the ends were folded up
180 to cover the end of the petiole to prevent desiccation. The dishes were checked daily
181 until egg hatch. Once larvae were present, a new leaf and/or leaflet was added to the
182 dish twice a week to assure that fresh food was available to the larvae, and water was
183 added to moisten the paper towel as needed until adult emergence. Daily observations
184 were made to record insect development.

185

186 Pupal Size

187 To measure pupal size, four to five plants of each species or cultivar (in the case of
188 tomato) were infested *ad-hoc*. Each group of plants were introduced in a Bugdorm cage
189 (47.5 cm x 47.5 cm x 47.5 cm) together with one pair of *T. absoluta* adults per plant.
190 Cages were placed in a growth chamber and insects were removed after 48 h. The plants
191 were maintained under the same conditions as for the larval development study. Prior to
192 pupation, the plants were placed horizontally on top of a tray lined with paper toweling to
193 facilitate collection of pupae. Pupae in the tray were collected every 72 h. The pupae
194 were sexed according to Coelho and França (1987). Eight female and eight male pupae
195 from each host plant were weighed individually using a precision Sartorius Analytic
196 A2005 balance (Sartorius AG, Goettingen, Germany).

197

198 **Data Analysis**

199 Data from the greenhouse experiment, daily fecundity in the no-choice experiment, total
200 number of eggs laid in the choice experiment and developmental time of eggs, larvae
201 and pupae of *T. absoluta* were analyzed with Kruskal-Wallis test and the Chi Square
202 approximation of the H-statistic because the data could not be normalized. Mann-
203 Whitney-Wilcoxon tests with Bonferroni-weighted test corrections ($P < 0.05$) were used

204 to observe pairwise differences between treatments in each of the studies. Two-way
205 analysis of variance (ANOVA) was used to analyze square-root transformed longevity
206 data and log-transformed pupal weight data. When statistically significant differences
207 were detected, means were separated using Tukey's HSD post-hoc test ($P < 0.05$).
208 Survivorship affected by host plant was evaluated using Kaplan-Meier survival platform
209 and log-rank tests were used to compare the survival curves. All analyses were
210 performed using JMP version 13.1.0 (SAS Institute Inc., Cary, NC, USA).

211

212 **Results**

213 **Greenhouse Experiment**

214 No galleries were found on the two cultivars of tomatillo or on *D. stramonium* plants
215 (Figure 1). The distribution of damage ratings was significantly different among the other
216 plant species. The damage rating was more variable on *S. nigrum* with half of the plants
217 having no visible galleries. The tomato "Patio Princess" had the greatest number of
218 damaged plants with only one plant having no visible galleries (Figure 1).

219 There was no statistical difference in the number of progeny produced between
220 the four host species on which *T. absoluta* reproduced ($\chi^2 = 3.91$; $df = 3$; $P = 0.27$) (Table
221 1). The sex ratio was slightly female-biased for tomato cultivars averaging 63.2%, and
222 slightly male-biased for *S. nigrum* and *S. sarrachoides* (56.7% and 50.8%, respectively).
223 Given the methods used in this experiment, 67 to 80% of the *T. absoluta* adults emerged
224 from the soil and the rest from the caged plant material, indicating that pupation occurred
225 primarily in the soil (Table 1).

226

227 **Laboratory Experiments**

228 **Adult Survival and Fecundity**

229 No statistical differences were observed in the adult survival curves for *T. absoluta*
230 females ($\chi^2 = 11.42$; $df = 6$; $P = 0.08$) or males ($\chi^2 = 4.15$; $df = 6$; $P = 0.66$) reared on the
231 seven host plants tested (Figs. 2 and 3, respectively).

232 There was no significant interaction between sex and host plant on longevity
233 ($F_{6,154} = 1.13$; $P = 0.35$) (Table 2). *Tuta absoluta* males survived significantly fewer days
234 than females (9.64 ± 0.73 vs. 12.79 ± 0.73 (mean \pm SE), respectively; ($F_{1,154} = 11.25$; $P <$
235 0.01)), but no differences were observed among the different host plants ($F_{6,154} = 0.10$;
236 $P = 0.43$).

237 All the females laid eggs on tomato leaflets, whereas 50% of those that were
238 offered “Purple” tomatillo leaves did not lay eggs at all (Table 3). The number of females
239 that did not lay eggs on leaves of the other host plants varied from 1 to 4 (Table 3). Daily
240 fecundity of females over their lifespan was significantly higher for both tomato varieties
241 ($\chi^2 = 27.26$; $df = 6$; $P < 0.01$) while the daily fecundity for the other species varied from
242 0.81 ± 0.61 eggs per day for adults on the “Purple” tomatillo to 3.23 ± 1.01 eggs per day
243 on *S. nigrum* (Table 3).

244 Host Preference for Oviposition

245 When *T. absoluta* females were presented a choice of hosts on which to oviposit,
246 the number of eggs laid in the tomato leaflets was significantly more than the number on
247 *S. sarrachoides* ($\chi^2 = 15.31$; $df = 3$; $P < 0.01$) (Table 4).

248

249 Pre-imaginal Development

250 Percent egg hatch was similar and fairly high on all host plants, ranging from 78 to 88%
251 of the eggs that were laid (Table 5). However, the mean developmental time to egg hatch
252 was significantly longer on *D. stramonium* than on *S. sarrachoides*, “Toma Verde”
253 tomatillo and “Qualit 23” tomato ($\chi^2 = 23.06$; $df = 6$; $P < 0.01$), with almost a full day
254 difference between the longest and shortest hatch time (Table 5).

255 None of the larvae that hatched from *T. absoluta* eggs on *D. stramonium* and the
256 two tomatillo varieties were able to develop in these hosts plants (Table 5). In fact, few
257 larvae survived more than 24 h. The survival rate for larvae feeding on “Qualit 23” tomato
258 was the greatest (67%), whereas the lowest survival rate was recorded for larvae feeding
259 on “Patio Princess” tomato (32%). Larval developmental time was significantly shorter
260 on *S. sarrachoides* and “Qualit 23” tomato than on *S. nigrum* ($\chi^2 = 20.75$; $df = 3$; $P <$
261 0.01) (Table 5). Between 61% and 83% of pupae successfully developed into adults.
262 Pupal duration was not significantly different among the different hosts ($\chi^2 = 1.76$; $df = 3$;
263 $P = 0.62$) (Table 5).

264

265 Pupal Size

266 Two-way ANOVA revealed that pupal size (Table 6) was significantly influenced
267 by sex ($F_{1,56} = 46.28$; $P < 0.01$) and by host plant ($F_{3,56} = 3.68$; $P = 0.02$) but the interaction
268 between these factors was not significant ($F_{3,56} = 2.14$; $P = 0.11$). Analysis of pupal
269 weights by sex reared on different host plants showed that no significant differences
270 were found for the females ($F_{3,28} = 0.86$; $P = 0.48$), but in males, size was significantly

271 affected by plant species ($F_{3,28} = 6.40$; $P < 0.01$). Male pupae from *S. nigrum* and “Patio
272 Princess” tomato were significantly heavier than those from “Qualit 23” tomato (Table 6).

273

274 Discussion

275 In our experiments with four host plant species other than tomato, *D. stramonium* and
276 tomatillo were unable to sustain *T. absoluta* larval development in either greenhouse or
277 laboratory studies. Neonate larvae died as they began to feed on the leaves of these two
278 species, and never lived longer than 48 h. As a result, feeding galleries were never
279 observed on the leaves.

280 Regarding *D. stramonium*, our results agree with those of Abbes et al. (2016)
281 who also reported no larval development. In addition, Bawin et al. (2015) reported larval
282 development on this species when eggs were laid by tomato-reared females, but found
283 little survival from egg to adult and no adult females were produced in their experiment.
284 Both papers suggest that poor quality of *D. stramonium* as host for *T. absoluta* is due to
285 the presence of tropane alkaloids in this plant species that are implicated in herbivore
286 resistance. By contrast, this plant species has been mentioned as a host plant in
287 Argentina, Chile (as chamico azul), and Sudan (García and Espul 1982, Larrain 1987,
288 Mohamed et al. 2015). The various results obtained among these studies regarding the
289 suitability of *D. stramonium* as a host may be due to variable biotic and abiotic conditions
290 (e.g. Moore et al. 2014, Han et al. 2016) or to the different geographical origins of *T.*
291 *absoluta* populations (Sylla et al. 2019). It is notable that our study results were similar
292 to those reported by Bawin et al. (2015) and Abbes et al. (2016) who also conducted
293 studies with populations from the Mediterranean, where this plant species is broadly
294 distributed (CABI 2019).

295 The two tomatillo varieties tested were not able to sustain larval development.
296 This may be due to the presence of pyrrolizidine alkaloids in species of the genus
297 *Physalis* (Pomilio et al. 2008) that are considered important in plant defense (Hartmann
298 and Ober 2000). Tropea-Garzia (2009) reported *P. peruviana* as a host of *T. absoluta* in
299 a Sicilian greenhouse close to a tomato crop. However, there are no other records of
300 *Physalis* spp. infestation by *T. absoluta*, although the genus is widely distributed in areas
301 infested by this pest (CABI 2019).

302 Although *T. absoluta* larval development was not successful on *D. stramonium*
303 and tomatillo, both species were suitable for egg-laying. Daily fecundity on these species
304 was numerically lower, but not statistically different, from that on the two tomato cultivars

305 and the two *Solanum* species in our study. These results differ from those of Proffit et al.
306 (2011) who reported that *T. absoluta* preferred tomato over the wild *Solanum*
307 *habrochaites* Knapp & Spooner, a species that does not support larval development.
308 Adult *T. absoluta* females search for host plants by responding to a blend of volatile
309 compounds released by suitable host plants. However, oviposition also depends upon
310 additional stimuli like leaf surface morphology and chemistry (Proffit et al. 2011, Caparros
311 Megido et al. 2014). In our study, *T. absoluta* females laid eggs on plants that were not
312 suitable for larval development. This mismatch between adult preference and larval
313 performance is not unusual (Hilker and Fatouros 2015), and it has been observed for
314 other Lepidoptera-plant associations. For example, *Barbarea vulgaris* (R. Br.) is very
315 attractive to *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) for egg-laying, yet the plant
316 does not sustain the development of larvae and therefore, acts as a “dead-end” trap crop
317 for the pest (Shelton & Badenes-Perez 2006).

318 Hatchability of eggs laid in all the tested plants, even in those that are unsuitable
319 for larval development, was high (>78%). Although some differences in the duration of
320 embryonic development were recorded, these differences did not appear to be related
321 to the host plant that was provided as oviposition substrate. For example, one of the
322 shortest embryonic developmental periods leading to egg hatch was on the tomatillo
323 “Toma Verde”, a cultivar on which the larvae did not develop in our studies. In
324 Lepidoptera, oogenesis is largely influenced by nourishment during the larval stages of
325 the parental female (Wheeler 1996). However, although the main role of the leaf is to
326 provide a suitable microclimate where eggs may develop, some leaf chemicals may alter
327 egg development (Hilker and Meiners 2011), and this might also influence embryonic
328 development time on different plants. In our studies, adult survival was not affected by
329 the plant species on which adults lived suggesting that the moths did not feed on the
330 plant. Hence, plant characteristics did not negatively influence the survival of the adults.
331 Rather, *T. absoluta*, as do many moths, feed on nectar and other sugary substances to
332 survive (Balzan and Wackers 2013, Arnó et al. 2018).

333 The results of our greenhouse experiment documented that the two tomato
334 varieties and the two other solanaceous weeds, *S. nigrum* and *S. sarrachoides*, share a
335 similar potential as reproductive and developmental hosts of *T. absoluta*. Previous
336 studies have documented that *T. absoluta* can develop on the nightshade species *S.*
337 *nigrum* (Desneux et al. 2010) and *S. sarrachoides* (Salas Gervasio et al. 2016) and may
338 therefore serve as alternative host species. Daily oviposition on *S. sarrachoides* was less
339 than half that on tomato, and this observation may be due to previous experience of the
340 source insects on tomato. However, larval development on *S. sarrachoides* was

341 significantly shorter than that on *S. nigrum* in our study, but was similar to that found for
342 *S. nigrum* by other authors (Bawin et al. 2015, Abbes et al. 2016). Since *S. nigrum* is
343 considered one of the most suitable plant species for *T. absoluta* development (Biondi et
344 al. 2018), our results suggest that *S. sarrachoides* has the potential to play a similarly
345 important role as an alternative host in the potential invasion and establishment of
346 *T. absoluta* in new regions such as California where both species are very common
347 weeds (Aegerter et al. 2011). Total survival from egg to adult was similar for both weed
348 species (between 22% and 24%). Total survival on tomato "Patio Princess" (23%) was
349 similar to these nightshade species, but numerically lower than those reared on tomato
350 "Qualit 23" (39%). This suggests that both *Solanum* weed species might be as suitable
351 as some tomato varieties for larval development. Differences in *T. absoluta* fitness
352 among tomato cultivars have been reported in several studies (e.g. Silva et al. 2015,
353 Ghaderi et al. 2017, Krechmer and Foester 2017).

354 The potential for an invasive herbivore to survive in an environment it has invaded
355 is strongly linked to the availability of host plants. Host plant availability in open fields,
356 greenhouses and nurseries has surely contributed to the rapid spread and establishment
357 of *T. absoluta* in Europe and Asia (Biondi et al. 2018). In addition to commercial crops
358 where pest sampling and control protocols are routinely implemented, wild vegetation
359 and home gardens may pose an additional and important risk. Tomatillo is produced in
360 small plots in many parts of Mexico, the United States, and Central America (Smith et al.
361 1999). Our laboratory and greenhouse experiments indicate that tomatillo is not likely to
362 pose a risk in the event of a North American invasion by *T. absoluta*, since neither of the
363 two cultivars tested were able to sustain larval development, and as previously
364 mentioned, tomatillo has not been reported as a potential host despite wide distribution
365 in *T. absoluta* infested areas. Similarly, *D. stramonium* would not likely contribute to the
366 establishment of *T. absoluta* in the event of an invasion with Mediterranean populations
367 because our results and as well as those of Bawin et al. (2015) and Abbes et al. (2016)
368 indicate that it is not a host, or a poor host at best. In contrast, *S. nigrum* and *S.*
369 *sarrachoides*, along with crops such as potatoes and eggplants that are known to be
370 hosts could play an important role in the establishment of *T. absoluta* in California and
371 elsewhere where these plants are common.

372

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384

385 **References Cited**

386 **Aegerter, B. J., R. M. Davis, C. F. Fouche, K. J. Hembree, W. T. Lanini, G. Miyao, A.**
387 **Ploeg, C. S. Stoddard, K. V. Subbarao, C. G. Summers, J. J. Stapleton, J. T.**
388 **Trumble, and F. G. Zalom. 2011.** UC IPM Pest Management Guidelines Tomato.
389 UC ANR Publication 3470. Oakland, CA.

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

394 **Arnó, J., M. F. Oveja, and R. Gabarra. 2018.** Selection of flowering plants to enhance
395 the biological control of *Tuta absoluta* using parasitoids. *Biol. Control* 122: 41–
396 50.

397 **Balzan, M. V., and F. L. Wäckers. 2013.** Flowers to selectively enhance the fitness of a
398 host-feeding parasitoid: adult feeding by *Tuta absoluta* and its parasitoid
399 *Necremnus artynes*. *Biol. Control.* 67: 21–31.

400 **Bawin, T., D. Dujeu, L. De Backer, M. L. Fauconnier, G. Lognay, P. Delaplace, F.**
401 **Francis, and F. J. Verheggen. 2015.** Could alternative solanaceous hosts act
402 as refuges for the tomato leafminer, *Tuta absoluta*? *Arthropod-Plant Inte.* 9: 425–
403 435.

404 **Bawin, T., D. Dujeu, L. De Backer, F. Francis, and F. J. Verheggen. 2016.** Ability of
405 *Tuta absoluta* (Lepidoptera: Gelechiidae) to develop on alternative host plant
406 species. *Can. Entomol.* 148: 434–442.

- 407 **Biondi, A., R. N. C. Guedes, F. H. Wan, and N. Desneux. 2018.** Ecology, worldwide
408 spread, and management of the invasive south american tomato pinworm, *Tuta*
409 *absoluta*: past, present, and future. *Ann. Rev. Entomol.* 63: 239–258.
- 410 **CABI (Centre for Agriculture and Bioscience International). 2018.** *Tuta absoluta*
411 CABI website. <https://www.cabi.org/isc/datasheet/49260>. (Accessed August 7,
412 2018).
- 413 **CABI (Centre for Agriculture and Bioscience International). 2019.** Invasive Species
414 Compendium. Wallingford, UK: CAB International. www.cabi.org/isc. (Accessed
415 July 25, 2019).
- 416 **CDFA (California Department of Food and Agriculture). 2017.** California agricultural
417 statistics review, 2016-2017. CDFA website.
418 <https://www.cdfa.ca.gov/Statistics/PDFs/2016-17AgReport.pdf> (Accessed
419 October 30, 2018).
- 420 **Caparros Megido, R., L. De Backer, R. Ettaïb, Y. Brostaux, M. L. Fauconnier, P.**
421 **Delaplace, G. Lognay, M. S. Belkhadi, E. Haubruge, F. Francis, and F.**
422 **Verheggen. 2014.** Role of larval host plant experience and solanaceous plant
423 volatile emissions in *Tuta absoluta* (Lepidoptera: Gelechiidae) host finding
424 behavior. *Arthropod-Plant Inte.* 8: 293–304.
- 425 **Coelho, M. C. F., and F. H. França. 1987.** Biologia e quetotaxia da larva e descrição da
426 pupa e adulto da traça do tomateiro. *Pesq. Agro. Brasil.* 22:129–135.
- 427 **Desneux, N., E. Wajnberg, K. Wyckhuys, G. Burgio, S. Arpaia, C. A. Narvaez-**
428 **Vasquez, J. González-Cabrera, D. Catalán-Ruescas, E. Tabone, J. Frandon,**
429 **J. Pizzol, C. Poncet, T. Cabello, and A. Urbaneja. 2010.** Biological invasion of
430 European tomato crops by *Tuta absoluta*: ecology, geographic expansion and
431 prospects for biological control. *J. Pest Sci.* 83: 197–215.
- 432 **García, M.F., and J.C Espul. 1982.** Bioecología de la polilla del tomate (*Scrobipalpula*
433 *absoluta*) en Mendoza, República Argentina. *RIA INTA* 17: 135–145.
- 434 **Ghaderi, S., Y. Fathipour, and S. Asgari. 2017.** Susceptibility of seven selected tomato
435 cultivars to *Tuta absoluta* (Lepidoptera: Gelechiidae): implications for its
436 management. *J. Econ. Entomol.* 110: 421–429.
- 437 **Han, P., N. Desneux, T. Michel, J. Le Bot, A. Seassau, E. Wajnberg, A. Amiens-**
438 **Desneux, and A. V. Lavoit. 2016.** Does plant cultivar difference modify the

439 bottom-up effects of resource limitation on plant-insect interactions? *J. Chem.*
440 *Ecol.* 42: 1293–1303.

441 **Hartmann, T., and D. Ober. 2000.** Biosynthesis and metabolism of Pyrrolizidine
442 alkaloids in plants and specialized insect herbivores, pp. 207-243. In F. J. Leeper
443 and J. C. Vederas (eds.), *Biosynthesis. Topics in Current Chemistry*, vol. 209.
444 Springer, Berlin, Heidelberg, Germany.

445 **Hilker, M., and T. Meiners. 2011.** Plants and insect eggs: How do they affect each
446 other? *Phytochemistry* 72: 1612–1623.

447 **Hilker, M., and N. E. Fatouros. 2015.** Plant responses to insect egg deposition. *Annu.*
448 *Rev. Entomol.* 60: 493–515.

449 **Krechemer F. S., and L. A. Foester. 2017.** Development, reproduction, survival, and
450 demographic patterns of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) on
451 different commercial tomato cultivars. *Neotrop. Entomol.* 46: 694–700.

452 **Larrain, P. 1987.** Plagas del tomate, I parte: descripción, fluctuación poblacional, daño,
453 plantas hospederas, enemigos naturales de las plagas principales. *IPA La*
454 *Platina* 39: 30–35.

455 **Mohamed, E. S. I., M. E. E. Mahmoud, M. A. M. Elhaj, S. A. Mohamed, and S. Ekesi.**
456 **2015.** Host plants record for tomato leaf miner *Tuta absoluta* (Meyrick) in Sudan.
457 *EPPO Bull.* 45(1): 108–111.

458 **Moore, B. D., R. L. Andrew, C. Külheim, and W. J. Foley. 2014.** Explaining
459 intraespecific diversity in plant secondary metabolites in an ecological context.
460 *New Phytol.* 201: 733–750.

461 **Muruvanda, D. A., D. Holden, M. Juarez, C. Ramos, T. Figueroa-Cano, and R. Lee.**
462 **2012.** Surveillance protocol for the tomato leaf miner, *Tuta absoluta*, for NAPPO
463 member countries. *N. Am. Plant Prot. Org.*, Raleigh, NC, accessed July 5, 2017.
464 [https://www.aphis.usda.gov/import_export/plants/plant_exports/downloads/Tuta](https://www.aphis.usda.gov/import_export/plants/plant_exports/downloads/Tuta_absoluta_surveillanceprotocol_08-06-2012-e.pdf)
465 [_absoluta_surveillanceprotocol_08-06-2012-e.pdf](https://www.aphis.usda.gov/import_export/plants/plant_exports/downloads/Tuta_absoluta_surveillanceprotocol_08-06-2012-e.pdf)

466 **Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E.**
467 **Wong, L. Russel, J. Zern, T. Aquino, and T. Tsomondo. 2001.** Economic and
468 environmental threats of alien plant, animal, and microbe invasions. *Agr. Ecosyst.*
469 *Environ.* 84: 1–20.

470 **Pomilio, A. B., E. M. Falzoni, and A. A. Vitale. 2008.** Toxic chemical compounds of the
471 *Solanaceae*. *Nat. Prod. Commun.* 3: 593–628.

- 472 **Portakaldali, M., S. Öztemiz, and H. Kütük. 2013.** A new host plant for *Tuta absoluta*
473 (Meyrick) (Lepidoptera: Gelechiidae) in Turkey. *J. Entomol. Res. Soc.* 15(3): 21–
474 24.
- 475 **Proffit, M., G. Birgersson, M. Bengtsson, R. Jr. Reis, P. Witzgall, and E. Lima. 2011.**
476 Attraction and oviposition of *Tuta absoluta* females in response to tomato leaf
477 volatiles. *J. Chem. Ecol.* 37: 565–574
- 478 **Salas Gervasio, N. G., M. G. Luna, S. Lee, A. Salvo, and N. E. Sánchez. 2016.** Trophic
479 web associated with the South American tomato moth *Tuta absoluta*: implications
480 for its conservation biological control in Argentina. *Agr. Forest Entomol.* 18: 137–
481 144.
- 482 **Shelton, A. M., and F. R. Badenes-Perez. 2006.** Concepts and applications of trap
483 cropping in pest management. *Ann. Rev. Entomol.* 51: 285–308.
- 484 **Smith, J. D., T. Dubois, R. Mallogo, E. F. Njau, S. Tua, and R. Srinivasan. 2018.** Host
485 range of the invasive tomato pest *Tuta absoluta* Meyrick (Lepidoptera:
486 Gelechiidae) on solanaceous crops and weeds in Tanzania. *Fla. Entomol.* 101:
487 573–579.
- 488 **Smith, R., M. Jimenez, and M. Cantwell. 1999.** Tomatillo production in California.
489 University of California Division of Agriculture and Natural resources. Publication
490 No. 7246. Oakland, CA.
- 491 **Silva, D. B., V. H. P. Bueno, J. C. Jr. Lins, and J. C. van Lenteren. 2015.** Life history
492 data and population growth of *Tuta absoluta* at constant and alternating
493 temperatures on two tomato lines. *Bull. Insectol.* 68: 223–232.
- 494 **Sylla, S., T. Brévault, L. S. Monticelli, K. Diarra, N. Desneux. 2019.** Geographic
495 variation of host preference by the invasive tomato leaf miner *Tuta absoluta*:
496 implications for host range expansion. *J. Pest Sci.* 92: 1387–1396
- 497 **Tropea-Garzia, G. 2009.** *Physalis peruviana* L. (Solanaceae), a host plant of *Tuta*
498 *absoluta* in Italy. *IOBC/wprs Bull.* 49: 231–232.
- 499 **Urbaneja, A., R. Vercher, V. Navarro, F. García-Marí, and J. L. Porcuna. 2007.** La
500 polilla del tomate, *Tuta absoluta*. *Phytoma Esp.* 194:16–23.
- 501 **Wheeler, D. 1996.** The role of nourishment in oogenesis. *Ann. Rev. Entomol.* 41: 407–
502 431.
- 503

504 **Figure Captions**

505 **Fig. 1.** Number of plants rated in each class according to the damage inflicted by *T.*
506 *absoluta* infestation.

507

508 **Fig 2.** Kaplan–Meier estimates of proportional survivorship for *T. absoluta* females on
509 different host plant material. Time was measured in days.

510

511 **Fig 3.** Kaplan–Meier estimates of proportional survivorship for *T. absoluta* males on
512 different host plant material. Time was measured in days.

513

514

515

516 **Table 1.** Progeny resulting from a mating pair of *T. absoluta* over 48 hours (mean number
 517 of adults \pm SE), percentage of females in the offspring and percentage of individuals
 518 emerging from the soil. Calculations have included zeros from plants that yielded no
 519 progeny.

Host plant	No. individuals/plant	% of females	% individuals from soil
Tomato Patio Princess	4.58 \pm 1.64	63.64	72.73
Tomato Qualit 23	3.75 \pm 2.02	62.79	66.67
<i>S. nigrum</i>	2.50 \pm 1.31	43.33	80.00
<i>S. sarrachoides</i>	5.00 \pm 1.55	49.15	80.00

520

521

522 **Table 2.** Longevity (mean \pm SE number of days) of *T. absoluta* adults when exposed to
 523 different host plants and supplied with a 10% sugar solution (n = 12 females and 12
 524 males).

Treatment	Females	Males
Tomato Patio Princess	15.25 \pm 1.33	11.08 \pm 2.25
Tomato Qualit 23	9.25 \pm 1.38	8.33 \pm 1.54
Tomatillo Purple	12.83 \pm 2.13	8.58 \pm 2.18
Tomatillo Toma Verde	14.00 \pm 2.19	11.08 \pm 2.03
<i>D. stramonium</i>	13.08 \pm 1.09	8.00 \pm 1.21
<i>S. nigrum</i>	15.17 \pm 2.55	8.75 \pm 2.48
<i>S. sarrachoides</i>	9.92 \pm 1.96	11.67 \pm 1.94

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528 **Table 3.** Daily fecundity (mean number of eggs laid per female \pm SE) during a *T. absoluta*
 529 female's lifespan and number of unfertile females (n = 12).

Treatment	No. unfertile females	Eggs/day/ female
Tomato Qualit 23	0	5.97 \pm 1.24 A
Tomato Patio Princess	0	5.06 \pm 1.16 A
<i>S. nigrum</i>	1	3.23 \pm 1.01 AB
Tomatillo Toma Verde	3	2.12 \pm 0.61 AB
<i>S. sarrachoides</i>	4	2.05 \pm 0.90 AB
<i>D. stramonium</i>	1	1.36 \pm 0.44 AB
Tomatillo Purple	6	0.81 \pm 0.61 B

530 Means followed by different letters are significantly different after Bonferroni correction
 531 was used to weigh the 21 pairwise comparisons done among plants ($P < 0.05/21 =$
 532 0.0024)

533

534

535 **Table 4:** Mean (\pm SE) number of eggs laid by a single *T. absoluta* female over 48 hours
 536 in a choice experiment when the four plant species were provided at the same time (n =
 537 13)

Host plant	Eggs/female
Tomato Qualit 23	9.31 \pm 2.68 A
Tomato Patio Princess	7.46 \pm 2.05 A
<i>S. nigrum</i>	3.15 \pm 1.09 AB
<i>S. sarrachoides</i>	0.31 \pm 0.24 B

538 Means followed by different letters are significantly different after Bonferroni correction
 539 was used to weigh the six pairwise comparisons done among plants ($P < 0.05/6 =$
 540 0.0083)

541

542

543 **Table 5.** Percent survival of each *T. absoluta* life stage and mean development times
 544 (days ± SE) on the different host plant species.
 545

Host plant	EGGS		LARVAE		PUPAE	
	% survival	developmental time	% survival	developmental time	% survival	developmental time
Tomato Qualit 23	84.31	4.16±0.07 B	67.44	12.79±0.34 B	68.97	6.95±0.15
Tomato Patio	88.24	4.47±0.20 AB	31.58	13.00±0.51 AB	83.33	7.30±0.15
<i>S. nigrum</i>	86.27	4.24±0.11 AB	40.91	15.17±0.47 A	61.11	7.36±0.88
<i>S. sarrachoides</i>	88.24	3.98±0.10 B	35.56	12.13±0.30 B	75.00	7.17±0.24
<i>D. stramonium</i>	78.43	4.85±0.18 A	0.00	-	-	-
Tomatillo Purple	80.39	4.39±0.13 AB	0.00	-	-	-
Tomatillo Toma Verde	86.27	4.11±0.10 B	0.00	-	-	-

546 Within column means followed by different letters are significantly different after
 547 Bonferroni correction was used to weigh the multiple pairwise comparisons done among
 548 plants regarding the developmental time of eggs ($P < 0.05/21 = 0.0024$) and larvae ($P <$
 549 $0.05/6 = 0.0083$).

550

551

552 **Table 6.** Mean (±SE) pupal weight (in mg) for *T. absoluta* reared on different host
 553 plants (n = 8).

Host Plant	FEMALES	MALES
Tomato Patio	4.19±0.27	3.20±0.15 A
Tomato Quality 23	3.74±0.23	2.36±0.19 B
<i>S. nigrum</i>	3.93±0.46	3.29±0.19 A
<i>S. sarrachoides</i>	4.30±0.24	2.81±0.16 AB

554 For males, means followed by different letters are significantly differences between
 555 treatments ($P < 0.05$, Tukey's HSD test).