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1 **THE POTENTIAL OF HOST PLANTS FOR BIOLOGICAL CONTROL OF *TUTA***
2 ***ABSOLUTA* BY THE PREDATOR *DICYPHUS ERRANS***

3

4 B.L. Ingegno, V. Candian, I. Psomadelis, N. Bodino, L. Tavella

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6 Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), ULF Entomologia Generale e
7 Applicata, University of Torino, Largo P. Braccini 2, 10095 Grugliasco (TO), Italy

8 E-mail: luciana.tavella@unito.it

9 Phone number: +390116708533

10

11 **ABSTRACT**

12 *Dicyphus errans* (Wolff) has been shown to be a suitable biocontrol agent for *Tuta absoluta*
13 (Meyrick). This generalist predator shares various host plants with the exotic pest, and these
14 interactions could be exploited to enhance pest control. Therefore, host preference, survival rate and
15 development times of the predator and prey were investigated on crop and non-crop plant species.
16 Among the tested plants, the favourite hosts were *Solanum* species for *T. absoluta*, and herb Robert,
17 European black nightshade, courgette and tomato for *D. errans*. *Tuta absoluta* accepted the same
18 plant species as hosts for oviposition, but it never developed on herb Robert and courgette in all the
19 experiments. Based on our results, we would suggest the use of courgette and herb Robert in
20 consociation with tomato and as a companion plant, respectively, which may keep pest densities
21 below the economic threshold. Moreover, the omnivorous and widespread *D. errans* could be a key
22 predator of this exotic pest, allowing a high encounter probability on several cultivated and non-
23 cultivated plant species.

24

25 **Keywords:** Hemiptera Miridae, Lepidoptera Gelechiidae, host plants, developmental time, habitat
26 management

27

28 INTRODUCTION

29 The success of augmentative biological control depends on the efficacy of the released beneficial
30 organisms but also on suitability of the hosting agro-ecosystem, which could be an unfavourable
31 environment due to high levels of disturbance or adverse climatic conditions (Landis et al. 2000;
32 Hatherly et al. 2008). Therefore, to evaluate the potential of a biological control agent (BCA), in
33 addition to its effectiveness in pest population control (acceptability of the pest, developmental times,
34 reproduction fitness, etc.), its capacity to establish itself in a given agro-ecosystem (crop species,
35 abundance of natural host plants surrounding the crop, thermal requirements, photoperiod, etc.)
36 should also be carefully considered for optimal performance. Its ability to feed and survive on
37 alternative nutritional sources, such as plant material, may be an advantage in stabilising natural
38 enemy population dynamics (Lalonde et al. 1999). This characteristic is well represented in generalist
39 predator mirid bugs belonging to the tribe Dicyphini (Hemiptera: Miridae) (Perdikis & Lykouressis
40 2000; Perdikis et al. 2011; Biondi et al. 2016; Naselli et al. 2016).

41 Among these generalist predators, the Palearctic *Dicyphus errans* (Wolff) is widespread throughout
42 Europe (Kerzhner & Josifov 1999), living omnivorously on various host plants (over 150 species)
43 and preying on a wide range of small arthropods (Voigt 2005), characteristics that endow it with a
44 high potential for successful establishment in an agro-ecosystem. In NW Italy it occurs naturally in
45 tomato crop [*Solanum lycopersicum* L. (Solanaceae)], where organic or integrated pest management
46 (IPM) are applied, located in complex agro-ecosystems, preying upon several pests such as whiteflies,
47 mites and thrips (Tavella & Goula 2001; Ingegno et al. 2009). Due to both morphological and
48 behavioural adaptations to pubescent surfaces (Voigt et al. 2007), this mirid prefers hairy plants,
49 including crop plants, such as tomato, eggplant (*Solanum melongena* L.), potato (*Solanum tuberosum*
50 L.) (Solanaceae), courgette (*Cucurbita pepo* L.) (Cucurbitaceae) and pot marigold (*Calendula*
51 *officinalis* L.) (Asteraceae) and non-crop plants, such as European black nightshade (*Solanum nigrum*
52 L.) (Solanaceae), *Geranium* spp. (Geraniaceae), *Stachys sylvatica* L. (Lamiaceae) and *Urtica dioica*

53 L. (Urticaceae) (Arzone et al. 1990; Calabrò & Nucifora 1993; Tavella & Goula 2001; Voigt 2005;
54 Ingegno et al. 2008). Considering its wide host plant range and its large distribution, probably, this
55 species gets a flexible odour-coding system, which allows it to adapt to environmental changes (Bruce
56 and Pickett 2011), relying on ubiquitous compounds for the identification of host plants instead of
57 using specific compounds, as already reported for other dicyphine species, i.e. *Macrolophus*
58 *pygmaeus* (Rambur) and *Macrolophus melanotoma* (Costa) (Ingegno et al. 2016).
59 Recently, *D. errans* has proven to be a suitable BCA against the exotic tomato borer *Tuta absoluta*
60 (Meyrick) (Lepidoptera: Gelechiidae), which is responsible for severe yield losses in tomato crops in
61 the Mediterranean area (Ingegno et al. 2013; Zappalà et al. 2013). Native to South America, this
62 multivoltine pest, characterised by cryptic habits and high pesticide resistance, has rapidly invaded
63 Europe since its accidental introduction into Spain in 2006 (Desneux et al. 2010; Tropea Garzia et al.
64 2012). Both sexes of the mirid prey actively on the eggs and 1st-instar larvae of the tomato borer
65 (Ingegno et al. 2013) as reported in other dicyphine species, such as *M. pygmaeus* and *Nesidiocoris*
66 *tenuis* (Reuter) (Urbaneja et al. 2009; Mollá et al. 2014). Compared to this latter species in Europe *D.*
67 *errans* has a wider distribution (Kerzhner & Josifov 1999). In NW Italy, it is the most abundant
68 species (Ingegno et al. 2008) even in tomato crops where other BCAs (e.g. *M. pygmaeus*) have been
69 released (Ingegno et al. 2014). Moreover, this indigenous mirid seems to share many host plants with
70 the exotic tomato borer. In fact, in addition to tomato, *T. absoluta* has been reported on potato,
71 eggplant and various wild solanaceous species, such as the European black nightshade, datura
72 (*Datura stramonium* L.) and *Nicotiana glauca* Graham (Tropea Garzia et al. 2012). In terms of
73 conservation biological control, knowledge of the host plant species shared by *D. errans* and *T.*
74 *absoluta* could be exploited using various techniques of habitat modification (Messelink et al. 2014)
75 in order to enhance the presence of spontaneously occurring indigenous natural enemies of the exotic
76 pest in agro-ecosystems. In fact, at the end of the growing season, predatory bugs are compelled to
77 abandon the cropped area and search for food and shelters, consequently, new releases of BCAs have
78 to be applied at the beginning of the following crop cycle. This migration could be substantially

79 avoided using companion plants suitable to attract and maintain natural enemies (Perdikis et al. 2011)
80 or intercropping, winter shelters, field borders, landscape diversification, etc. (Ingegno & Messelink
81 2016).
82 Therefore, to improve our knowledge on the correct management of the exotic pest, an in-depth
83 analysis on the most promising plants to grow in consociation with and/or surrounding tomato crop
84 for the control of *T. absoluta* and the enhancement of *D. errans* was carried out. Biological and
85 behavioural aspects of this predator-prey system, with particular regard to shared host plants, were
86 investigated. In particular, the preference, survival rate and developmental times of both the predator
87 and prey were compared on different plant species, crop and non-crop plants usually grown in agro-
88 ecosystems in NW Italy. Furthermore, the role of a crop plant and a non-crop plant to use in tomato
89 cultivation in consociation or as a companion plant, respectively, to manage pest outbreaks was
90 assessed in laboratory conditions.

91

92 **MATERIALS AND METHODS**

93 **Insect and plant rearing**

94 Colonies of *D. errans* were started from individuals collected on European black nightshade in
95 different localities in Piedmont (NW Italy) and reared on European black nightshade, tomato cv
96 Marmande and tobacco *Nicotiana tabacum* L. (Solanaceae) inside insect cubic cages, 47.5 cm edge
97 (BugDorm, MegaView, Taiwan). Individuals were fed with eggs of *Ephestia kuehniella* Zeller
98 (Lepidoptera: Pyralidae) (Bioplanet s.c.a., Cesena, Italy) and with dehydrated and decapsulated cysts
99 of *Artemia salina* (L.) (Anostraca: Artemiidae) (La Mangrovia, Ostuni, Italy). Mass rearing was
100 carried out in climatized chambers, at 24±1 °C, 55±5% RH, with a L 16:D 8 photoperiod.
101 Colonies of *T. absoluta* were established from individuals provided by Bioplanet laboratories
102 (Bioplanet s.c.a., Cesena, Italy). Continuous mass rearing was maintained on tomato plants in net
103 cages (150 W × 150 L × 110 H cm) consisting of a stainless steel frame structure supporting an

104 insect-proof net (mesh 0.23×0.23 mm). Mass rearing was carried out in an experimental greenhouse
105 at 27±3 °C and 55±23% RH.

106 The following 10 plant species were selected among the most common hosts and non-hosts of *D.*
107 *errans* and *T. absoluta*, in tomato crop environments in Piedmont, and used in laboratory assays:
108 tomato cv Marmande, potato cv Villastellone, eggplant cv Bellezza nera, pepper cv Quadrato d'Asti,
109 datura, European black nightshade, courgette cv Nero di Milano, herb Robert *Geranium robertianum*
110 L. (Geraniaceae), common bean *Phaseolus vulgaris* L. cv Borlotto and broad bean *Vicia faba* L. cv
111 Aguadulce Supersimonia (Fabaceae). Seeds from seed companies were used, except seeds of
112 European black nightshade and herb Robert that were collected from wild plants grown in Turin area.
113 Seeds were sown in plastic pots (Ø 14 cm), watered daily and fertilized. All the plants were grown
114 in an experimental heated greenhouse and used in the experiments when they reached approximately
115 25–40 cm in height with a similar leaf area.

116

117 **Host plant selection**

118 The host plant selection experiments were set up as multi-choice assays and performed separately
119 with the predator *D. errans* or the pest *T. absoluta*. Potted plants of each of the 10 selected plant
120 species were randomly placed in a net cage (150 W×150 L×110 H cm) with a stainless steel frame
121 structure supporting the insect-proof net (mesh 0.23×0.23 mm), together with predator or prey
122 individuals. All the experiments were conducted in a heated experimental greenhouse at 27±3 °C and
123 55±23% RH.

124 The predator *D. errans*

125 To assess the preference of *D. errans* adults toward the 10 tested plant species, two potted plants of
126 each species were randomly placed inside a net cage in the experimental greenhouse. Two 1-week-
127 old females and one male were released per plant (a total of 40 females and 20 males per cage) at the
128 centre of the cage. After 72 h, each plant was inspected to count the surviving adults. The plants were

129 then singly isolated in Plexiglas cylinders (\varnothing 12 cm, height 50 cm), placed in climatised chambers at
130 24 ± 1 °C, $65\pm 5\%$ RH and L 16:D 8 and checked for nymph emergences every 48 h until no nymphs
131 were found for one week. All emerged nymphs were removed and counted. The plant preference was
132 expressed as the proportion of nymphs emerged from each plant species per cage. Seven repetitions
133 were conducted.

134 The pest *T. absoluta*

135 To assess the oviposition preference and generated offspring on the 10 tested plant species, three
136 potted plants of each species were placed inside a net cage in the experimental greenhouse. Four adult
137 *T. absoluta* were released per plant (a total of 120 adults per cage) at the centre of the cage. After
138 48 h, the adults were removed and each plant was inspected to count the eggs. The plants were then
139 singly isolated in Plexiglas cylinders (\varnothing 12 cm, height 50 cm) and after one week they were checked
140 for egg hatching and larval emergence. Five repetitions were conducted.

141

142 **Survival rate and development time**

143 The survival rate and development time of the predator *D. errans* and of the pest *T. absoluta* were
144 evaluated on six plant species selected from the most promising ones for future field applications. All
145 the bioassays were carried out in climatised chambers at 24 ± 1 °C, $65\pm 5\%$ RH and L 16:D 8.

146 The predator *D. errans*

147 To estimate the embryonal development time of *D. errans* on the tested plants, the number of days
148 between the exposure of each plant species to the predator females and the first nymph emergence
149 was recorded. For this purpose, the plants coming from the host plant selection experiment or other
150 plants specifically set, if the number of nymphs was not high enough, were used. Newly emerged
151 nymphs (<1 day old) were placed individually on leaf disks (\varnothing 25 mm) from each plant species in
152 single cells of 12-well tissue culture plates (Falcon™ Tissue Culture Plates, Corning, NY, USA) on
153 wet Gypsum plaster to maintain humidity, and provided with *A. salina* cysts (about 0.02 g). The cells

154 were then closed with Parafilm®. For each plant species, 20 nymphs were observed during their
155 development until adulthood or death. Moulting, evidence of the presence of the exuvia or death of a
156 nymph were recorded daily and used to determine the duration and survival rate of each nymphal
157 instar. All the emerged adults were sexed, measured (from the head vertex to the end of the hemelytra)
158 under a stereomicroscope and weighed with a precision (0.01 mg) balance (ABS 120-4, Kern & Sohn
159 GmbH, Germany) after 1 min of cold anaesthesia.

160 The pest *T. absoluta*

161 For each plant species, 15 fresh eggs (less than 48 h) of the tomato borer were gently transferred to a
162 healthy potted plant. Each plant was placed separately inside a Plexiglas cage (20×20×30 cm) with
163 two sides, a lid of fine gauze (30/10 net) and a mesh sleeve inserted in the middle of one side
164 (Ø 11 cm). All the emerged adults were counted. Six repetitions were conducted.

165

166 **Role of a crop plant and a non-crop plant on the pest *T. absoluta***

167 On the basis of the results obtained in the host selection and developmental trials, the plants resulting
168 to be interesting for their possible field application to manage *T. absoluta* in tomato cultivation, in
169 consociation with and/or as companion plants, were further tested. In particular, three plant species
170 (tomato, a crop plant and a non-crop plant) were used in: i) dual choice experiments on leaves and on
171 entire plants to evaluate the preference by the tomato borer; ii) a field simulation laboratory trial to
172 assess the effects of three tomato field conditions on the pest. All the experiments were carried out in
173 climatised chambers at 24±1 °C, 65±5% RH and L 16: D 8.

174 Dual choice experiments with the pest *T. absoluta*

175 In dual choice experiments on both leaves and entire potted plants, the following six comparisons
176 were performed: 1) tomato vs tomato, 2) tomato vs crop plant, 3) tomato vs non-crop plant, 4) crop
177 plant vs crop plant, 5) non-crop plant vs non-crop plant, 6) crop plant vs non-crop plant.

178 Dual choice experiments on leaves were carried out in Petri dishes (\varnothing 9 cm), half-filled with agar
179 2%, on which leaves of the two plants in comparison were equally distributed to cover the entire
180 surface. A glass cylinder (\varnothing 8 cm, height 15 cm), covered with a fine net on the top to prevent insect
181 escaping, was placed on each Petri dish. Five individuals of *T. absoluta* were inserted in each cylinder
182 and removed after 24 h. Leaves were then inspected to count the eggs. At least 10 repetitions were
183 conducted for each comparison.

184 Dual choice experiments on entire potted plants were carried out to evaluate, besides the number of
185 laid eggs, also the number of hatched larvae and of emerged adults. A pair of plants (one per each
186 plant in comparison) was placed in an insect cubic cage, 47.5 cm edge (BugDorm, MegaView,
187 Taiwan), in which 10 *T. absoluta* adults were inserted. After 48 h, the adults were removed and each
188 plant was inspected to count the eggs. The plants were then singly isolated in Plexiglas cages
189 (20×20×30 cm), and checked for larval hatching after one week, and then every two days for adult
190 emergence. Five repetitions were conducted for each comparison.

191 Field simulation laboratory trial with the pest *T. absoluta*

192 To evaluate the effects of three tomato field conditions (i.e., monoculture, crop consociation,
193 companion planting), the following three comparisons were performed: 1) tomato vs tomato, 2)
194 tomato vs crop plant, 3) tomato vs non-crop plant. The laboratory trial was carried out in insect cubic
195 cage, 47.5 cm edge (BugDorm, MegaView, Taiwan), in which six plants (three per each plant in
196 comparison) were placed in two opposite rows. The plants were infested introducing 12 adults of *T.*
197 *absoluta* (two adults per plant) in each cage. After 2 weeks, the adults were removed and the plants
198 were inspected to count the larvae, and then checked every two days to monitor adult emergence.
199 Four repetitions were conducted for each comparison.

200

201 **Statistical analyses**

202 In the host plant selection experiment on *D. errans*, the percentages of nymphs that emerged from
203 each plant species in each cage (repetition) were arcsine square root transformed, checked for

204 homogeneity of variance (Levene test) and normality (Shapiro-Wilk test) and compared using a one-
205 way ANOVA; in the case of significant differences the means were separated by a Tukey's test. In
206 the host plant selection experiment on *T. absoluta*, the percentages of laid eggs and of emerged larvae
207 for each plant species in each cage were compared using Kruskal Wallis analysis and, in the case of
208 significant differences, the means were separated using a Mann-Whitney U test, as they were not
209 homogeneous. After testing them for homogeneity of variance (Levene test) and normality (Shapiro-
210 Wilk test), developmental time data for *D. errans* and *T. absoluta* were analysed using a one-way
211 ANOVA and, in the case of significant differences, the means were separated using a Tukey's test.
212 Data on the weight and length of *D. errans* that emerged in the developmental trials were compared
213 using Kruskal Wallis analysis and the means were separated using a Mann-Whitney U test if the
214 assumptions of an ANOVA were not met, otherwise the means were separated using a Tukey's test.
215 In the dual choice experiments and field simulation laboratory trial with the pest *T. absoluta*, data
216 were expressed as percentage of laid eggs, hatched larvae or emerged adults per plant species on the
217 total number of laid eggs, hatched larvae or emerged adults per comparison; then, they were arcsine
218 square root transformed and tested for normality. When data were normally distributed, a Student's
219 T test pairwise comparison was applied to test the hypothesis that the distribution deviated from a
220 null model in which plant sources were chosen with equal frequency. Otherwise, if data were not
221 normally distributed, the non-parametric Wilcoxon test was performed. Moreover, in the field
222 simulation laboratory trial to compare the mean number of larvae and of adults emerged in each
223 comparison, because of non-homogeneity of variances, raw data were analysed with Kruskal Wallis
224 analysis and, in the case of significant differences, means were separated by Mann-Whitney U test.
225 The statistical analyses were performed using SPSS v21.0 (SPSS Inc., Chicago, IL, USA).

226

227 **RESULTS**

228 **Host plant selection**

229 The predator *D. errans*

230 In the multi-choice experiment *D. errans* females laid eggs on all 10 tested plant species. The six
231 species showing the most abundant offspring were, in decreasing order, herb Robert, European black
232 nightshade, eggplant, courgette, tomato and common bean (Figure 1). The least favourite plant
233 species was the broad bean from which only three nymphs out of 142 emerged. The mean proportion
234 of emerged nymphs was significantly higher on herb Robert than on broad bean, pepper, datura and
235 potato (ANOVA, DF=9, 69, F=3.194, P=0.003) (Figure 1).

236 The pest *T. absoluta*

237 In the multi-choice experiment, *T. absoluta* females laid eggs on all 10 offered plant species but
238 mostly, in decreasing order, on tomato, European black nightshade, eggplant, courgette and potato
239 (Figure 2). Nevertheless, newly emerged larvae were found almost exclusively on species of the
240 genus *Solanum* (Figure 2). The mean proportions of eggs and larvae were significantly higher on
241 plants belonging to this genus than any other genera (Kruskal Wallis: eggs, DF=9, $\chi^2=94.307$,
242 $P<0.001$; larvae, DF=9, $\chi^2=115.438$, $P<0.001$) (Figure 2). In particular, tomato was the favourite
243 species for both oviposition (1500 out of 3572 eggs) and larval emergence (1054 out of 2445 larvae).
244 Although numerous eggs were found on courgette (392) only six hatched and no larvae developed.

245

246 **Survival rate and developmental time**

247 The predator *D. errans*

248 The interval from exposure of the plant to the females to the first nymph emergence ranged from
249 13.1 ± 0.4 days to 16.0 ± 1.0 days on herb Robert and tomato respectively, showing a shorter embryonal
250 development of *D. errans* on herb Robert (ANOVA, DF=5, F=4.68, $P<0.001$) (Table 1). The interval
251 from nymph emergence to adulthood ranged from 14.7 ± 0.4 days on European black nightshade to
252 17.3 ± 0.3 days on eggplant and was significantly different between these two plants (ANOVA, DF=5,
253 66, F=2.625, $P=0.032$) (Table 2). Moreover, significant differences were found in the developmental
254 times of each instar between plant species without a constant order (Table 2). Rate of adult emergence
255 was significantly higher on herb Robert and tomato than on common bean and eggplant (Table 2).

No significant differences were observed in sex ratio of newly emerged *D. errans* from different plant species (Table 2). Within the sexes, females reared on different plant species showed no significant differences in either weight or length; males were significantly heavier when reared on courgette and herb Robert than on bean and longer when reared on herb Robert compared to tomato and European black nightshade (Table 3).

The pest *T. absoluta*

In the developmental trials, no adult *T. absoluta* emerged from courgette and herb Robert, showing a 100% mortality, significantly higher than that on the other plant species (Kruskal Wallis, DF=5, $\chi^2=27.341$, $P<0.001$) (Table 4). Preimaginal developmental time was significantly shorter on tomato and European black nightshade than on eggplant, (ANOVA, DF=3, 164, $F=7.040$, $P<0.001$) (Table 4). Overall, newly emerged larvae took less than 20 days to reach adulthood.

Role of a crop plant and a non-crop plant on the pest *T. absoluta*

On the basis of the results obtained in the host selection and developmental trials, courgette and herb Robert were selected among the crop and non-crop plants, respectively, to assess their suitability as crop plants and/or companion plants to grow in consociation with and/or surrounding tomato crop.

Dual choice experiments with the pest *T. absoluta*

In the dual choice experiment on leaves, the tomato borer oviposited on all the tested plant species, however showing a preference toward the leaves of tomato when offered together with leaves of courgette (Wilcoxon test: $Z=-2.536$; $P=0.011$) or of herb Robert (Wilcoxon test: $Z=-3.051$; $P=0.002$) (Table 5). On the contrary, no significant difference were found between leaves of courgette and herb Robert (Wilcoxon test: $Z=-0.090$; $P=0.928$), as well as when the same plant species was offered in the arena (Wilcoxon test: tomato, $Z=-0.161$; $P=0.872$; courgette, $Z=-1.156$; $P=0.248$; herb Robert, $Z=-1.675$; $P=0.098$) (Table 5).

Also, in the dual choice experiment on entire plants, *T. absoluta* oviposited on all the tested plant species. Similarly, for oviposition tomato was preferred to courgette (Student's T test: $df=4$; $t=5.976$;

282 P=0.004) and herb Robert (Student's T test: df=4; t=2.772; P=0.050) (Table 6). Moreover, no
283 significant difference was found between courgette and herb Robert (t=-0.952; P=0.395), as well as
284 when plants of the same species were offered in the cage (Student's T test: courgette, df=4; t=-0.820;
285 P=0.458; herb Robert, t=1.185; P=0.302; tomato, t=-0.939; P=0.401) (Table 6). The larval hatching
286 and adult emergence on tomato varied from 85.3±8.6 to 97.7±1.4% and from 68.8±9.7 to 96.7±2.2%,
287 respectively, whereas despite the presence of eggs, no larvae and consequently no adults of the tomato
288 borer emerged from courgette and herb Robert (Table 6).

289 Field simulation laboratory trial with the pest *T. absoluta*

290 No larvae and consequently no adults of *T. absoluta* emerged from courgette and herb Robert,
291 therefore numbers of both larvae and adults were significantly different between tomato and courgette
292 (Wilcoxon test: larvae, Z=-2.000; P=0.046; adults, Z=-2.000; P=0.046) and between tomato and herb
293 Robert (Wilcoxon test: larvae, Z=-2.000; P=0.046; adults, Z=-2.000; P=0.046) (Table 7). No
294 differences were found when tomato was the only plant species offered for both larva hatching and
295 adult emergence (Wilcoxon test: larvae, Z=-0.365; P=0.715; adults, Z=-1.095; P=0.273) (Table 7).
296 Moreover, even if the mean number of larvae or adults of *T. absoluta* emerged in each comparison
297 was variable, no significant differences were found on tomato plants (U Mann Whitney test; P>0.05)
298 (Table 7).

299

300 **DISCUSSION**

301 Habitat management may occur at different levels, i.e. within-crop, within-farm or at landscape
302 levels, to improve the availability of the resources required by natural enemies (Landis et al. 2000).
303 Focusing on the within-crop level, in organic and IPM farming systems the use of pest resistant
304 cultivars, pest repellent plants, pest trapping plants or predator attractive companion plants might
305 preserve crop production from pest attacks (Parker et al. 2013). In our study, we investigated shared
306 hosts in order to identify crop plants and/or companion plants to grow in consociation with and/or
307 surrounding tomato crops.

308 In this study, among the tested crop plants, tomato, eggplant and potato were the most attractive to *T.*
309 *absoluta*, whereas eggplant, courgette and tomato were the most preferred by *D. errans*. Therefore,
310 tomato was confirmed as the favourite crop plant of the exotic pest for both oviposition and
311 preimaginal development. In fact, all the epigeal plant parts are suitable for moth development
312 (Tropea Garzia et al. 2012) and fecundity on this host is twofold higher than on potato and European
313 black nightshade (Bawin et al. 2015). Tomato was also one of the favourite hosts of *D. errans* in both
314 the multi-choice and developmental experiments, showing an adult emergence rate of 85%. This crop
315 plant is potentially even more attractive to the predator when attacked by the tomato borer (Ingegno
316 et al. 2013), as also reported for other dicyphines, *M. pygmaeus* and *N. tenuis* (Ingegno et al. 2011;
317 Lins et al. 2014).

318 Eggplant and potato were attractive to *T. absoluta*, confirming the previously reported high capacity
319 of the pest to develop on these crops (Tropea Garzia et al. 2012; Megido et al. 2013). Indeed, the
320 preimaginal developmental time on potato did not differ from that observed on tomato, contrary to
321 the results previously reported by Bawin et al. (2015) where it was found to develop faster in different
322 experimental conditions (i.e., on excised plant leaves). By contrast, only eggplant, not potato, even
323 though it has been reported as a host (Goula & Alomar 1994), was found to be among the favourite
324 hosts of *D. errans* in a multi-choice experiment, even though the developmental time and emergence
325 rate were longer and lower respectively than on the other host plants.

326 Although courgette was selected by moth females for oviposition in all the experiments, it did not
327 result in larval development of *T. absoluta*. To our knowledge, this is the first report of developmental
328 inhibition in the tomato borer on this crop plant. Such inhibition could be due to morphological plant
329 features or defence mechanisms in response to the presence of the eggs. Therefore, further
330 investigations on the inhibition properties of courgette, such as analyses of the plant's chemical
331 profile, which may include some repellent substances, are needed. In the field simulation trial, despite
332 the same number of *T. absoluta* adults inserted into the cages, larva and adult emergence was
333 considerably lower in the comparison tomato vs courgette than in the one tomato vs tomato. Besides

possible inhibition properties of the courgette, such reduction could be also due to the intrinsic limit of tomato plants to tolerate high pest density that should be further investigated. On the other hand, beside courgette, *D. errans* has already been observed on several cucurbits (Voigt et al. 2007; Balzan & Moonen 2014). Moreover, in the field this mirid species is frequently found in large numbers inside courgette flowers (personal observations). However, field experiments should be carried out to validate our results in order to recommend a consociation of tomato and courgette for both controlling the tomato borer and enhancing the mirid predator.

The three non-crop plants tested in our study revealed different levels of attractiveness for both prey and predator. *Datura*, even though it has been reported as a host plant of the tomato borer (Tropea Garzia et al. 2012), was unattractive to *T. absoluta*, as already observed by Bawin et al. (2015), and *D. errans*, showing no apparent advantage for pest management. However, European black nightshade was highly attractive for both prey and predator in the multi-choice experiment. Indeed, *D. errans* developed faster on this host than on the other tested plant species, showing also an adult emergence rate of 70%, not significantly lower than the one on tomato (85%). Hence, the role of this plant species in the agro-ecosystem should be carefully evaluated as it could act as a reservoir or as a source. In fact, during winter, in the absence of tomato crops, the predator may take refuge and carry on its pest control activity on European black nightshade. However, both prey and predator could move from this plant to the tomato crop in spring, thwarting its advantages as a predator winter reservoir.

Finally, herb Robert was the favourite host plant for *D. errans* in terms of attractiveness and suitability, as it was unattractive to *T. absoluta*. In fact, moth females laid few eggs on this plant and no larvae were found or developed. These characteristics make herb Robert a potentially promising companion plant. Moreover, in the field simulation trial, in the comparison tomato vs herb Robert, a high reduction of larva and adult emergence of *T. absoluta* was observed. As previously reported for the comparison tomato vs courgette, this reduction should be further investigated to assess the causes, such as possible inhibition properties of herb Robert and/or intrinsic limits of tomato plants to tolerate

360 high pest density. This plant species has a wide ecological amplitude covering the whole distribution
361 range of the predator (Kerzhner & Josifov 1999); it has spread everywhere in world temperate zones,
362 including Europe, the Americas, northern Africa and western Asia (Tofts 2004). Therefore, in terms
363 of habitat management, herb Robert could be used in plant strips next to vegetable cultivations to
364 enhance early crop colonization by the predatory mirid. In fact, a prior to pest establishment of *D.*
365 *errans* in cropping systems should be considered to prevent high pest populations and to contribute
366 to effective and stable pest control strategies in organic greenhouses. For this purpose, field
367 experiments, like those performed using marigold in tomato crops to enhance the presence of *D.*
368 *errans* and *M. pygmaeus* (Lambion 2010), should be carried out to evaluate their efficacy as BCAs.
369 In conclusion, our outcomes underline the potential role of some crop and non-crop plants (e.g. a
370 consociation of courgette and tomato and/or herb Robert as a companion plant) for the correct
371 management of this prey-predator system to keep pest densities below the economic threshold.
372 Moreover, based on our results, as well as on the great plasticity of mirids in exploiting food sources
373 (Biondi et al. 2016), the omnivorous and widespread *D. errans* could be a key predator of the exotic
374 pest *T. absoluta*. Its ability to survive in various environments may result in a high encounter
375 probability with the tomato borer on several cultivated and non-cultivated plant species and a more
376 successful pest control.

377

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382

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484

485

486 **Table 1.** Developmental time in days (mean±SE, no. of individuals) occurring from eggs to nymph
 487 emergence of *Dicyphus errans* on six plant species. Means followed by different letters are
 488 significantly different (Tukey test, P>0.05).

Plant species	Time from egg to nymph emergence
<i>Cucurbita pepo</i>	13.61±0.54 (18) ab
<i>Geranium robertianum</i>	13.11±0.41 (38) b
<i>Phaseolus vulgaris</i>	15.64±0.83 (7) ab
<i>Solanum lycopersicum</i>	16.00±1.04 (16) a
<i>Solanum melongena</i>	14.82±0.50 (28) ab
<i>Solanum nigrum</i>	15.47±0.38 (33) a

489

490 **Table 2.** Developmental time in days (mean±SE, no. of individuals) occurring for each nymphal instar of *Dicyphus errans* on six plant species,
 491 adult emergence rate, and sex ratio [no. of females/(no. of females + no. of males)]. In columns, means followed by different letters are significantly
 492 different.

Plant species	I-II	II-III	III-IV	IV-V	V-adult	Total	Emergence rate	Sex ratio
<i>Cucurbita pepo</i>	2.30±0.21 (20) b	3.30±0.31 (20) a	2.89±0.21 (18) bc	2.94±0.25 (16) ab	4.45±0.43 (11) ab	16.00±0.70 ab	55% ab	0.55
<i>Geranium robertianum</i>	3.40±0.39 (20) a	2.55±0.18 (20) b	2.85±0.25 (20) bc	2.70±0.21 (20) b	3.89±0.30 (18) ab	15.22±0.40 ab	90% a	0.39
<i>Phaseolus vulgaris</i>	3.00±0.00 (20) ab	1.73±0.30 (11) b	5.60±0.60 (5) a	2.40±0.24 (5) ab	3.00±0.55 (5) ab	15.40±0.60 ab	25% b	0.20
<i>Solanum lycopersicum</i>	3.00±0.22 (20) ab	2.55±0.20 (20) ab	2.30±0.11 (20) c	2.80±0.22 (20) b	4.65±0.26 (17) a	15.29±0.34 ab	85% a	0.53
<i>Solanum melongena</i>	3.30±0.21 (20) a	3.55±0.21 (11) a	3.71±0.42 (7) b	4.14±0.26 (7) a	2.86±0.26 (7) b	17.29±0.29 b	35% b	0.14
<i>Solanum nigrum</i>	2.45±0.14 (20) b	3.55±0.21 (20) a	2.90±0.22 (20) bc	2.80±0.30 (20) b	3.14±0.36 (14) b	14.71±0.44 a	70% ab	0.64
	Kruskal Wallis	ANOVA	ANOVA	ANOVA	ANOVA	ANOVA	GLM	GLM
	DF=5	DF=5, 96	DF=5, 84	DF=5, 82	DF=5, 66	DF=5, 66	DF=5, 114	DF=5, 66
	$\chi^2=26.34$	F=7.25	F=10.75	F=2.43	F=4.32	F=2.62	$\chi^2=31.26$	$\chi^2=7.59$
	P<0.001	P<0.001	P<0.001	P=0.042	P=0.002	P=0.032	P<0.001	P=0.180

493

494

495 **Table 3.** Mean weight (\pm SE) and length (\pm SE) of newly emerged females and males of *Dicyphus*
 496 *errans* on different plant species. In columns, means followed by different letters are significantly
 497 different.

Plant species	♀			♂		
	No.	Weight (mg)	Length (mm)	No.	Weight (mg)	Length (mm)
<i>Cucurbita pepo</i>	6	1.85±0.03 a	4.90±1.24 a	5	1.50±0.00 a	4.83±0.48 ab
<i>Geranium robertianum</i>	7	2.04±0.05 a	5.27±0.71 a	11	1.52±0.04 a	4.99±0.39 a
<i>Phaseolus vulgaris</i>	1	1.71 a	5.1 a	4	1.15±0.03 c	4.80±0.41 ab
<i>Solanum lycopersicum</i>	9	1.94±0.08 a	4.98±1.23 a	8	1.39±0.05 ab	4.76±0.75 b
<i>Solanum melongena</i>	1	1.8 a	5.2 a	6	1.37±0.05 ab	4.87±0.56 ab
<i>Solanum nigrum</i>	9	1.93±0.06 a	5.20±0.83 a	5	1.24±0.06 bc	4.68±1.02 b
		Kruskal Wallis	Kruskal Wallis		Kruskal Wallis	ANOVA
		DF=5	DF=5		DF=5	DF=5, 32
		$\chi^2=9.556$	$\chi^2=7.007$		$\chi^2=19.947$	F=3.34
		P=0.089	P=0.220		P=0.001	P=0.015

498

499 **Table 4.** Developmental time in days (mean±SE) from egg to adult and emergence rate of *Tuta*
 500 *absoluta* on different plant species. In columns means followed by different letters are significantly
 501 different (Tukey test, P>0.05).

Plant species	Developmental time	Emergence rate
<i>Cucurbita pepo</i>	-	0.0%
<i>Geranium robertianum</i>	-	0.0%
<i>Solanum lycopersicum</i>	25.37±0.26 a	43.3%
<i>Solanum melongena</i>	27.80±0.09 b	30.0%
<i>Solanum nigrum</i>	26.12±0.35 ab	44.4%
<i>Solanum tuberosum</i>	24.32±0.98 a	68.9%

502

503 **Table 5.** Mean number (\pm SE) of laid eggs of *Tuta absoluta* in the dual choice experiment on leaves
504 of the three plant species in comparison. Wilcoxon test tested the hypothesis that the tomato borer
505 distribution deviated from a null model in which plant sources were chosen with equal frequency for
506 oviposition ($P<0.05$). Data are shown before transformation for an easier interpretation. * $P<0.05$;
507 ** $P<0.01$; *** $P<0.001$.

Comparison (no. of repetitions)	Plant species	No. of eggs (mean \pm SE)	Plant species	No. of eggs (mean \pm SE)	Z	P
1 (18)	<i>Solanum lycopersicum</i>	12.33 \pm 3.17	<i>Solanum lycopersicum</i>	13.33 \pm 3.86	-0.161	0.872
2 (15)	<i>Solanum lycopersicum</i>	8.10 \pm 1.64	<i>Cucurbita pepo</i>	1.40 \pm 0.43	-2.536	0.011*
3 (20)	<i>Solanum lycopersicum</i>	9.73 \pm 2.72	<i>Geranium robertianum</i>	0.09 \pm 0.09	-3.051	0.002**
4 (10)	<i>Cucurbita pepo</i>	2.44 \pm 0.83	<i>Cucurbita pepo</i>	4.56 \pm 1.89	-1.156	0.248
5 (11)	<i>Geranium robertianum</i>	0.70 \pm 0.38	<i>Geranium robertianum</i>	0.90 \pm 0.32	-1.656	0.098
6 (15)	<i>Cucurbita pepo</i>	2.07 \pm 1.40	<i>Geranium robertianum</i>	2.20 \pm 1.56	-0.90	0.928

508

509

510 **Table 6.** Mean number (\pm SE) of laid eggs, hatched larvae and emerged adults of *Tuta absoluta* in the
511 dual choice experiment on entire plants of the three plant species in comparison. Student's T test
512 pairwise (T) or Wilcoxon test (Z) tested the hypothesis that tomato borer distribution deviated from
513 a null model in which plant sources were chosen with equal frequency ($P < 0.05$). Data are shown
514 before transformation for an easier interpretation. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
515

Stage	Comparison (no. of repetitions)	Plant species	Mean no. \pm SE	Plant species	Mean no. \pm SE	T or Z	P
eggs	1 (5)	<i>Solanum lycopersicum</i>	29.60 \pm 8.61	<i>Cucurbita pepo</i>	2.20 \pm 0.66	T=-5.976	0.004**
	2 (5)	<i>Solanum lycopersicum</i>	58.20 \pm 20.68	<i>Geranium robertianum</i>	13.40 \pm 3.43	T=-2.772	0.050*
	3 (5)	<i>Solanum lycopersicum</i>	21.40 \pm 10.78	<i>Solanum lycopersicum</i>	19.20 \pm 6.82	T=-0.939	0.401
	4 (5)	<i>Cucurbita pepo</i>	7.00 \pm 4.23	<i>Cucurbita pepo</i>	9.60 \pm 4.07	T=-0.820	0.458
	5 (5)	<i>Geranium robertianum</i>	10.80 \pm 3.09	<i>Geranium robertianum</i>	6.20 \pm 2.73	T=-1.185	0.302
	6 (5)	<i>Cucurbita pepo</i>	7.40 \pm 2.60	<i>Geranium robertianum</i>	7.00 \pm 1.67	T=-0.952	0.395
larvae	1 (5)	<i>Solanum lycopersicum</i>	28.60 \pm 7.92	<i>Cucurbita pepo</i>	0.00 \pm 0.00	Z=-2.236	0.025*
	2 (5)	<i>Solanum lycopersicum</i>	43.00 \pm 10.04	<i>Geranium robertianum</i>	0.00 \pm 0.00	Z=-2.236	0.025*
	3 (5)	<i>Solanum lycopersicum</i>	20.40 \pm 10.04	<i>Solanum lycopersicum</i>	17.60 \pm 5.79	Z=-0.674	0.500
	4 (5)	<i>Cucurbita pepo</i>	0.00 \pm 0.00	<i>Cucurbita pepo</i>	0.00 \pm 0.00	Z=0.000	1.000
	5 (5)	<i>Geranium robertianum</i>	0.00 \pm 0.00	<i>Geranium robertianum</i>	0.00 \pm 0.00	Z=0.000	1.000
	6 (5)	<i>Cucurbita pepo</i>	0.00 \pm 0.00	<i>Geranium robertianum</i>	0.00 \pm 0.00	Z=0.000	1.000
adults	1 (5)	<i>Solanum lycopersicum</i>	28.00 \pm 7.37	<i>Cucurbita pepo</i>	0.00 \pm 0.00	Z=-2.236	0.025*
	2 (5)	<i>Solanum lycopersicum</i>	37.80 \pm 11.77	<i>Geranium robertianum</i>	0.00 \pm 0.00	Z=-2.236	0.025*
	3 (5)	<i>Solanum lycopersicum</i>	19.80 \pm 9.62	<i>Solanum lycopersicum</i>	17.20 \pm 5.41	Z=-0.674	0.500
	4 (5)	<i>Cucurbita pepo</i>	0.00 \pm 0.00	<i>Cucurbita pepo</i>	0.00 \pm 0.00	Z=0.000	1.000
	5 (5)	<i>Geranium robertianum</i>	0.00 \pm 0.00	<i>Geranium robertianum</i>	0.00 \pm 0.00	Z=0.000	1.000
	6 (5)	<i>Cucurbita pepo</i>	0.00 \pm 0.00	<i>Geranium robertianum</i>	0.00 \pm 0.00	Z=0.000	1.000

516

517 **Table 7.** Mean number (\pm SE) of larvae and adults of *Tuta absoluta* emerged on the three plants of
 518 each plant species tested in the trial. In column, mean numbers of larvae and of adults followed by
 519 different letters are significantly different (U Mann Whitney test, $P<0.05$). Wilcoxon pairwise test
 520 tested the hypothesis that the tomato borer emergence deviated from a null model in which plant
 521 sources were chosen with equal frequency ($P<0.05$). Data are shown before transformation for easier
 522 interpretation. * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

523

Stage	Plant species	Mean no. \pm SE	Plant species	Mean no. \pm SE	Z	P
larvae	<i>Solanum lycopersicum</i>	118.75 \pm 39.52 a	<i>Solanum lycopersicum</i>	106.00 \pm 28.86 a	-0.365	0.715
		79.00 \pm 19.03 a	<i>Cucurbita pepo</i>	0.00 b	-2.000	0.046*
		82.25 \pm 25.12 a	<i>Geranium robertianum</i>	0.00 b	-2.000	0.046*
adults	<i>Solanum lycopersicum</i>	73.25 \pm 27.12 a	<i>Solanum lycopersicum</i>	45.50 \pm 10.77 a	-1.095	0.273
		30.75 \pm 8.29 a	<i>Cucurbita pepo</i>	0.00 b	-2.000	0.046*
		46.00 \pm 18.14 a	<i>Geranium robertianum</i>	0.00 b	-2.000	0.046*

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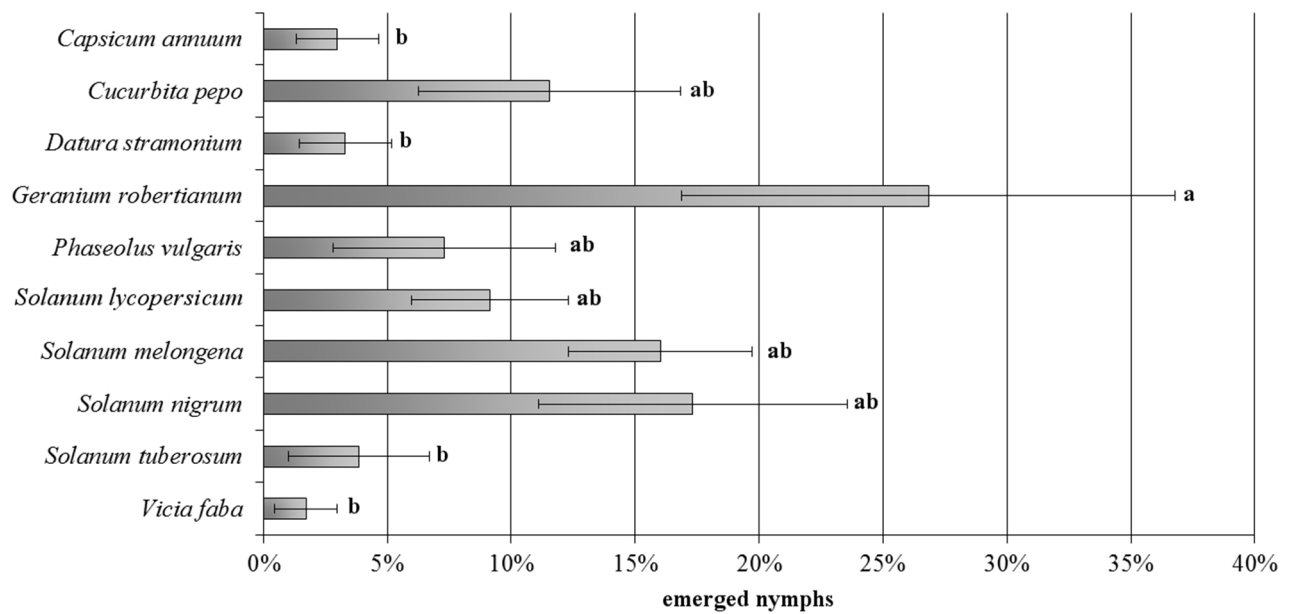


Figure 1. Mean percentage (\pm SE) of total emerged nymphs (no.=142) of *Dicyphus errans* on 10 plant species tested in the multi-choice experiment. Bars followed by different letters are significantly different (Tukey's test, $P<0.05$). Data are shown before transformation for easier interpretation.

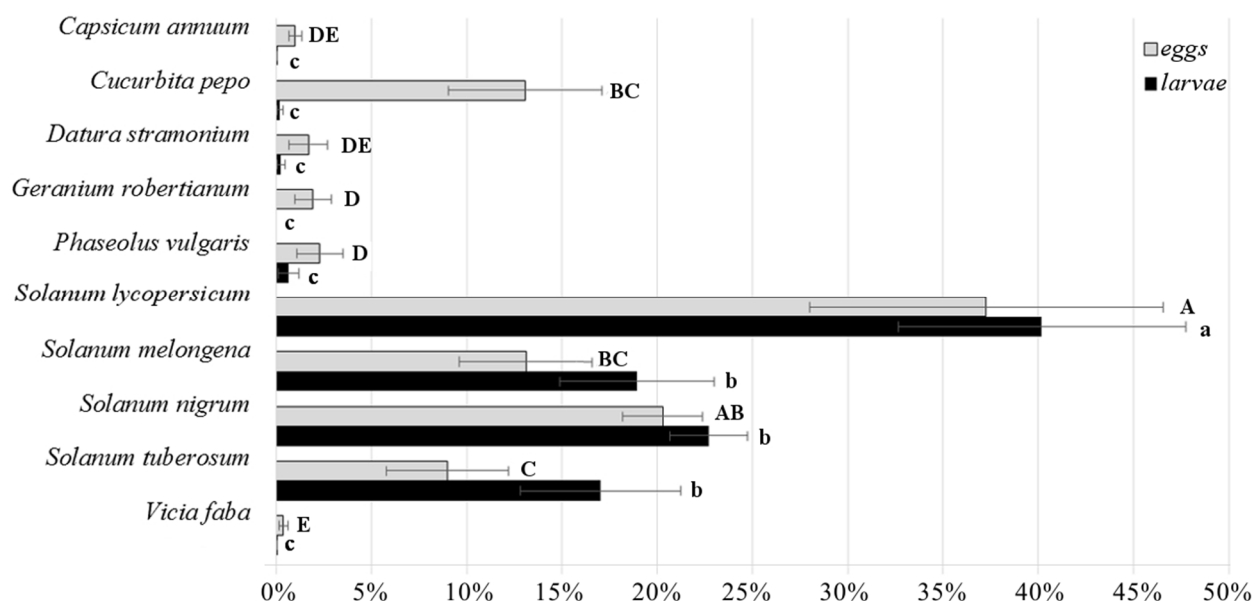


Figure 2. Mean percentage (\pm SE) of total eggs (no.=3572) and emerged larvae (no.=2445) of *Tuta absoluta* on 10 plant species tested in the multi-choice experiment. Bars followed by different letters (upper and lower case refer to eggs and larvae, respectively) are significantly different (Mann-Whitney U test, $P < 0.05$). Data are shown before transformation for easier interpretation.