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(Article begins on next page)



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1 **Plant preference in the zoophytophagous generalist predator *Macrolophus pygmaeus***

2 **(Heteroptera: Miridae)**

3

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9 **Abstract**

10 *Macrolophus pygmaeus* (Heteroptera: Miridae) is an omnivorous predator used to control
11 several pests of horticultural greenhouses. With the aim to explore the relationship between
12 *M. pygmaeus* and different host plants compared with tomato, plant preferences and bio-cycle
13 traits were studied using: *Capsicum annuum*, *Calendula officinalis*, *Salvia officinalis*,
14 *Parietaria officinalis* and *Solanum nigrum*. Species were selected among natural host crop
15 and wild plants. Plant preference was measured by multi-choice host plant selection and
16 olfactometric bioassays. Bio-cycle traits were assessed on reproduction and on nymphal
17 development with and without animal diet support. Among tested plants, *P. officinalis* was the
18 least attractive under laboratory conditions. Furthermore the availability of prey was crucial
19 for the successful establishment of *M. pygmaeus* on tested plants, suggesting the inability of
20 nymphs to complete development to adulthood on a strictly phytophagous diet. Nevertheless
21 *M. pygmaeus* seemed to prefer plants where phytophagy provides a fitness benefit.

22

23 **Key words**

24 Dicyphini, olfactometer bioassay, host plant selection, oviposition preference, biological
25 control, tomato

26

27 **Introduction**

28 Species of *Macrolophus* (Heteroptera: Miridae) belonging to the subfamily Bryocorinae, tribe
29 Dicyphini, are generalist predators well-known for their role in the control of several pests
30 (e.g. aphids, mites, moths, thrips, whiteflies) in horticultural crops in Europe (Avilla et al.,
31 2004). In fact, starting from the end of the '80s, their presence was reported in IPM vegetable
32 crops of different regions of southern Europe, as a consequence of the reduced insecticide
33 pressure (Tavella and Goula, 2001). In particular, unlike other predatory bugs, such as
34 anthocorids of the genus *Orius*, that are hampered by glandular trichomes (Coll and Ridgway,
35 1995), tomato plants represent a very suitable host for Dicyphini (Riudavets and Castañé
36 1998; Tavella and Goula, 2001).

37 Dicyphini are characterized by zoophytophagous behaviour, thus they are strictly related to
38 the plant besides the prey. Zoophytophagy is positive because predators can survive in the
39 crop even when prey are scarce or totally absent (Eubanks and Denno, 1999). The plant can
40 provide not only water essential for predation (Sinia et al., 2004), but also nutrients. In fact,
41 some species can develop and reproduce in the absence of prey by feeding on plants, but only
42 on some plant species or even on some parts of them (Lucas and Alomar, 2001). For example,
43 in previous laboratory trials *Macrolophus* species proved to develop on various crop plants,
44 i.e. leaves of tomato, eggplant, pepper, cucumber, melon and broad bean (Perdikis and
45 Lykouressis, 1997, 1999, 2000), and French bean pods (Tavella and Arzone, 1996), whereas
46 they are unable to reach adulthood feeding on Chinese cabbage, cabbage and Brussel sprouts
47 (Hatherly et al., 2009). Anyway, the developmental time on a plant diet is often considerably
48 longer, while emergence rate and adult size are smaller, as a further confirmation of their
49 improved performance in the presence of prey.

50 Plants release volatile compounds varying quantitatively and qualitatively depending on plant
51 species and attacks of specific pests, and able to attract predators (Paré and Tumlinson, 1999;

52 Dudareva et al., 2006). The tritrophic interactions regulating the plant-prey-predator
53 relationships are very complicated in these zoophytophagous mirid bugs. In spring, predatory
54 bugs, especially fertile females, migrate from winter refuges onto tomato where, if not
55 disturbed by chemicals, they establish and contribute efficiently to control pest outbreaks
56 (Tavella et al., 1997). An earlier colonization of tomato seems to be affected by the presence
57 and abundance of natural host plants, rather than by their abundance in the agroecosystem
58 (Alomar et al., 2002; Ingegno et al., 2009). Their density within crops in fact can be related to
59 composition and abundance of the surrounding vegetation and to topographic characteristics,
60 suggesting the importance of host plant proximity to enhance early movement of these
61 predators into the fields (Alomar et al., 1994; Gabarra et al., 2004). Concerning host range,
62 Dicyphini show a preference for glandular and sticky plants; in fact, most of the northwestern
63 Italian species have been collected on hairy plant species belonging to Solanaceae, Lamiaceae
64 and Geraniaceae (Ingegno et al., 2008; Tavella and Goula, 2001).

65 Among the Dicyphini species colonizing tomato crops in the Mediterranean region, the
66 species initially identified as *M. caliginosus* Wagner seemed to be the most promising: in fact,
67 it is now reared by several commercial producers and largely used in programmes of
68 biological control and IPM. Recent studies on molecular taxonomy of *Macrolophus* species
69 revealed that species marketed for several years as *M. caliginosus* is actually *M. pygmaeus*
70 (Rambur) (Martinez-Cascales et al., 2006 a, b).

71 Due to their effectiveness as pest control agents, bio-ethological studies on *Macrolophus*
72 species have been carried out to assess their predatory activity in different conditions
73 (temperature, humidity, photoperiod) and on different prey (whiteflies, aphids, thrips, mites),
74 and their functional response (Montserrat et al., 2000; Enkegaard et al., 2001; Perdakis 2002;
75 Perdakis and Lykouressis 2002; Montserrat et al., 2004; Lykouressis et al., 2007). Artificial
76 diets have also been tested and developed for rearing of predatory bugs to improve their

77 massive production (Castañé and Zapata, 2005; Zapata et al., 2005). Furthermore, laboratory
78 trials were carried out to evaluate the side-effects of the most widely used pesticides in
79 horticulture (Figuls et al., 1999; Tedeschi et al., 2001; Tedeschi et al., 2002). Recently, studies
80 on responses of some Dicyphini species to volatile compounds produced by plants and prey
81 were carried out above all in laboratory conditions (McGregor and Gillespie, 2004; Moayeri
82 et al., 2006a, b; Moayeri et al., 2007a, b).

83 To enhance the presence and activity of Dicyphini in the crops, the factors stimulating
84 predatory bugs to leave the natural host plants and colonize the crop should be investigated
85 thoroughly for an economically and ecologically sustainable farming. Thus the present
86 research has been aimed at assessing preference and bio-ethological responses of the
87 zoophytophagous *M. pygmaeus* on different plant species in comparison with tomato, the crop
88 plant where it is more frequently and abundantly found.

89

90 **Material and methods**

91 Insect mass rearing and plant growing

92 *M. pygmaeus* used in the experiments came from a laboratory colony derived from Bioplanet,
93 Italy, and reared in insect cages (MegaView, Taiwan) on tobacco plants [*Nicotiana tabacum*
94 L. (Solanaceae)], supplemented with eggs of *Ephestia kuehniella* (Zeller) (Lepidoptera:
95 Pyralidae). Identity of *M. pygmaeus* was further assessed by molecular analyses as described
96 in Martinez-Cascales et al. (2006 a, b). Mass rearing was maintained at $24\pm 1^{\circ}\text{C}$, RH $65\pm 5\%$
97 and L16:D8.

98 Among crop (vegetable and garden) and wild plants, reported as host plants for Dicyphini
99 species in NW Italy (Ingegno et al., 2008, 2009, personal observation), the following six plant
100 species were selected: tomato [*Lycopersicon esculentum* Miller, cv Marmande (Solanaceae)],
101 pepper [*Capsicum annuum* L., cv Quadrato d'Asti giallo (Solanaceae)], pot marigold

102 [*Calendula officinalis* L. (Asteraceae)], sage [*Salvia officinalis* L. (Lamiaceae)], pellitory-of-
103 the-wall [*Parietaria officinalis* L. (Urticaceae)], and European black nightshade [*Solanum*
104 *nigrum* L. (Solanaceae)]. To obtain plants of similar age and size (approximately 20cm high),
105 they were periodically seeded, and afterwards transplanted in plastic pots (Ø 12cm), and
106 maintained in a heated greenhouse without any pesticide use.

107 Reproduction and development on different plant species

108 Reproduction of *M. pygmaeus* was studied on single plants of the six species, supplemented
109 with eggs of *E. kuehniella*. Each plant was isolated in a Plexiglas cylinder (height 195mm, Ø
110 110mm), wedged in the pot soil, and enclosed at the upper extremity by net. Three females
111 and two males 1-week-old of *M. pygmaeus* were introduced in each cylinder and removed
112 after one week. *E. kuehniella* eggs glued on a paper strip with a honey solution were
113 periodically supplied as food source. Egg hatching and nymph emergence were monitored
114 every 48 hours until no nymphs were seen for four days; all newly-emerged nymphs were
115 removed and counted. Five replications (i. e. five cylinders) were performed for each plant
116 species.

117 The survival rate and time of nymphal development were studied on the six plant species in
118 presence and absence of *E. kuehniella* eggs. Freshly hatched nymphs (<1-day-old) from each
119 plant species were placed individually on leaf discs of the same plant in cells of 2cm² (24-well
120 tissue culture plate, Sarstedt, Germany). For each plant species 24 nymphs, 12 with *E.*
121 *kuehniella* eggs (directly supplied on leaf discs) and 12 without *E. kuehniella* eggs, were
122 observed during their life span. Moulting, evident from the presence of the exuvia, or death of
123 each nymph were daily recorded and used to determine time and survival at each nymphal
124 instar. All the emerged adults were examined under stereo-microscope to determine their sex,
125 and to measure their length (from vertex to the end of hemielytra).

126 All the assays were carried out in climatic chambers at 24±1°C, RH 65±5%, and L16:D8.

127 After performing tests of homogeneity of variance (Levene) and normality (Kolmogorov-
128 Smirnov), data of reproduction and development, and of measures of the adults emerged on
129 each plant species were analyzed with one-way ANOVA; means were then separated by
130 Tukey's test ($P < 0.05$) (SPSS version 12.0; SPSS Inc., Chicago, IL, USA).

131 Host plant selection experiments

132 The host plant selection experiments were set up as multi-choice assays where whole plants or
133 single leaves of the six plant species were simultaneously offered to *M. pygmaeus*.

134 *Whole plant choice*

135 To assess the adult preference for the six plants being to be tested, one potted plant of each
136 species was placed inside a 47.5×47.5×93cm net insect cage (MegaView, Taiwan). Five cages
137 as five replications were set up. The position of the plant species in a 2×3 matrix was assigned
138 randomly, taking care that the plants did not touch each other. Five 1-week-old females and
139 two males were released on each plant (for a total of 30 females and 12 males per cage). After
140 one week, each plant was wrapped in a net bag, removed from the cage, and inspected to
141 count the adults of *M. pygmaeus*. Then the plants were singly isolated in Plexiglas cylinders
142 (height 195mm, Ø 110mm), and checked to observe egg hatching and nymph emergence
143 every 48 hours until no nymphs were seen for four days. All emergent nymphs were removed
144 and counted.

145 *Single leaf choice*

146 The plant preference by ovipositing females was tested by offering a single leaf or, in the case
147 of the plants with small leaves (i.e. *P. officinalis*), a piece of stem with some leaves, of the six
148 plant species simultaneously in a 20×20×30cm net cage (MegaView, Taiwan). Ten cages as
149 ten replications were set up. The single leaf or the piece of stem with some leaves were put
150 into a 1.5mL plastic tube filled with water, and introduced through equidistant hole in a
151 polystyrene support randomly in a 2×3 matrix. Leaf areas were about equivalent for the six

152 plant species. Oviposition preference was tested in presence of prey, *E. kuehniella* eggs,
153 supplied in the centre of the matrix on paper strip glued with a honey solution. Two 1-week-
154 old females and one male were released for each plant species (for a total of 12 females and
155 six males per cage). The adults of *M. pygmaeus* were removed after 48 hours. The number of
156 eggs laid on each plant species was counted under a stereo-microscope five days later. The
157 plant preference by ovipositing females was expressed as the proportion of eggs laid on each
158 plant species in the cage as described by Thompson (1988).

159 All the multi-choice assays were carried out at $24\pm 1^{\circ}\text{C}$, RH $65\pm 5\%$, and L16:D8.

160 In the whole plant multi-choice experiment the relationship between percentage of recaptured
161 adults and number of emerged nymphs was estimated with Pearson's correlation (SPSS
162 version 12.0). In the leaf multi-choice experiment, the percentages of eggs laid on each plant
163 species in the cages were compared, after arcsine square-root transformation, using ANOVA,
164 and means were separated by Tukey's test ($P < 0.05$) (SPSS version 12.0).

165 Olfactometric bioassays

166 In the bioassays, 1-week-old females, kept without prey and plant in a glass tube (length
167 120mm, \varnothing 23mm) for 18 hours, were used to assess olfactory responses of *M. pygmaeus* to
168 the odours of tomato compared with those of the other tested plants. The bioassays were
169 carried out in a Y-shaped Pyrex tube (internal \varnothing 23mm) formed by an entry arm, 250mm
170 long, and two side arms, 200mm long (70° angle), and positioned vertically as in other studies
171 with Dicyphini (McGregor and Gillespie, 2004; Moayeri et al., 2006a, b; Moayeri et al.,
172 2007a, b). Each side arm was connected to a glass cylindrical chamber (height 500mm, \varnothing
173 130mm) as an odour-source container. Airflow was provided by an air pump (Air 275R, Sera,
174 Germany). Before reaching the odour-source chambers, air passed in an activated CO_2 filter,
175 in a flow meter (EK-2NRK, Comer, Italy) to set the airflow, and in a 1-L water bubbler half-

176 filled with deionized water. The odour-source chambers were held behind a black panel, so
177 that *M. pygmaeus* females could not see the plants during the bioassays in the Y-tube.
178 In all experiments, the flow rate through flow meter was set at 2.5L min^{-1} and measured at the
179 downwind end with a digital anemometer (TA-410, PCE Group, Italy) to control any flow
180 leak. Before each trial, an air flow was established in the Y-tube by adjusting the flow rate
181 using the air pump knob and the flow meter. After the flow was established, a single *M.*
182 *pygmaeus* female was introduced into the tube. Each female was observed until she had
183 walked at least 6cm up one of the side arms or until 20min had elapsed. Females that did not
184 choose a side arm within 20min were considered as “no choice” and were not counted in the
185 subsequent data analysis. Each female was tested only once. The odour sources chosen by
186 females that responded were recorded. Twenty-five responses were recorded for each pair of
187 odour sources.

188 After testing a batch of five females, the odour sources were switched between the left-hand
189 and right-hand side arms to minimize any spatial effect on choices, whereas after testing two
190 batches (i.e. after 10 insect responses) the Y-tube was cleaned with neutral soap and alcohol
191 (70%_v). Chambers were washed after each trial with neutral soap and alcohol (70%_v) and
192 sterilised in autoclave at 120°C for 20 min. The olfactometric bioassays were conducted at
193 $24\pm 1^\circ\text{C}$, RH 25-30%, and $540\pm 30\text{lux}$.

194 Two experiments were carried out to assess: i) the preference of *M. pygmaeus* to tomato and
195 the other five plants; ii) the responses of *M. pygmaeus* to the odours of tomato plants
196 uninfested, presently infested and previously infested by the whitefly *Trialeurodes*
197 *vaporariorum* Westwood (Hemiptera: Aleyrodidae) (Table 1). The odour sources consisted of
198 one entire potted plant. The infested plants were grown separately from uninfested plants.
199 Moreover, to evaluate an eventual systemic effect of whitefly infestation, about 50 individuals
200 of *T. vaporariorum* were introduced into a fine mesh net covering the apex of the plant. After

201 15 days, the apex was cut to remove the parts that hosted the pest. Also the apex of the
202 uninfested tomato plants used in comparison with these ones was cut to prevent any influence
203 due to the mechanic damage.

204 In the olfactometric bioassays, responses of *M. pygmaeus* females were analyzed by Chi-
205 square test with significance levels of 90% and 95% (SPSS version 12.0). The null hypothesis
206 was that predatory females had 50:50 distribution across the two odour sources. Females that
207 did not make a choice were excluded from the statistical analysis.

208

209 **Results**

210 Reproduction and development on different plant species

211 Nymphal hatching from the tested plant species supplemented with eggs of *E. kuehniella* was
212 significantly different only between *C. officinalis* and *P. officinalis* (ANOVA: df=29,
213 F=2.844, P=0.037), with on average 27.4±6.2 and 2.8±0.7 nymphs emerged, respectively
214 (Figure 1).

215 The development times from egg-hatching to adulthood on the six plant species with prey
216 were significantly different (ANOVA: df=53, F=4.182, P=0.003), the longest on *S. officinalis*
217 (19.3 days) and the shortest on *C. officinalis* and *C. annuum* (14.4 and 15.5 days,
218 respectively) (Table 2). The percentage of individuals that reached adulthood ranged from
219 58% on tomato and *S. officinalis* to 100% on *S. nigrum*, (Table 2). The sex ratio was variable
220 on the tested plants, ranging from 0.30 on *P. officinalis* to 0.75 on *C. annuum* and *S. nigrum*;
221 however we could analyze only the measures of females because we did not obtain males
222 enough on all tested plants. The length of female adults was significantly different between *S.*
223 *officinalis* (3.144±0.045 mm) and *P. officinalis* (3.367±0.035 mm) (ANOVA: df=31,
224 F=2.673, P=0.045).

225 *M. pygmaeus* was able to complete development on all the tested plants when supplemented
226 with *E. kuehniella* eggs, whereas no nymphs reached adulthood when fed on plant alone of
227 the different species without prey (Table 2). Many 1st instar nymphs could reach the 2nd instar,
228 but after only on *C. officinalis* and *S. nigrum* very few nymphs reached the 5th instar whereas
229 on *P. officinalis* and *S. officinalis* no nymphs got over the 2nd instar (Table 2).

230 Host plant selection and oviposition multi-choice experiments

231 In the whole plant multi-choice experiment, no significant differences were found between
232 numbers of nymphs emerged on the tested plant species (ANOVA: df=29, F=0.794, P=0.565),
233 ranging on average from 27.0 on *L. esculentum* to 12.6 on *P. officinalis* (Table 3). As
234 surveyed for the emerged nymphs, also the numbers of adults recaptured on each plant at end
235 of experiment were not significantly different between the six plant species. However, the
236 lowest percentage of *M. pygmaeus* adults was recaptured on *P. officinalis*, on which the
237 lowest number of nymphs was also observed (Table 3). Furthermore, a positive correlation
238 was found between the percentage of recaptured adults and the number of emerged nymphs
239 on the same plant species (Pearson's correlation=0.507, P=0.004; n=30) (Figure 2).

240 In the leaf multi-choice experiment, the percentage of eggs laid per plant in each cage was
241 significantly higher on tomato compared to sage (ANOVA: df=59, F=2.946, P=0.020), on
242 which on average 30.8% and 2.5% of eggs were laid respectively (Table 4).

243 Olfactometric bioassays

244 In the first experiment (Table 1), no significant preference was detected between healthy
245 tomato and the following plants (Figure 3): *C. officinalis* ($\chi^2=0.04$, P=0.84), *C. annuum*
246 ($\chi^2=0.04$, P=0.84), *S. officinalis* ($\chi^2=0.36$, P=0.55) and *S. nigrum* ($\chi^2=0.36$, P=0.55). By
247 contrast, *P. officinalis* resulted unattractive in comparison with tomato ($\chi^2=4.84$, P=0.03) as
248 well as the empty chamber ($\chi^2=3.24$, P=0.07). The females that did not choose any odour

249 sources were always very few; at the most three non-responding females were observed in the
250 comparison with *C. officinalis*, *C. annuum* and *S. officinalis*.

251 In the second experiment (Table 1), *M. pygmaeus* females proved to be more attracted by the
252 whitefly infested tomato compared to the uninfested tomato ($\chi^2=3.24$, $P=0.07$) and by the
253 uninfested tomato compared to the whiteflies ($\chi^2=3.24$, $P=0.07$) (Figure 4). No significant
254 differences in responses of *M. pygmaeus* females were found comparing the healthy tomato
255 with the previously infested one ($\chi^2=1.00$, $P=0.32$), as well as comparing whitefly odours with
256 the empty chamber ($\chi^2=0.36$, $P=0.55$) (Figure 4). As in the first experiment, the females non-
257 responding to the compared odorous source were always very few, at the maximum two
258 females in the comparison with whitefly alone and whitefly infested tomato.

259

260 **Discussion**

261 The obtained results confirmed that host plant selection in *M. pygmaeus* has a substantial
262 influence on survival and development, and that the benefits of particular host plants vary in
263 the presence or absence of prey. When *M. pygmaeus* nymphs were provided with both plant
264 and prey, they were able to complete development on all plant species showing similar
265 survival rates between plants, whereas without prey no nymphs reached adulthood in the same
266 experimental conditions. Nevertheless, our results showed that the absence of prey could be
267 tolerated longer on *S. nigrum*, *C. officinalis*, *C. annuum* and tomato than on *S. officinalis* and
268 *P. officinalis*. Development times on tested plants without prey varied greatly from the second
269 instar, probably due to the various nutritional values of the plants or to the presence of
270 inhibitor compounds. The availability of prey seems to be crucial for successful establishment
271 of *M. pygmaeus* on tested plants in our experimental conditions. However, even if in other
272 laboratory experiments (Perdikis and Lykouressis, 1999, 2000; Tavella and Arzone, 1996) *M.*
273 *pygmaeus* could reach the adulthood on prey-free plants, worse biological traits (i.e. longer

274 development time and higher mortality) observed on plants without prey than with prey
275 suggest the difficulty of the species to complete development to adulthood on a strictly
276 phytophagous diet. This need was observed also in other omnivorous mirid bugs as
277 *Nesidiocoris tenuis* (Reuter) (Heteroptera: Miridae) (Urbaneja et al., 2005), *Dicyphus errans*
278 (Wolff) (Guidone et al., 2005) and *D. hesperus* Knight (Sanchez et al., 2004) that did not
279 complete development when feeding on tomato alone. Phytophagy mainly provides the water
280 necessary for vital functions and although plants appear to be a much poorer food resource
281 than prey for *M. pygmaeus*, nutrients collected from them may greatly improve the survival of
282 individuals as prey become scarce.

283 Among the host plants tested in laboratory experiments, *P. officinalis* was the least attractive,
284 even if during field surveys in NW Italy individuals of *M. pygmaeus* were often collected on
285 this plant (Tavella and Goula, 2001). Although in the whole plant selection experiment no
286 significant differences were found, an obvious separation emerged in positive relationship
287 among percentages of recaptured adults and emerged nymphs of *M. pygmaeus* between *P.*
288 *officinalis* and the other tested plants. The colonization of *P. officinalis* in natural conditions
289 by Dicyphini (Alomar et al., 1994; Gabarra et al., 2004; Tavella and Goula, 2001), in contrast
290 with the unattractiveness in laboratory assays, is probably due both to the location of this
291 plant, usually grown on walls in sheltered sites, and to the concurrent presence of prey,
292 possible source of food. These facts make *P. officinalis* a suitable refuge for *M. pygmaeus*,
293 especially during winter in absence of tomato crop. In fact, a previous study showed that
294 abundance and vicinity of this plant to the tomato crop facilitate the early entrance of
295 predatory bugs (Gabarra et al., 2004).

296 Other plant species confirming their important role as natural hosts also in laboratory
297 experiments were *S. nigrum* and *C. officinalis*. *S. nigrum* is one of the most common weeds in
298 the vegetable agroecosystems of NW Italy, and also the most favourite host for another

299 predatory bug widespread in the area, *D. errans* (Tavella and Goula, 2001; Ingegno et al.,
300 2008). In the development experiments, *S. nigrum* supported the highest survival rate of *M.*
301 *pygmaeus* nymphs with prey and, even if no nymphs could complete the development to
302 adulthood, also without prey. This weed therefore can contribute to the conservation of
303 predatory bugs in the field as suggested also in another recent study (Lykourressis et al.,
304 2008). On the other hand, *C. officinalis* is a common garden plant, now widely naturalized
305 throughout NW Italy, where it represents one the most favourite natural host of *M. pygmaeus*
306 (Tavella and Goula, 2001). Like *S. nigrum*, *C. officinalis* supported a longer nymphal
307 development in absence of prey; moreover, in the reproduction experiments the highest
308 numbers of nymphs emerged on this plant species.

309 Natural presence of predatory bugs in vegetable agroecosystems of NW Italy seems to be
310 strictly related to the environmental conditions; in fact, Dicyphini are found mainly in
311 agroecosystems characterized by a high environmental complexity, i.e. patchy landscape
312 where vegetable crops are surrounded by natural corridors wasteland and woodland (Ingegno
313 et al., 2009). Therefore, since abundance of natural host plants acting as source affects greatly
314 the presence of predatory bugs, plants species, like *S. nigrum* and *C. officinalis*, can carry out
315 an important role in conserving and augmenting *M. pygmaeus* in agroecosystems. To
316 implement natural control augmentation strategies in vegetable crops these plants should be
317 conserved and, if scarcely present, increased. Conservation of natural host plant, such as
318 *Dittrichia viscosa* L. (Asteraceae) for *M. melanotoma* (Costa) (Perdikis et al., 2007), or their
319 use as banker plants in vegetable greenhouses, e.g. tobacco for *Macrolophus* sp. (Arnó et al.,
320 2000) and mullein [*Verbascum thapsus* L. (Scrophulariaceae)] for *D. hesperus* (Sanchez et al.,
321 2003a), have been already proposed to favour the early establishment of native predators on
322 tomato crops in other geographic areas.

323 Concerning the two vegetables compared in our experiments, besides tomato also pepper
324 appeared rather attractive for *M. pygmaeus*, especially in leaf multi-choice experiments. By
325 contrast, in the field this mirid species was surveyed on pepper (Goula and Alomar, 1994), but
326 only occasionally (Tavella and Goula, 2001), and not everywhere (Sanchez et al., 2003b). In
327 fact, *M. pygmaeus* is found on various vegetable crops in southern Europe but it is primarily
328 used in conservative and inoculative biological control strategies, sometimes in combination
329 with parasitoids, to control whiteflies and other pests in tomato greenhouses, as documented
330 by a rich literature (Avilla et al., 2004; Castañé et al. 2004). Therefore, some producers
331 suggest to release the species as control agents on tomato and egg-plant. Moreover, *M.*
332 *pygmaeus* also shows potential for the control of whiteflies in greenhouse melons (Alomar et
333 al., 2006).

334 The differences in plant preference between field surveys and laboratory experiments are
335 probably due to several environmental factors that may influence the zoophytophagous
336 behaviour of these omnivorous mirid bugs. In fact, even if Dicyphini are abundant and
337 widespread in the Mediterranean Basin, the species colonizing vegetable crops vary from
338 region to region, probably in relation to the presence and abundance of natural host plants
339 growing in the agroecosystem. Various species mainly belonging to the genera *Macrolophus*,
340 *Dicyphus* and *Nesidiocoris* were reported in different areas of Europe (Alomar et al., 1994;
341 Carnero-Hernández et al., 2000; Gabarra et al., 1988; Perdikis and Lykouressis, 1996;
342 Sanchez et al., 2003b; Sanchez et al., 2006; Tavella et al., 1997; Tavella and Goula, 2001).
343 Therefore, results obtained under laboratory conditions should be validated in the field in
344 specific situation in order to suggest successful control augmentation strategies.

345 Besides the plant, the prey and above all the interaction plant-prey are fundamental (Dicke
346 and Loon, 2000). In olfactometric bioassays, *M. pygmaeus* females were attracted from
347 whitefly infested tomato as previously observed for *D. hesperus* (McGregor and Gillespie,

348 2004), while no differences emerged between the previously infested tomato and the healthy
349 one, likely excluding a systemic effect of whitefly infestation on plant. The actual presence of
350 the prey on tomato is important for attracting *M. pygmaeus*, consistent with the results of
351 another study conducted in Y-tube olfactometer where the predatory species preferred spider
352 mite infested green bean plants to uninfested plants (Moayeri et al., 2006b). However, the
353 only presence of the whitefly, without host plant, was not sufficient for attracting *M.*
354 *pygmaeus*, as observed with other potential prey, the aphid *Myzus persicae* (Sulzer) and the
355 spider mite *Tetranychus urticae* Koch (Moayeri et al., 2006a, b). Although in the bioassays
356 the infested plants after prey removal were not significantly attractive, further research on
357 responses of *M. pygmaeus* is needed to investigate thoroughly a possible systemic effect due
358 to prey feeding on tomato, and to identify plant volatiles that, acting as indirect defences,
359 constitutive and/or induced, can affect adversely the herbivorous victim by attracting the
360 predatory bug.

361

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519

520 **Tables**

521 **Table 1.** Theses in comparison in the two experiments in olfactometric bioassays.

Experiment 1			Experiment 2		
clean air	vs	tomato	clean air	vs	uninfested tomato
<i>C. officinalis</i>	vs	tomato	clean air	vs	whitefly
<i>C. annuum</i>	vs	tomato	whitefly	vs	uninfested tomato
<i>P. officinalis</i>	vs	tomato	infested tomato	vs	uninfested tomato
<i>S. officinalis</i>	vs	tomato	uninfested tomato	vs	previously infested tomato
<i>S. nigrum</i>	vs	tomato			

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524 **Table 2.** Development times (days±SE) of *M. pygmaeus* (n=12), for each nymphal instar and
 525 to reach adulthood on six plant species supplemented or not with *E. kuehniella* eggs.
 526 Percentages of survivorship for each nymphal instar. In the column means followed by
 527 different letters are significantly different (Tukey's test, P<0.05).

Plant	Instar						sex ratio $\frac{\Omega}{(\Omega + \delta)}$
	First	Second	Third	Forth	Fifth	Total	
<i>C. officinalis</i>	3.4 ± 0.4	2.4 ± 0.3	2.2 ± 0.2	2.6 ± 0.3	3.2 ± 0.6	14.4 ± 0.7 b	0.67
	100.0%	100.0%	100.0%	83.3%	90.0%	75.0%	
<i>C. annuum</i>	2.8 ± 0.3	2.9 ± 0.3	2.8 ± 0.2	2.7 ± 0.3	3.8 ± 0.4	15.5 ± 0.7 b	0.75
	100.0%	91.7%	90.9%	80.0%	100.0%	66.7%	
<i>L. esculentum</i>	3.3 ± 0.4	2.5 ± 0.2	2.6 ± 0.2	2.8 ± 0.3	5.1 ± 0.4	16.8 ± 0.8 ab	0.43
	100.0%	100.0%	91.7%	81.8%	77.8%	58.3%	
<i>P. officinalis</i>	3.0 ± 0.4	3.0 ± 0.4	3.0 ± 0.3	2.7 ± 0.3	5.4 ± 0.5	17.0 ± 0.8 ab	0.30
	100.0%	83.3%	100.0%	100.0%	100.0%	83.3%	
<i>S. officinalis</i>	4.8 ± 0.5	3.5 ± 0.4	2.6 ± 0.2	3.8 ± 0.7	3.7 ± 0.4	19.3 ± 0.8 a	0.71
	100.0%	91.7%	90.9%	70.0%	100.0%	58.3%	
<i>S. nigrum</i>	2.8 ± 0.3	3.0 ± 0.3	2.9 ± 0.2	3.5 ± 0.5	4.4 ± 0.2	16.7 ± 0.7 ab	0.75
	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	
<i>C. officinalis</i>	2.7 ± 0.4	3.0 ± 0.7	1.0	2.0	-	-	-
	83.3%	50.0%	20.0%	100.0%	0.0%	0.0%	
<i>C. annuum</i>	2.0 ± 0.2	1.0	1.0	-	-	-	-
	83.3%	10.0%	100.0%	0.0%	0.0%	0.0%	
<i>L. esculentum</i>	2.0 ± 0.4	3.4 ± 0.7	8.5 ± 1.5	-	-	-	-
	91.7%	45.5%	40.0%	0.0%	0.0%	0.0%	
<i>P. officinalis</i>	2.8 ± 0.6	-	-	-	-	-	-
	41.7%	0.0%	0.0%	0.0%	0.0%	0.0%	
<i>S. officinalis</i>	2.8 ± 0.5	-	-	-	-	-	-
	83.3%	0.0%	0.0%	0.0%	0.0%	0.0%	
<i>S. nigrum</i>	2.6 ± 0.3	4.0 ± 0.6	2.7 ± 0.7	3.0	-	-	-
	100.0%	75.0%	33.3%	33.3%	0.0%	0.0%	

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531 **Table 3.** *M. pygmaeus* adults recaptured (mean % \pm SE) and nymphs emerged (mean number
532 \pm SE) on each whole plant of the six species in multi-choice selection experiment. Significant
533 differences between these were not found (ANOVA, $P>0.05$).

Plant species	Mean % of adult recaptured \pm SE	Mean no. of nymphs \pm SE
<i>C. officinalis</i>	17.7 \pm 4.5	24.0 \pm 2.3
<i>C. annuum</i>	17.4 \pm 4.9	21.8 \pm 11.1
<i>L. esculentum</i>	17.8 \pm 4.9	27.0 \pm 4.6
<i>P. officinalis</i>	8.0 \pm 3.0	12.6 \pm 3.6
<i>S. officinalis</i>	19.7 \pm 6.1	25.4 \pm 8.1
<i>S. nigrum</i>	19.5 \pm 2.5	21.8 \pm 5.9

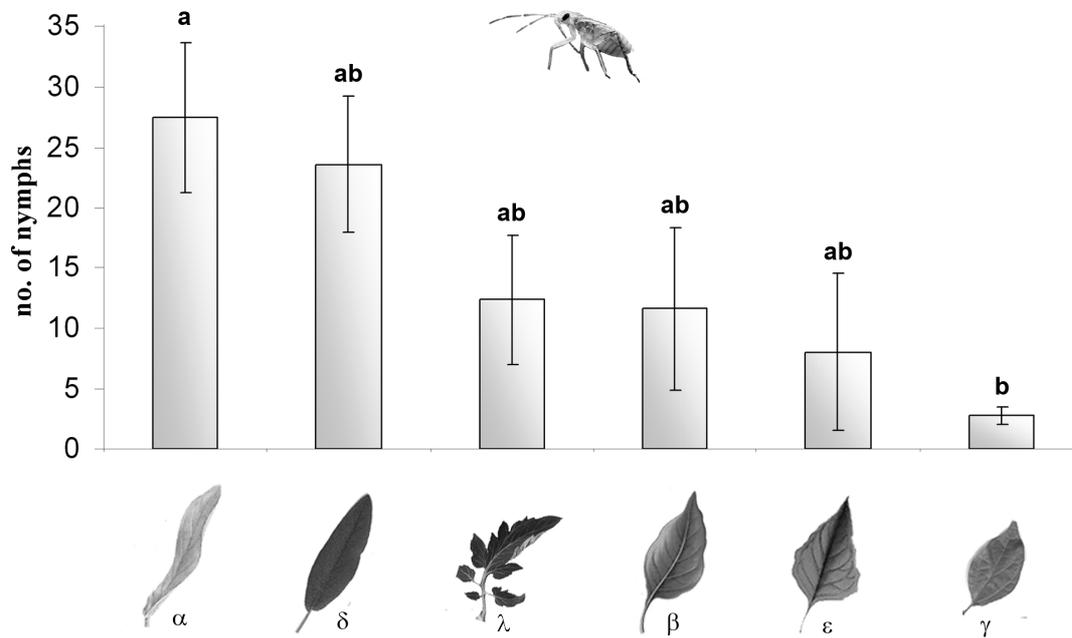
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536 **Table 4.** Percentage of eggs (means \pm SE) laid by *M. pygmaeus* females on leaf area of each
537 plant species in multi-choice oviposition experiment. Mean percentages followed by different
538 letters are significantly different (Tukey's test, $P < 0.05$).

Plant species	Mean percentage of eggs \pm SE
<i>C. officinalis</i>	18.53 \pm 5.48 ab
<i>C. annuum</i>	26.49 \pm 8.35 ab
<i>L. esculentum</i>	30.77 \pm 9.16 a
<i>P. officinalis</i>	6.33 \pm 4.12 ab
<i>S. officinalis</i>	2.48 \pm 1.12 b
<i>S. nigrum</i>	15.40 \pm 9.58 ab

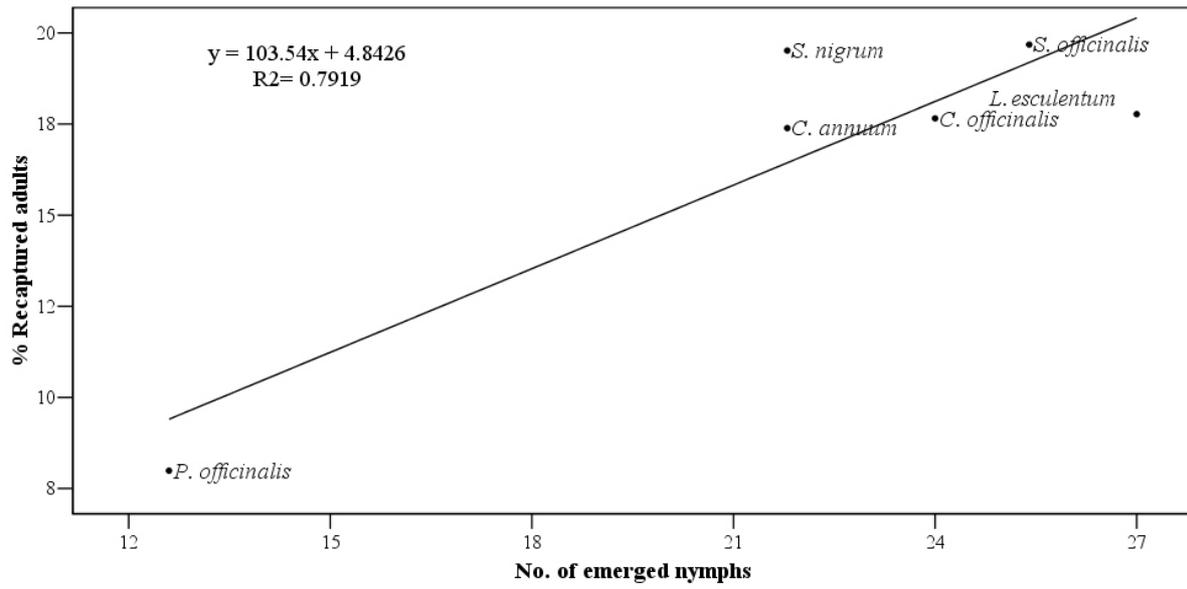
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541

542 **Figure 1.** Nymphs of *M. pygmaeus* (mean number \pm SE) emerged on the six plants in
 543 reproduction experiment: α = *C. officinalis*; δ = *S. officinalis*; λ = *L. esculentum*; β = *C.*
 544 *annuum*; ϵ = *S. nigrum*; γ = *P. officinalis*. Means characterized by different letters are
 545 significantly different (Tukey's test, $P < 0.05$).

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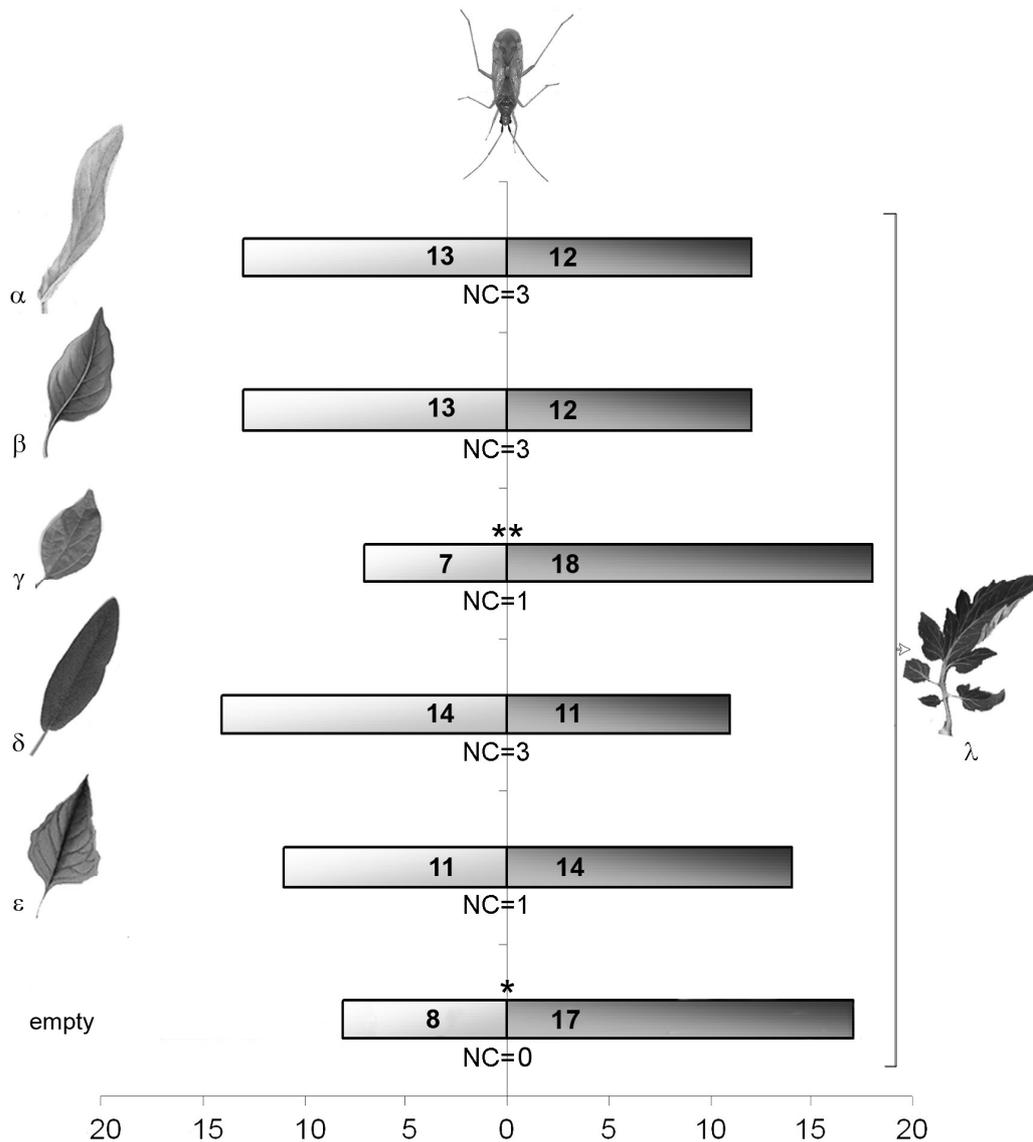
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Figure 2. Relationship between percentage of recaptured adults of *M. pygmaeus* in multi-

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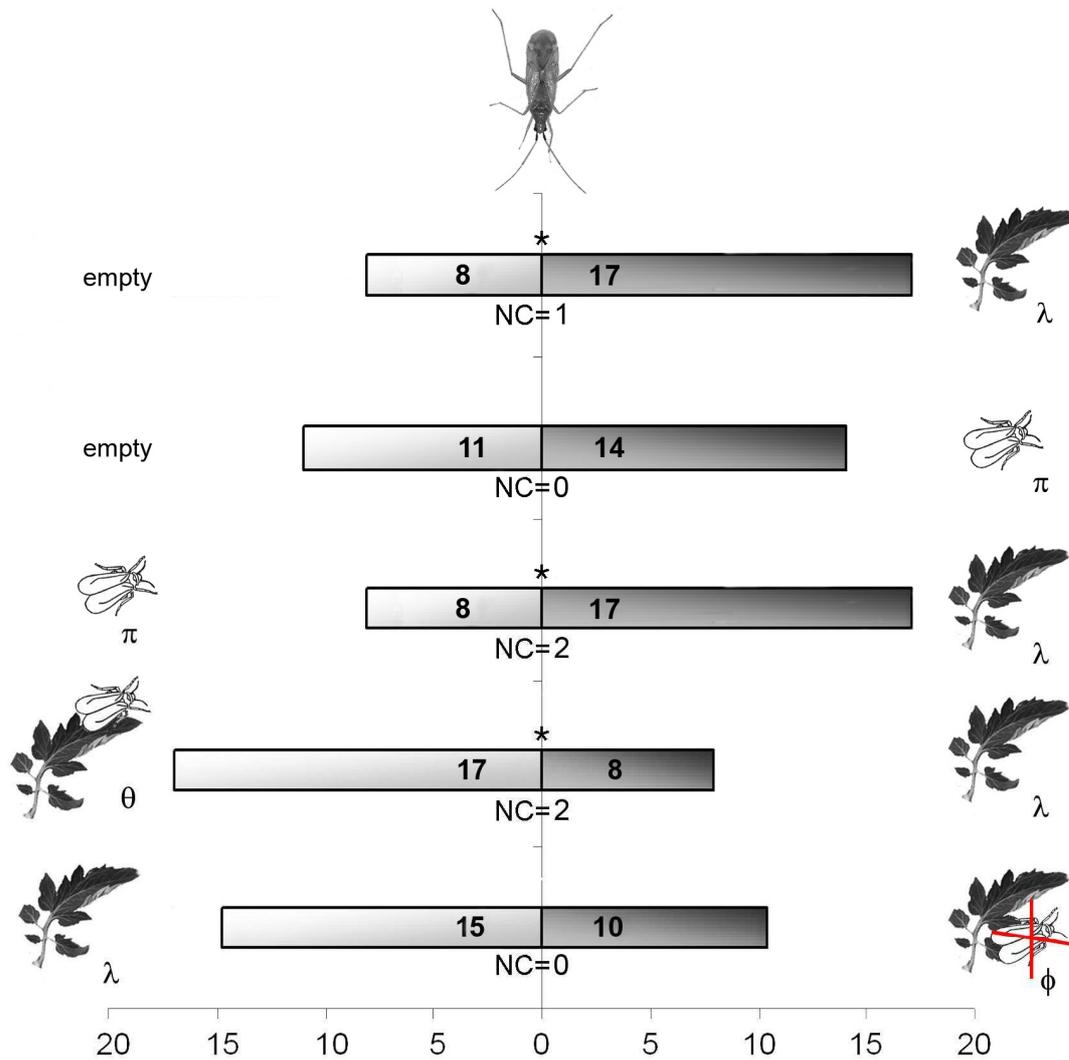
choice selection experiment and number of emerged nymphs (Pearson's correlation, $P < 0.01$).

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552

553 **Figure 3.** Responses of *M. pygmaeus* (no. of responding females in bars) in a Y-tube
 554 olfactometer and number of non-responding individuals (NC) to the odours of the plants for
 555 each compared pair. The following plants were tested against healthy tomato individuals (λ =
 556 *L. esculentum*): α = *C. officinalis*; β = *C. annuum*; γ = *P. officinalis*, δ = *S. officinalis*; ϵ = *S.*
 557 *nigrum*. Numbers in bars represent individual mirids that moved toward the volatiles. χ^2
 558 statistics (** $P < 0.05$, * $P < 0.10$; df:1) tested the hypothesis that the distribution of side-arm
 559 choices deviated from a null model where odour sources were chosen with equal frequency.



560

561 **Figure 4.** Responses of *M. pygmaeus* (no. of responding females in bars) in a Y-tube
 562 olfactometer and number of non-responding individuals (NC) to the odours of infested (θ),
 563 previously infested (ϕ) or uninfested (λ) tomato with the whitefly *T. vaporariorum* (π) for
 564 each compared pair. Numbers in bars represent individual mirids that moved toward the
 565 volatiles. χ^2 statistics (* $P < 0.10$; $df: 1$) tested the hypothesis that the distribution of side-arm
 566 choices deviated from a null model where odour sources were chosen with equal frequency.