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1 Does the plant defense priming compound β -aminobutyric acid affect the
2 performance of *Macrolophus pygmaeus* when used to control *Bemisia*
3 *tabaci* in tomato?
4

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33 **Abstract**

34 The β -aminobutyric acid (BABA) is a plant defense priming compound highly effective in controlling
35 important tomato diseases and plant-parasitic nematodes. It has also been shown to induce resistance
36 against phytophagous insects such as aphids.

37 This study examines the effect of BABA on the performance of the tomato pest *Bemisia tabaci* (MEAM 1,
38 previously known as Biotype B) and its zoophytophagous predator *Macrolophus pygmaeus* under
39 laboratory and greenhouse conditions. Tomato plants were treated with BABA 25 mM applied by soil
40 drenching. The effect of BABA on the fertility and juvenile development of two generations of *B. tabaci*
41 and *M. pygmaeus* was evaluated.

42 Our results showed no effect of BABA on the juvenile development or adult fecundity/fertility of both the
43 whitefly and its predator. The non-interference of BABA with *M. pygmaeus* and *B. tabaci* assures that
44 the control of the whitefly with this mirid bug will not be affected when this elicitor is applied to the crop.
45 Further studies are needed to clarify the mechanisms underlying BABA-plant-whitefly-predatory myrids
46 interactions.

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49 **Keywords** BABA, induced resistance, life history traits, zoophytophagous predator, whitefly

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53 **Introduction**

54 The sensitization of the plant innate immune system causing faster and stronger expression of the basal
55 defense mechanisms against a subsequent attack is referred to as ‘priming’ (Conrath et al. 2006). Priming
56 presents the advantage of increasing plant protection with low plant fitness costs (i.e., plant reproduction
57 and growth) (Van Hulten et al. 2006; Walters et al. 2009) because under enemy-free conditions (e.g., an
58 absence of pathogens or pests), priming-mediated resistance outweighs the costs associated with the direct
59 activation of plant defenses (Heil 2002; van Hulten et al. 2006). Priming is generally associated with root
60

61 colonization by symbiotic fungi (*Glomus* spp., *Rhizophagus* spp., *Trichoderma* spp.) or nonpathogenic
62 bacteria (Van der Ent et al. 2009; Estaún et al. 2010; Shores et al. 2010; Hermosa et al. 2012) but can also
63 be associated with the attack of a plant by arthropods (Pappas et al. 2015; Pérez-Hedo et al. 2015). In
64 addition to beneficial plant-microbe interactions, several chemicals have been reported to trigger induced
65 resistance, among which β -aminobutyric acid (BABA), a nonprotein amino acid, was recently indicated to
66 be a novel plant defense hormone (Bacelli et al. 2017).

67 The mechanisms of BABA-induced resistance (BABA-IR) are based on the ability of BABA to potentiate
68 different defense signaling pathways (Bacelli et al. 2017). β -Aminobutyric acid-induced resistance against
69 the bacterial pathogen *Pseudomonas syringae* Van Hall and the fungal pathogen *Botrytis cinerea* Persoon
70 follows the endogenous accumulation of salicylic acid and the NPR1 protein (Zimmerli et al., 2000, 2001).
71 Furthermore, in soybean, BABA induces the expression of 15 genes related to defense against aphids and
72 significant increases in the activities of several defense enzymes (Zhong et al., 2014). One of the
73 consequences of BABA-IR is the rapid deposition of callose-containing papillae. This event also occurs in
74 *Arabidopsis* genotypes with impairment of in salicylic acid, ethylene, or jasmonic acid signalling pathway
75 (Conrath et al. 2006). Callose induction is an important defense response to phloem-sucking pests because
76 callose occludes sieve elements, thus interfering with their food supply (Hao et al. 2008; Sun et al. 2018).
77 In some cases, direct toxicity of BABA to insects is highly likely, since unmetabolized BABA has been
78 detected in both aphids (Hodge et al., 2011; Cao et al. 2014) and parasitoids (Hodge et al., 2011).

79 β -Aminobutyric acid induces plant resistance in diverse crop species, such as grapevine, pepper, potato,
80 tobacco, and tomato (Jakab et al. 2001; Cohen 2002). β -Aminobutyric acid is effective against a wide range
81 of plant antagonists, including viruses, bacteria, fungi and phytopathogenic nematodes (Justyna and Ewa
82 2013). The main effect of BABA on insects has been demonstrated in phloem feeders such as aphids on
83 plants such as legumes, brassicas, wheat, soybean and apples: BABA-treated plants negatively alter the
84 fitness of *Acyrtosiphon pisum* (Harris), *Myzus persicae* (Sulzer), *Brevicoryne brassicae* (L.) and *Aphis*
85 *plantaginea* (Passerini) by reducing their survival, prolonging juvenile development and reducing adult
86 fecundity (Hodge et al. 2005, 2006; Cao et al. 2014; Zhong et al. 2014; Robert et al. 2016). Moreover,
87 BABA has been shown to promote resistance against the Asian citrus psyllid *Diaphorina citri* Kuwayama
88 in citrus plants by affecting all developmental stages of the insect (Tiwari et al. 2013). More specifically, a
89 drench application of BABA, at concentration 25 mM, significantly reduced the mean number of *D. citri*
90 eggs, nymphs and adults, produced per plant, as compared with a water control.

91 Few studies have addressed the effects of BABA on the behavior and fitness of natural enemies. The
92 priming of plant defenses usually induces the release of volatile compounds that increase the attractiveness
93 of plants to predators and parasitoids (Shimoda et al. 2002; Lou et al. 2005; Moraes et al. 2009; Battaglia
94 et al. 2013; Duran et al. 2017). Conversely, it has been shown that the predator *Coccinella septempunctata*
95 L. avoids broad bean plants treated with BABA (Williams and Flaxman 2012). No effect on the behavior
96 of the parasitoid *Aphidius ervi* (Haliday) has been detected (Hodge et al. 2011). Regarding the effects on
97 the fitness of natural enemies, a reduction in the size and survival of *A. ervi*-parasitizing *A. pisum* has been
98 observed (Hodge et al. 2011). The extent of the adverse effects varies with the dose of BABA applied to
99 the host plant *Vicia faba* L.

100 Currently, BABA is not marketed as a plant protection product although it can play an important role in the
101 protection of tomato plants. Indeed ,it has been demonstrated that this compound is highly effective in
102 controlling important tomato diseases caused by pathogens such as *Phytophthora infestans* (Mont.) de Bary
103 and *Oidium neolycopersici* L. and plant-parasitic nematodes (Fatemy et al. 2012; Justyna and Ewa 2013;
104 Mutar and Fattah 2013). However, the BABA-mediated effects have not been studied in the tomato pests
105 or their natural enemies with the sole exception of *Aulacorthum solani* (Kaltenbach) (Hodge and Powell
106 2012).

107 One of the most serious pests of tomato crops is the sweet potato whitefly, *Bemisia tabaci* (Gennadius)
108 (Hemiptera: Aleurodidae) (McKenzie et al. 2004), a polyphagous species that is now recognized as a cryptic
109 species complex (De Barro and Ahmed 2011). The increases in pest resistance to many insecticides and the
110 need to develop environmentally friendly agricultural practices have promoted the use of biological control
111 agents as an effective control strategy for *B. tabaci* (Gerling et al. 2001; Shah et al. 2015). The predator
112 *Macrolophus pygmaeus* Rambur is used across Europe in integrated pest management (IPM) programmes
113 for tomato pests including *B. tabaci*, especially in the Mediterranean region (Alomar et al. 2002; Castañé
114 et al. 2004; Alomar et al. 2006; Arnó et al. 2010; Perdakis et al. 2011; Moreno-Ripoll et al. 2012; Aviron et
115 al. 2016). This zoophytophagous predator is highly polyphagous and is linked to the host plant for feeding
116 and oviposition (Castañé et al. 2011; Hamdi et al. 2013; Han et al. 2015; Duran et al. 2016, 2018).

117 BABA used against plant pathogens may have side effects on tomato pests. In this case, it is very likely
118 that predators will also be affected. One of the effects of BABA on insects is a reduction in size. Host size
119 is a constraint for parasitoids. Conversely, the size of the prey may not be a limiting factor for predators if
120 there is an abundance of prey. On the other hand, by consuming more prey items, predators may be

121 particularly affected by the presence of nonmetabolized toxic chemicals in their prey (Kos et al. 2011).
122 Finally, in the case of zoophytophagous predators, BABA can directly affect the predator through the host
123 plant. In this study, we evaluated the effect of BABA on the juvenile development and adult fecundity of
124 *B. tabaci*. These parameters affect population growth and therefore the availability of prey for *M. pygmaeus*.
125 We also assessed the effect of BABA on the fecundity and juvenile development of *M. pygmaeus* fed either
126 *B. tabaci* or an alternative prey that has no nutritional relationship with the plant, i.e. eggs of *Ephestia*
127 *kuehniella* Zeller (Lepidoptera: Pyralidae).

128

129 **Materials and methods**

130

131 **Insect and plant material**

132 *Bemisia tabaci* and *M. pygmaeus* were obtained from rearing cultures established at IRTA and maintained
133 under controlled conditions ($25 \pm 2^\circ\text{C}$, 16 h/8 h L:D and $70 \pm 10\%$ RH). *Bemisia tabaci* (MEAM 1,
134 previously known as biotype B) was originally collected in Murcia (Spain) in 1992 and was reared on
135 cabbage seedlings. *Macrolophus pygmaeus* was originally collected in tomato crops from the Maresme area
136 (Barcelona, Spain) and was reared on tobacco plants and fed with the eggs of *E. kuehniella*, as described
137 in Agustí and Gabarra (2009). *Ephestia kuehniella* eggs were purchased from Biotop (Valbonne, France).
138 The experiments were conducted using tomato plants of the San Marzano nano (dwarf) cultivar. This
139 tomato cultivar, characterized by small pear-shaped fruits, is native to southern Italy (Corrado et al. 2014).
140 The San Marzano nano cultivar has been used in previous studies mainly because of its susceptibility to
141 insect pests and plant pathogens (Battaglia et al. 2013; Chitarra et al. 2016; Coppola et al. 2017; Duran et
142 al. 2017). Tomato seeds were sown in trays containing a mixture of commercial propagating substrate
143 (Stender® propagation substrate A 210, Germany) composed of white and Irish peat and perlite (NPK 14-
144 16-18, pH 5.5-6.0). The seedlings were transferred to individual plastic pots (12 cm diameter), watered as
145 required and maintained in a heated greenhouse (temperature ranging between 20.35°C and 22.1°C ; relative
146 humidity ranging between 50.6 and 68.0%; both parameters were measured with a Testo 175-H2
147 Temperature and Humidity Data Logger - Spain).
148 Plants, at the 5 fully extended leaf stage (aprox. 40 cm) were treated with 50 ml/pot of BABA (Sigma-
149 Aldrich Co.; purity 97%) at a 25 mM concentration in distilled water, applied by soil drenching; the plants
150 were separated in trays depending on the treatment. The control plants were watered with 50 ml of distilled

151 water. The BABA-treated plants were allowed to undergo priming for 4 days in greenhouse conditions
152 before being used in the different tests. During this time interval, BABA-treated plants and controls were
153 not watered, as suggested by Hodge et al. (2005).

154 In several studies, a single application of 25 mM BABA has been reported to affect the performance of
155 sucking insects (Hodge et al. 2005, 2006; Hodge and Powell 2012; Cao et al. 2014; Zhong et al. 2014).

156 Preliminary tests showed that the concentration of 50 mM BABA (a single dose of 50 ml/pot) causes a
157 phytotoxic effect on tomato plants of the selected cultivar (unpublished results). This finding together with
158 the fact that 25 mM BABA has been shown to decrease the severity of pathogenic diseases without causing
159 any phytotoxic effects (Hassan and Buchenauer 2008) was the reason that we chose this concentration.

160 To reduce the variability in *B. tabaci* egg laying due to temperature fluctuation, the tests for evaluating the
161 fertility of whiteflies and predators were performed under the same controlled conditions applied in the
162 rearing colonies. The tests for evaluating the effect of BABA on the juvenile development of *B. tabaci* and
163 *M. pygmaeus* were performed in the winter-spring period in a heated greenhouse, which allowed us to
164 maintain similar environmental conditions to those applied in commercial greenhouse crops.

165

166 **Effect of BABA on *B. tabaci***

167 The effect of BABA on the fertility and juvenile development of two generations of *B. tabaci* was evaluated.
168 Egg deposition by the parental generation was assessed by confining *B. tabaci* adults from the rearing
169 colony to tomato leaves (10 females and 10 males per plant) inside muslin bags (5 cm width x 7 cm length)
170 (28 replicates for both BABA and untreated plants). The whitefly adults were allowed to lay eggs for 72 h
171 under controlled conditions ($25 \pm 2^\circ\text{C}$, 16 h/8 h light/dark and $70 \pm 10\%$ RH). After removing the muslin
172 bags, the number of eggs was recorded with the aid of a stereomicroscope without detaching the leaves
173 from the plants. Subsequently, 24 plants from the untreated group and 20 from the group treated with BABA
174 were individually isolated in transparent acrylic cylinders (20 cm diameter x 41 cm height with a muslin
175 cover on the top to allow ventilation) and moved to a greenhouse for whitefly juvenile development. The
176 remaining plants (4 from the untreated group and 8 from the BABA-treated group), which were accidentally
177 damaged during egg counting, were eliminated. Thirty-three days later, when adults started to emerge, the
178 numbers of nymphs, pupae and empty puparia were recorded.

179 A new set of 20 plants treated as described above was then prepared. Ten whitefly adults (5 females and 5
180 males per plant) that had emerged in the previous test (BABA and control first generation adults) were

181 confined to leaves inside muslin bags for egg laying and maintained for 72 hours under controlled
182 conditions. After removing the muslin bags, the number of eggs was counted. The BABA-treated plants
183 and untreated plants were then individually isolated in acrylic cylinders and moved to the greenhouse for
184 immature whitefly development (second generation). When adults started to emerge (35 days after
185 oviposition), the numbers of nymphs, pupae and empty puparia were recorded. As in the previous
186 experiment, the plants that were accidentally damaged during egg counting were discarded. Unfortunately,
187 some plants from the untreated group and few plants treated with BABA, but showing mild symptoms,
188 were attacked by *O. neolycoopersici* during the experiment. Plants showing symptoms, even mild ones, were
189 eliminated from the analysis. For this reason, only 8 and 12 plants were evaluated for the control and BABA
190 treatments, respectively.

191

192 **Effect of BABA on *M. pygmaeus***

193 The fertility of *M. pygmaeus* females from the rearing colony and the development of newly hatched
194 nymphs were evaluated on BABA-treated and untreated plants. Two different sources of food were tested
195 for the developing *M. pygmaeus* nymphs: *E. kuehniella* eggs and *B. tabaci* larvae, to discern two possible
196 effects: the effect of the consumption of BABA directly from the plant (the only possibility when feeding
197 on *E. kuehniella* eggs) and that of indirect BABA intake through the consumption of *B. tabaci* nymphs.
198 Emerging adults were weighed, and their fertility was recorded.

199 To evaluate fertility in the parental generation, five 7-day-old females and five males of *M. pygmaeus* were
200 allowed to interact and lay eggs on plants treated with BABA or control plants (11 replicates) without prey
201 for 72 h. Ten days later (the time period necessary for eggs to hatch at 25°C), the newborn nymphs were
202 counted.

203 To evaluate the survival of the nymphs fed with *E. kuehniella* eggs, twenty 1st-instar predator nymphs from
204 the rearing colony were released on a plant (5 fully extended leaves) that was either treated with BABA or
205 untreated and placed in a transparent acrylic cylinder (20 cm diameter x 41 cm height). Twelve replicates
206 (plants) were performed for both the BABA and control treatments. A small spoonful of *E. kuehniella* eggs
207 (approximately 600 eggs) was provided as food every two or three days. Between the 3rd and 4th weeks of
208 predator development, the number of adults was recorded daily. Adults were sexed and weighed with a
209 precision scale (Sartorius A200S Analytical Balance, readability 0.0001 g). Thereafter, the adults from each
210 treatment were maintained together on a non-treated plant for 7 days to allow their sexual maturation and

211 were then used for the subsequent fertility tests. *Ephestia kuehniella* eggs were also offered as prey during
212 this period. The fertility of the first-generation females that were obtained and allowed to mature as
213 described above was evaluated by placing 5 females and 5 males on an untreated plant for 72 h without
214 prey (12 replicates). After 10 days, the total number of newborn nymphs per plant was recorded.
215 Nymphal survival with *B. tabaci* larvae as prey was assessed by following the same experimental procedure
216 used in the previous experiment. However in this case, before starting the bioassay, the plants were infested
217 with *B. tabaci* by releasing 25 whitefly females and males per plant and maintaining them for 20 days under
218 controlled conditions in an acrylic cage (44 cm width x 67 cm length). Fourteen replicates were performed
219 for both the control and BABA-treated plants.

220

221 **Statistical Analyses**

222 To examine the effect of BABA on the mean number of eggs laid by *B. tabaci* females, fecundity data for
223 both the parental and first generations were independently analyzed with a two-sample *t*-test.

224 To evaluate whether the whitefly age distribution was influenced by BABA, a two-way factorial ANOVA
225 with “treatment” (two levels, controls and BABA-treated plants) and “whitefly instar” (three levels,
226 nymphs, pupae and empty puparia as a representation of emerged adults) as fixed effects was performed
227 independently for the parental and first generations.

228 The effect of BABA on predator fitness, measured as the survival of juvenile stages and female fertility,
229 was analyzed with a two-sample *t*-test. The weights of *M. pygmaeus* individuals fed with *E. kuehniella* or
230 with *B. tabaci* nymphs were independently analyzed in a two-way factorial ANOVA with sex and treatment
231 (controls and BABA-treated plants) as fixed effects.

232 All the statistical analyses performed in this study were carried out using R.3.6 software (R Core Team,
233 2019).

234

235 **Results**

236

237 **Effect of BABA on *B. tabaci***

238 The differences in the mean number of eggs laid by *B. tabaci* females on BABA-treated and control plants
239 were not statistically significant in the parental generation or the first generation (Table 1). The plants

240 treated with BABA were therefore accepted for oviposition by *B. tabaci* to the same extent as the control
241 plants. Furthermore, the development of juvenile stages on the plants treated with BABA did not
242 subsequently alter the fertility of emerging females.

243 Figure 1 shows the mean number of first-generation nymphs, pupae and empty puparia per plant 33 days
244 after egg deposition, grouped by instar and condition. The differences between the whitefly instars were
245 obviously significant ($F_{2,126}=19.59$; $P<0.001$). In contrast, the differences between treatments (BABA vs
246 control: $F_{1,126}=0.87$; $P=0.353$) and the interaction effect between the whitefly instars and treatments
247 ($F_{2,126}=0.13$; $P=0.876$) were not significant. A similar result was obtained in the second generation (whitefly
248 instars: $F_{2,54}=32.31$; $P<0.001$; treatments: $F_{1,54}=2.37$; $P=0.129$; interaction $F_{2,54}=0.32$; $P=0.729$; Fig. 2).
249 This result indicates that the development rate and survival of juvenile stages were not affected by BABA.

250

251 **Effect of BABA on *M. pygmaeus***

252 In *M. pygmaeus*, BABA had no significant effect on either female fertility or the development and survival
253 of juvenile stages (Table 2). The result was the same whether *M. pygmaeus* fed on plants with *E. kuehniella*
254 eggs or *B. tabaci* nymphs. In the first case, *M. pygmaeus* was only able to obtain BABA from the plant,
255 whereas, in the second case, BABA was available from both the plant and the prey.

256 The mean weights of the females and males that developed on the BABA-treated or control plants and were
257 fed with *E. kuehniella* eggs are shown in Figure 3. The difference in body weight between the sexes was
258 statistically significant ($F_{1,128}=387.19$, $P < 0.001$). In contrast, the differences between the treatments
259 ($F_{1,128}=0.85$, $P=0.359$) and the interaction between the two factors ($F_{1,128}=1.77$, $P=0.186$) were not
260 significant. The *M. pygmaeus* individuals fed with *B. tabaci* nymphs were smaller than those fed with *E.*
261 *kuehniella* eggs. The differences in body weight were statistically significant between sexes ($F_{1,155}=74.26$,
262 $P < 0.001$) and between treatments ($F_{1,155}=21.18$, $P < 0.001$), although the interaction between the two
263 factors was not significant ($F_{1,155}=2.37$, $P=0.125$) (Fig. 4). Males that developed on plants treated with
264 BABA were significantly heavier than those that developed on control plants (Tukey's test $P < 0.05$).

265

266 **Discussion**

267 The application of 25 mM BABA to tomato as a soil drench did not affect the overall fitness of *B. tabaci*
268 and its predator *M. pygmaeus*. Higher concentrations or multiple applications might lead to different results

269 since the effect of BABA on insects is dose dependent (Cao et al. 2014). However, the tested concentration
270 (25 mM) has been reported to affect the performance of sucking insects such aphids and one psilid species
271 on diverse host plant species (Hodge et al. 2005, 2006; Hodge and Powell 2012; Tiwari et al. 2013; Cao et
272 al. 2014; Zhong et al. 2014), including tomato (Hodge and Powell 2012). Previous studies on the effect of
273 BABA on whiteflies and zoophytophagous predators are not available for either tomato or other host plants.
274 Our data seem to demonstrate that BABA is ineffective against whiteflies, contrary to what has been
275 observed for aphids. We can hypothesize a few explanations for this finding that are not necessarily
276 mutually exclusive.

277 First, aphids and whiteflies, which are both hemipterans that feed on phloem, exhibit different life cycles
278 and feeding behaviors. Aphid adults and nymphs are mobile and change feeding sites on the plant during
279 their lifespan, while whitefly first-instar nymphs establish a unique feeding site that will be the same for
280 the next nymphal instars (Pollard 1955). Both insects use their stylets to penetrate the plant cuticle,
281 epidermis and mesophyll to reach the phloem sieve elements, where they feed on. Both insects also produce
282 stylet sheets with their saliva to insulate their stylets from the plant tissues, and these structures are very
283 useful for revealing the track followed to the phloem vessels. The difference is that the stylet sheets from
284 aphids are profusely branched, indicating that the insect punctures and probes most of the mesophyll cells
285 in its path to a major vein in the phloem and, depending on its size and the elicitors of its saliva, causes
286 moderate to extensive damage. In this process, wound signalling pathways are activated. In contrast, stylet
287 sheets from whiteflies are usually shorter and lead to the puncture of minor phloem vessels. Whitefly stylets
288 rarely puncture mesophyll cells, thus avoiding cell damage and the consequent activation of wound
289 responses in the plant (Pollard 1955). Therefore, whiteflies are known to mainly activate the salicylic acid
290 defensive pathway in plants (which is also activated by plant pathogens), while suppressing the activation
291 of the jasmonic acid (JA) pathway, which interferes with whitefly nymphal development (Kempema et al.
292 2007; Zarate et al. 2007; Walling 2000; 2008). We can speculate that BABA amplifies the plant's normal
293 response to *B. tabaci* by inducing faster and stronger accumulation of SA. As a result of negative cross-talk
294 between SA and JA (Koornneef & Pieterse 2008), the activation of the SA response will protect the whitefly
295 against the activation of effective defenses from the plant (Zarate et al. 2007; Puthoff et al. 2010). This
296 might explain the lack of effects mediated by BABA or other elicitors, such as Actigard (benzo (1,2,3)
297 thiazazole-7-carbothioic acid (S)-methyl ester), on *B. tabaci* performance (Inbar et al. 1997; Mayer et al.
298 2002).

299 A second aspect concerns the ability of whiteflies, particularly *B. tabaci* MEAM1, to detoxify toxic
300 chemicals obtained from the plant (Wang et al. 2017). For this reason, whiteflies appear to be immune to
301 the defenses elicited in the plant by other phytophagous species (Mayer et al. 2002; Pappas et al. 2015). We
302 cannot exclude the possibility that *B. tabaci* is able to metabolize defensive chemicals induced by BABA
303 or BABA itself.

304 The third aspect concerns the translocation and metabolism of BABA in the plant. Studies on this topic
305 have shown that when BABA is applied to the roots, it travels acropetally via the transpiration stream and
306 remains mostly unmetabolized in plant tissues (Cohen 2002). High concentrations of BABA have been
307 found in aphids feeding on BABA-treated plants (Hodge and Powell 2011; Cao et al. 2014). It is possible
308 that the different feeding behavior of whiteflies compared to aphids reduces the risk of taking in
309 unmetabolized BABA from the host plant.

310 We further must add that tomato genotypes display different levels of resistance to pests and diseases in
311 relation to environmental conditions (Goggin et al. 2001; Sharma et al. 2010; Rivelli et al. 2013). The
312 relationship between the genotype and the inducibility of resistance is complex and poorly studied. Tomato
313 accessions vary considerably in the inducibility of resistance by BABA, at least in relation to pathogens,
314 and the level of induction is not always related to the basal resistance level (Sharma et al. 2010).

315 The lack of an effect of BABA-primed plants on predator fitness is consistent with the absence of an effect
316 on the prey. *Macrolophus pygmaeus* is a zoophytophagous insect that activates plant defence mechanisms
317 itself (Pappas et al. 2015; Zhang et al. 2018). Nevertheless, the dependence of *M. pygmaeus* on plant
318 nutrients is much more limited than that of a strict phytophagous insect. This predator is more dependent
319 on its prey than on the plant, and it can be reared for several generations on a meat diet alone without the
320 presence of any plant material (Castañé and Zapata 2005), while it barely survives on a strict plant diet
321 (Perdikis and Lykouressis 2004). It is assumed that this mirid bug uses the host plant mainly as a water
322 source (Castañé et al., 2011) except in conditions of prey scarcity (Sampson and Jacobson 1999). The
323 limited dependence on the plant may explain the lack of direct negative effects of the BABA-treated plants
324 on the predator, apart from the lack of prey-mediated effects.

325 In conclusion, the application of BABA to tomato as a soil drench did not have an effect on the overall
326 fitness of *B. tabaci* or its predator *M. pygmaeus*. The non-interference of BABA with *M. pygmaeus* and *B.*
327 *tabaci* assures that the control of the whitefly with this mirid bug will not be disturbed when this elicitor is
328 applied to the crop. As previously mentioned, it is well established that the action of BABA is effective in

329 the control of tomato diseases caused by phytopathogens and nematodes, and the results obtained here
330 indicate that the use of BABA at the tested concentration will be compatible with the implementation of
331 biological control programmes targeting pests based on the use of *M. pygmaeus*. Further studies are needed
332 to clarify the mechanisms underlying BABA-plant-whitefly-predatory mirids interactions.

333 **Conflict of interest**

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

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340

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530

531 **Figure and table captions**

532

533 **Fig. 1.** First generation of *B. tabaci*: Individuals per plant (mean \pm SE) obtained as offspring of 10 females
534 left to lay eggs for 72 hours in controlled conditions; distribution by instar on the thirty-third day from
535 oviposition.

536

537 **Fig. 2.** Second generation of *B. tabaci*: Individuals per plant (mean \pm ES) obtained as offspring of 5 females
538 left to lay eggs for 72 hours in controlled conditions; distribution by instar on the thirty-fifth day from
539 oviposition.

540

541 **Fig. 3.** Mean weight (\pm SE) of *M. pygmaeus* individuals reared on control or BABA-treated tomato plants
542 and fed with *E. kuehniella* eggs as prey.

543

544 **Fig. 4.** Mean weight (\pm SE) of *M. pygmaeus* females and males reared on control or BABA-treated tomato
545 plants and fed with *B. tabaci*.

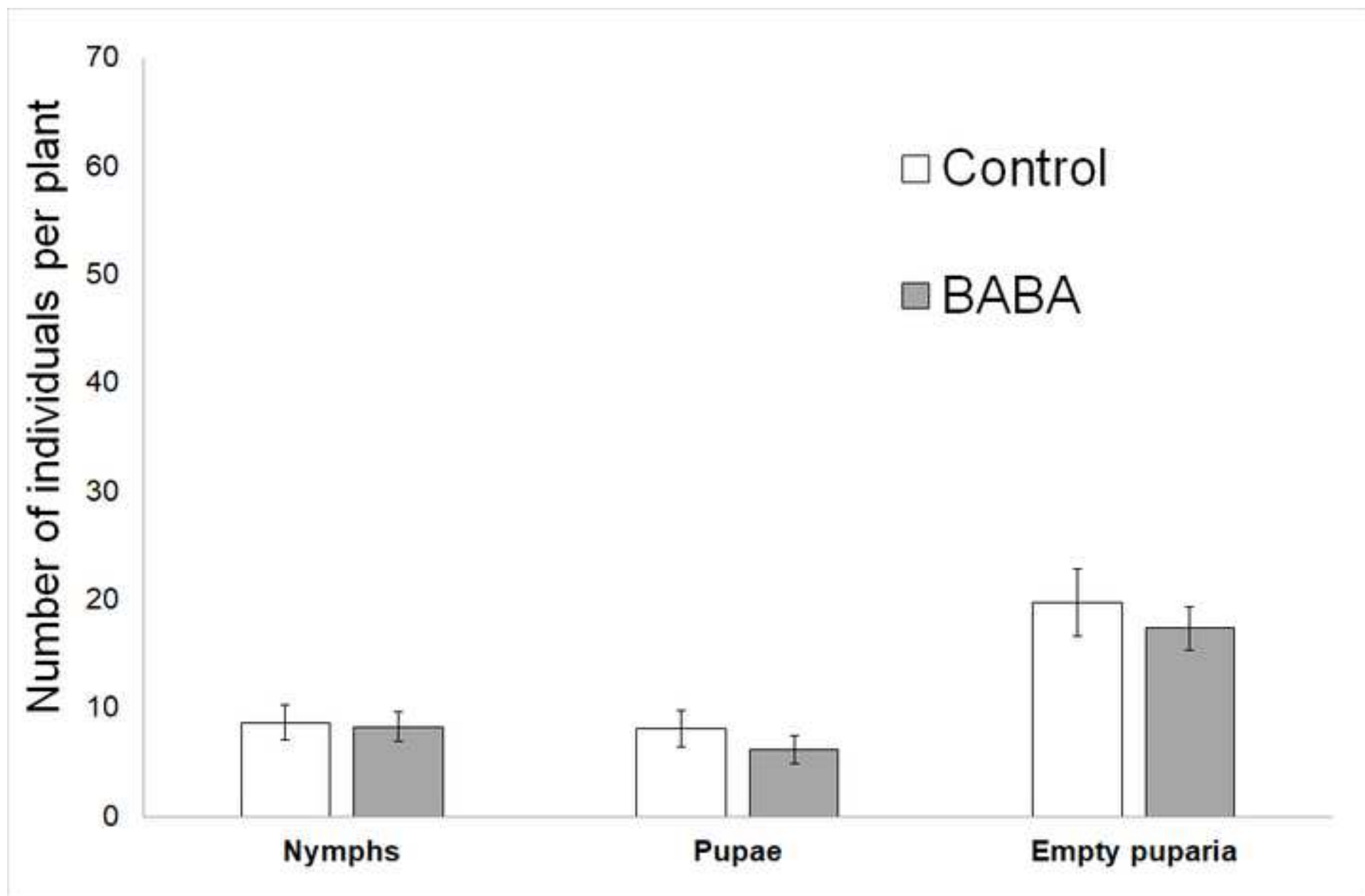
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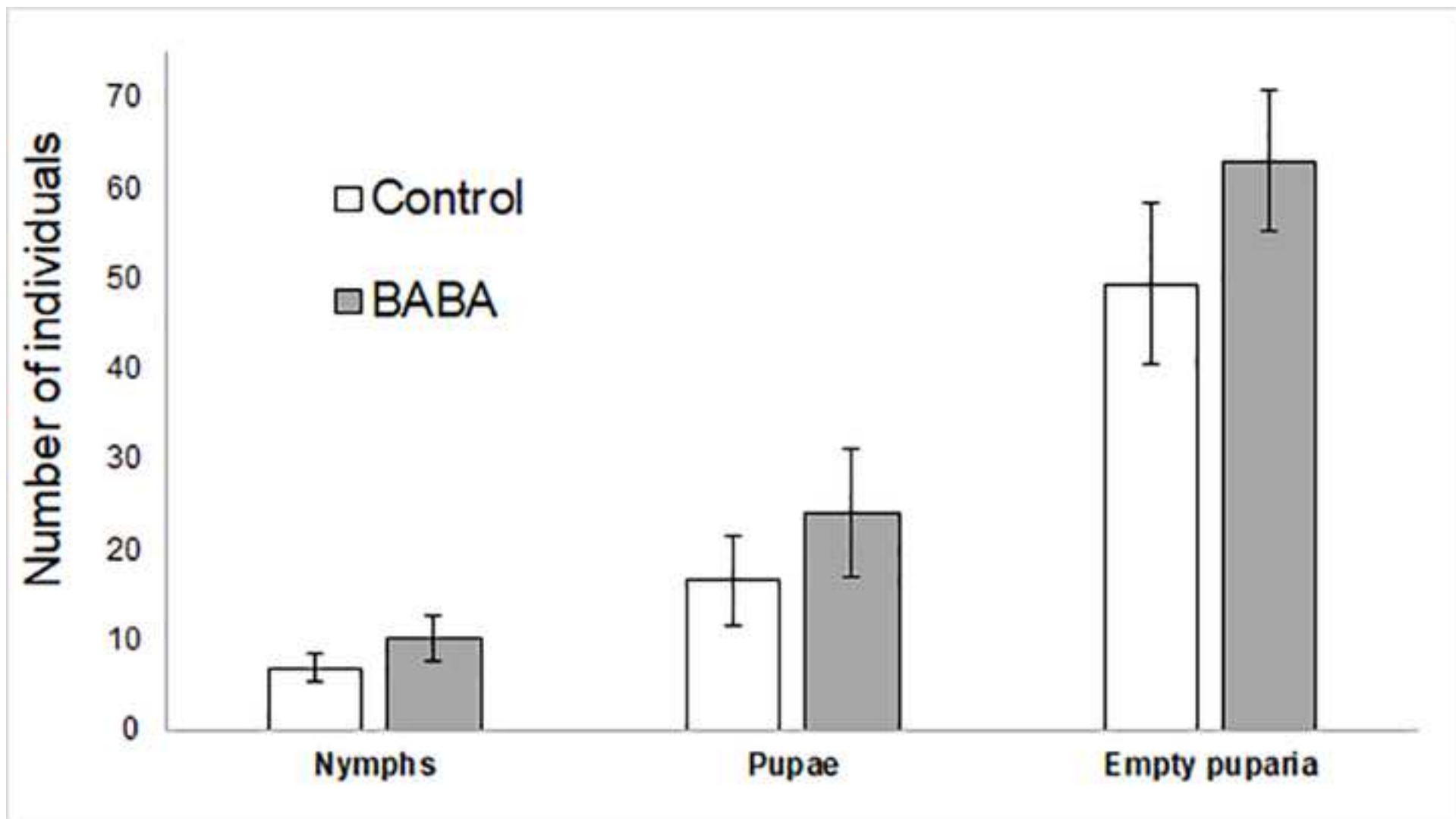
547 **Tab. 1.** Number of eggs laid by *B. tabaci* females in both the parental and first generations on BABA-
548 treated and control plants and the corresponding two-sample t-test results.

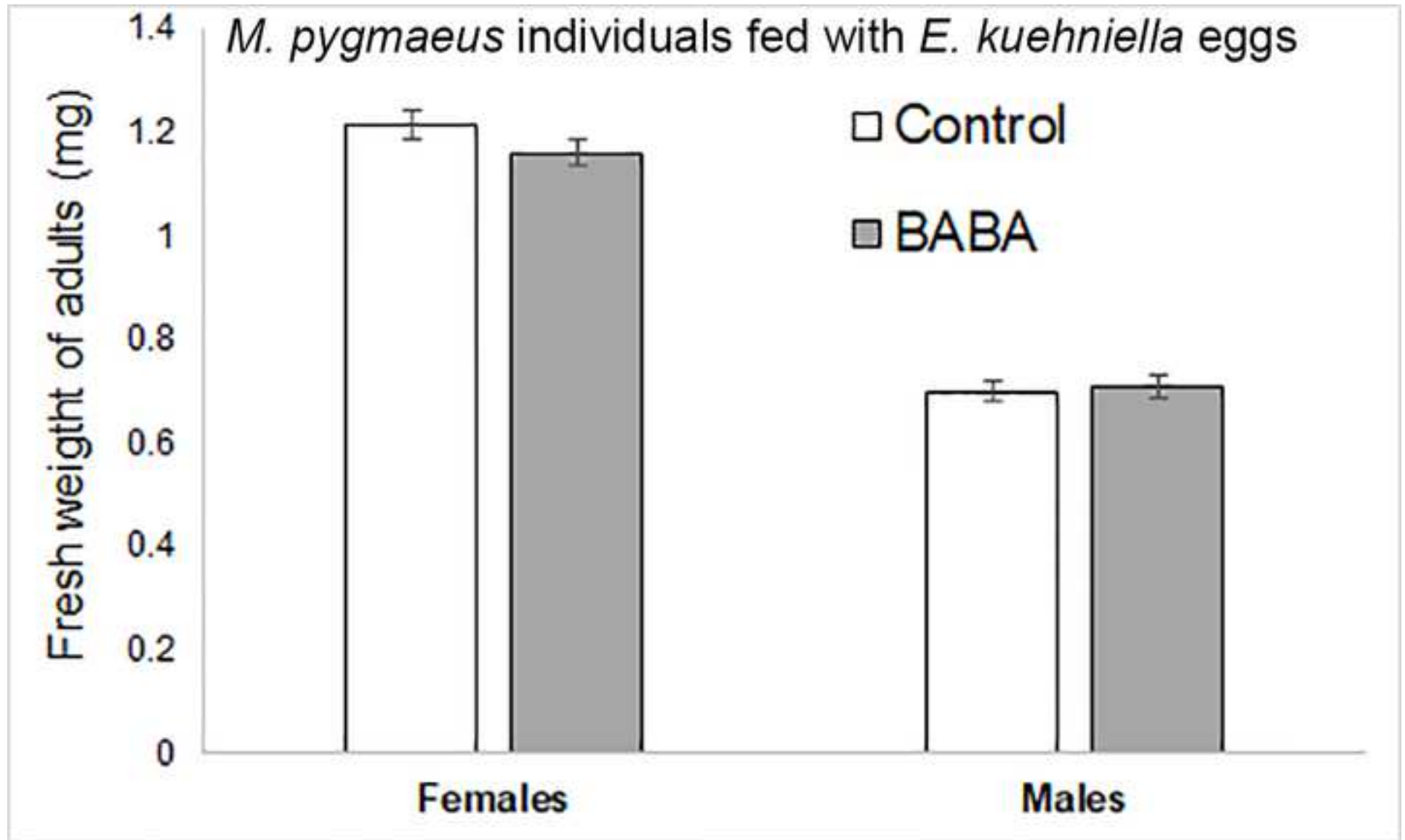
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550 **Tab 2.** *M. pygmaeus*: female fertility (number of newly emerged nymphs/female/plant/day of oviposition)
551 and the number of emerged adults per plant, including the corresponding two-sample t-test results.

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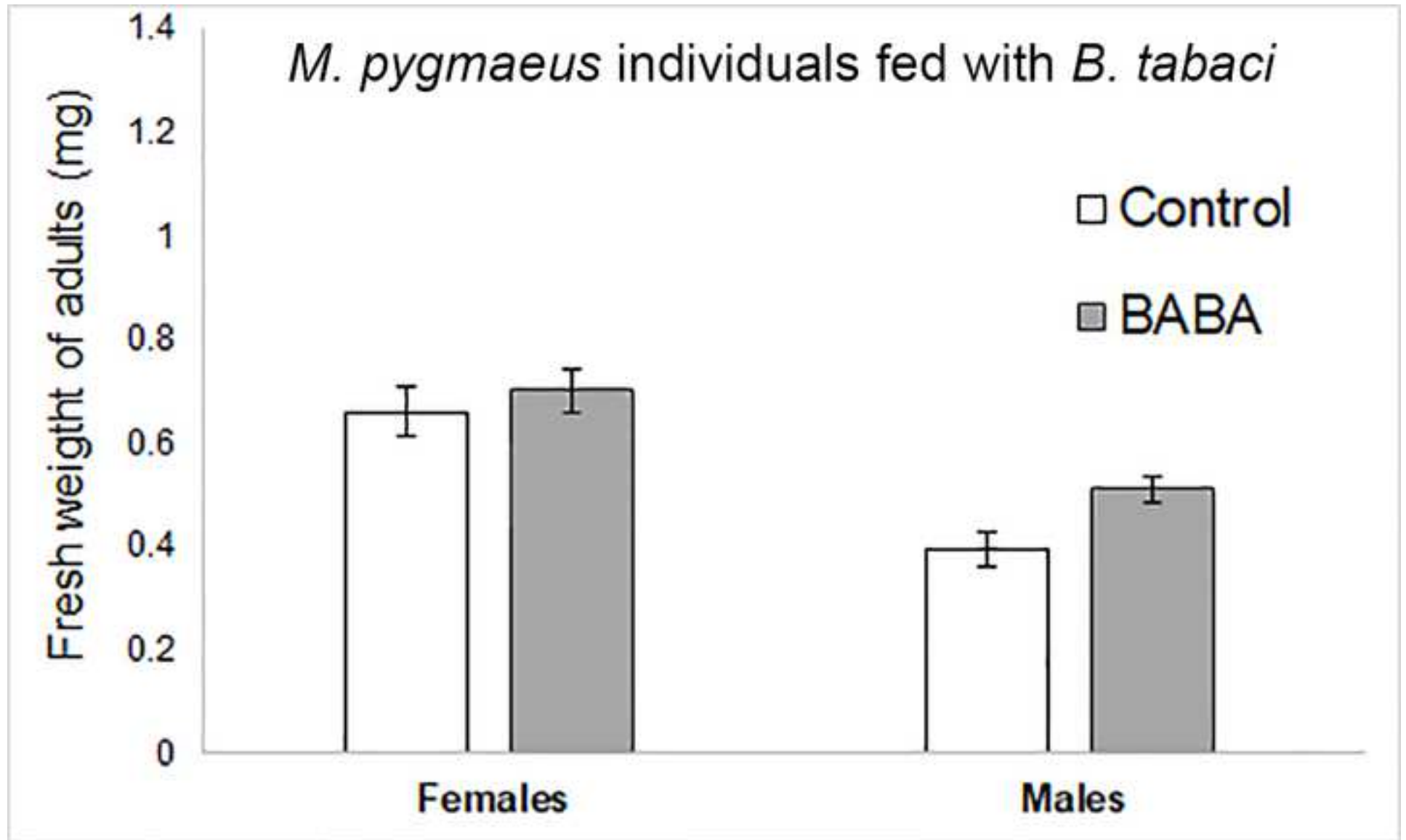


Table 1. Number of eggs laid by *B. tabaci* females in both the parental and first generations on BABA-treated and control plants and the corresponding two-sample t-test results.

	BABA (Mean \pm SE)	Control (Mean \pm SE)	Statistics
Eggs/female/day (parental generation)	3.88 \pm 0.49	3.81 \pm 0.42	$t_{54}=0.10$, $P=0.92$
Eggs/female/day (first generation)	7.56 \pm 0.67	6.80 \pm 0.61	$t_{38}=0.83$, $P=0.42$

Table 2. *M. pygmaeus*: female fertility (number of newly emerged nymphs/female/plant/day of oviposition) and the number of emerged adults per plant, including the corresponding two-sample t-test results.

	BABA (Mean ± SE)	Control (Mean ± SE)	Statistics
Fertility of parental generation adults	0.38±0.08	0.47±0.09	$t_{20} = -0.76, P=0.46$
Fertility of first-generation adults (<i>E. kueniella</i> eggs as prey)	2.7±0.37	2.2±0.31	$t_{26} = -0.40, P=0.45$
Fertility of first-generation adults (<i>B.tabaci</i> as prey)	0.9±0.22	1.0±0.09	$t_{33} = 0.40; P=0.69$
Number of emerged adults (<i>E. kueniella</i> eggs as prey)	10.75±0.95	9.75±0.98	$t_{22} = 0.73, P=0.47$
Number of emerged adults (<i>B.tabaci</i> as prey)	5.37±0.84	5.92±0.68	$t_{26} = -0.35, P= 0.73$