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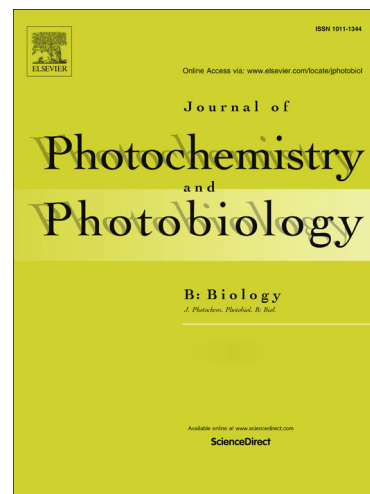
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1 **Impact of UV-A radiation on the performance of aphids and whiteflies and on the leaf**
2 **chemistry of their host plants**

3

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ABSTRACT

19 Ultraviolet (UV) radiation directly regulates a multitude of herbivore life processes, in
20 addition to indirectly affecting insect success *via* changes in plant chemistry and
21 morphogenesis. Here we looked at plant and insect (aphid and whitefly) exposure to
22 supplemental UV-A radiation in the glasshouse environment and investigated effects on
23 insect population growth. Glasshouse grown peppers and eggplants were grown from seed
24 inside cages covered by novel plastic filters, one transparent and the other opaque to UV-A
25 radiation. At a 10-true leaf stage for peppers (53 days) and 4-true leaf stage for eggplants (34
26 days), plants were harvested for chemical analysis and infested by aphids and whiteflies,
27 respectively. Clip-cages were used to introduce and monitor the insect fitness and populations
28 of the pests studied. Insect pre-reproductive period, fecundity, fertility and intrinsic rate of
29 natural increase were assessed. Crop growth was monitored weekly for 7 and 12 weeks
30 throughout the crop cycle of peppers and eggplants, respectively. At the end of the insect
31 fitness experiment, plants were harvested (68 days and 18-true leaf stage for peppers, and 104
32 days and 12-true leaf stage for eggplants) and leaves analysed for secondary metabolites,
33 soluble carbohydrates, amino acids, total proteins and photosynthetic pigments. Our results
34 demonstrate for the first time, that UV-A modulates plant chemistry with implications for
35 insect pests. Both plant species responded directly to UV-A by producing shorter stems but
36 this effect was only significant in pepper whilst UV-A did not affect the leaf area of either
37 species. Importantly, in pepper, the UV-A treated plants contained higher contents of
38 secondary metabolites, leaf soluble carbohydrates, free amino acids and total content of
39 protein. Such changes in tissue chemistry may have indirectly promoted aphid performance.
40 For eggplants, chlorophylls *a* and *b*, and carotenoid levels decreased with supplemental UV-
41 A over the entire crop cycle but UV-A exposure did not affect leaf secondary metabolites.
42 However, exposure to supplemental UV-A had a detrimental effect on whitefly development,
43 fecundity and fertility presumably not mediated by plant cues as compounds implied in pest
44 nutrition -proteins and sugars- were unaltered.

45

46 Keywords: Plant-insect interactions; UV-blocking covers; Insect pests; Pepper; Eggplant

47

48 Highlights:

- 49 • Supplemental UV-A causes a reduction in pepper stem height
- 50 • Aphids benefit from changes in pepper metabolites under supplemental UV-A
- 51 • There is a detrimental effect of UV-A radiation on whitefly performance
- 52 • UV-mediated changes appear to be highly dependent on each plant-insect complex

53

54 **1. Introduction**

55 Aphids and whiteflies are two of the most important pests worldwide, not only because of the
56 direct damage they cause, but also because their alimentary habits involve transmission of
57 plant viruses (Hull, 2002). Ultraviolet (UV) radiation plays a major role in herbivores,
58 including insect pests, by modifying their orientation toward potential hosts, flight activity,
59 alighting, arrestment, feeding behavior and interaction between sexes (Raviv and Antignus,
60 2004; Johansen *et al.*, 2011). Aphids (Hemiptera: Aphididae) and whiteflies (Hemiptera:
61 Aleyrodidae) are among the most studied insects concerning their flight behaviour. Aphids
62 have been reported to reduce their flight activity and ability to disperse in UV-deficient
63 environments (Díaz and Fereres, 2007; Döring and Chittka, 2007). Moreover, a decrease in
64 fecundity and population density has been also demonstrated (Antignus *et al.*, 1996; Chyzik
65 *et al.*, 2003; Díaz *et al.*, 2006; Kuhlmann and Müller, 2009a; Paul *et al.*, 2011; Legarrea *et*
66 *al.*, 2012). Conversely, UV radiation stimulates whitefly migration (Mound, 1962; Coombe,
67 1982). Among new integrated pest management strategies, UV-absorbent photoselective nets
68 have been successfully tested in field situations by reducing the impact of insect vectors and
69 plant pathogens on protected crops (Díaz and Fereres, 2007; Weintraub, 2009; Legarrea *et*
70 *al.*, 2012).

71 Knowledge on the effects of UV-B on plant growth and chemistry (nutritional characteristics
72 relevant to insects) has been developed due to past concerns about ozone depletion (Ballaré *et*
73 *al.*, 1996; Hunt and McNeil, 1999; Mackerness, 2000; Jansen, 2002; Comont *et al.*, 2012;
74 Mewis *et al.*, 2012). In contrast, understanding of the effects of the UV-A fraction of the solar
75 spectrum on plants and insect pests is very limited. Whilst UV-A radiation is unaffected by
76 ozone depletion, it is a significant component of the solar spectrum affected by latitude,
77 altitude and cloud cover. It is also often absent from the glasshouse/horticultural
78 environment. New environmental concerns suggest that understanding UV-A impacts on
79 plants could be important given that predictions by the United Nations Environment
80 Programme suggest that there will be a higher incidence of cloud free periods, particularly in
81 southern Europe and the Mediterranean Basin. This will result in higher exposure of crops to
82 ambient UV-A radiation (WMO, 2010). Only a few authors have considered UV-A impacts
83 on plant growth (Tezuka *et al.*, 1994; Jayakumar *et al.*, 2003, 2004; Verdaguer *et al.*, 2012).
84 The latter work shows that radiation in the UV-A range produces alterations in leaf
85 morphology and anatomy of several plants, with the most characteristic response mainly
86 observed in the adaxial epidermal cells, which were thicker and longer than those grown
87 without UV-A.

88 There are no known studies that have focused on how UV-A influences the relationship
89 between phytophagous insects and their plant hosts but there is large body of material
90 published on UV-A plant pollinator interactions (Stephanou *et al.*, 2000; Petropoulou *et al.*,
91 2001; Dyer and Chittka, 2004). Furthermore, research on spider mites by Sakai and Osakabe
92 (2010) concluded that *Tetranychus urticae* Koch (Acari: Tetranychidae) exploits UV-A
93 information to avoid ambient UV-B radiation. At the same time other work on *Panonychus*
94 *citri* McGregor (Acari: Tetranychidae) suggested that eggs were tolerant to UV-B radiation

95 and females successfully oviposited on the upper side of leaves exposed to UV-B via
96 artificial lamps (Fukaya *et al.*, 2013).

97 Our knowledge on the effects of UV-B on plant-insect interactions would suggest that typical
98 plant responses would include the accumulation of UV-screening metabolites, increased leaf
99 thickness and trichome density or reduction in cell elongation (Smith *et al.*, 2000; Paul and
100 Gwynn-Jones, 2003; Liu *et al.*, 2005; González *et al.*, 2009; Kulmann and Müller, 2009a).
101 These impacts have implications for host success because such physical and biochemical
102 traits affect host acceptance and success of future insect progeny (Vänninen *et al.*, 2010; Paul
103 *et al.*, 2011)

104 Understanding of the indirect effects of UV-A on insects *via* plants remains limited to what
105 we know about current practices in horticulture. On one hand, the horticulture industry
106 traditionally grows crop species under glass or plastic with opaque or lowered UV radiation
107 environments. However, evidence suggests that supplemental UV-A may improve plant
108 growth, yield and quality. For example, a combination of visible radiation and UV-A at a
109 particular ratio may be highly suitable for enhanced growth of soybean seedlings (Middleton
110 and Teramura, 1993). Similar findings have been observed on the yield of *Phaseolus mungo*
111 L., which was improved with UV-A exposure (Jayakumar *et al.*, 2003). UV cladding
112 materials have been shown to also have positive effects on crop growth by increasing stem
113 length, leaf toughness or trichome density (Hunt and McNeil, 1999; Kittas *et al.*, 2006;
114 Kuhlmann and Müller, 2009a, 2010; Paul *et al.*, 2011). There is also evidence that UV
115 transmitting environments could produce food plants commercially with increased human
116 health benefits (Tsormpatsidis *et al.*, 2011).

117 In this study, we hypothesise that UV-A is central to the trophic relationships between these
118 two global pests -aphids and whiteflies- and their plant hosts. We grew the horticultural hosts
119 *Capsicum annuum* L. (pepper) and *Solanum melongena* L. (eggplant) and their respective
120 insect pests, the green peach aphid *Myzus persicae* Sulzer (Hemiptera: Aphididae) and the
121 whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) in the presence and absence of
122 UV-A radiation. We targeted how UV-A impacts the success of insects *via* population
123 growth. In tandem with direct effect of UV-A, we also assessed how UV-A exposure
124 indirectly affects insects *via* changes in plant chemistry. Correlations between the different
125 responses found in leaf chemicals analysed and plant sensitivity to UV-A are considered.

126

127 **2. Methods and materials**

128 *2.1. Plant propagation*

129 Experiments were undertaken in a glasshouse facility at the Institute of Agricultural Sciences
130 of CSIC (Madrid, Spain) (40° 26' 23'' N, -3° 41' 14'' W) at a temperature of 23:20±2 °C
131 (day:night), a photoperiod of 14:10 (light:dark) and 70-80% RH. *C. annuum* cv California
132 Wonder (Ramiro Arnedo S.A., La Rioja, Spain) and *S. melongena* cv Black beauty (Batlle,
133 S.A., Barcelona, Spain) seeds were germinated in pots with a mixture of soil:vermiculite

134 (1:1). For both species, three seeds were placed in each pot and thinned to one post
135 germination. Plants were watered three times a week using 20-20-20 (N:P:K) Nutricem 60
136 fertiliser (Miller Chemical & Fertilizer Corp., Pennsylvania, USA) at a dose of 0.25 g L⁻¹.

137 2.2. UV-A treatments

138 UV-A radiation was supplied by two Osram Ultra-Vitalux UV lamps (Osram GmbH,
139 Munich, Germany). Lamps were switched on and off with no gradual transition for a
140 photoperiod of 14 hours every day throughout the entire length of experiments. The lamps
141 emitted no UV-C radiation and produced radiation levels representative of typical sunny
142 summer day conditions in the centre of the Iberian Peninsula (Gutiérrez-Marco *et al.*, 2007;
143 Häder *et al.*, 2007). However, it should be emphasised that our aim here was to expose plants
144 and insects to UV-A under glasshouse conditions rather than simulate UV-A outdoors. The
145 lamps used were heavily weighted for UV-A emission so throughout the text we will refer to
146 the treatment as UVA+ (supplemental UV-A). A set of two 1 x 1 x 1m (L x H x W) cages
147 were covered by filters. As a positive control that allowed UV-A radiation transmission but
148 blocked UV-B radiation (Table 1), the upper side of one cage was covered with a 200 µm
149 thickness film (Solplast S.A., Murcia, Spain). The four lateral sides were covered to a 50 cm
150 height with a UV-transparent net T 50 mesh (Polysack Plastic Industries Ltd., Nir Yitzhak,
151 Israel) to permit airflow inside the cage. The remaining upper 50 cm were covered with
152 plastic film. For the suppressed UV-A radiation treatment, a 200 µm thickness Antivirus UV-
153 blocking film (Solplast S.A., Spain) and a UV-absorbing Optinet 50 mesh (Polysack Plastic
154 Industries Ltd., Nir Yitzhak, Israel) were used. Optical properties (transmitted radiation) of
155 the UV-opaque and UV-transparent films were analysed at the CSIC Torres Quevedo
156 Institute (Madrid, Spain) using a double monochromator Lambda 900 UV/Visible/NIR
157 spectrophotometer (PerkinElmer Life and Analytical Sciences Ltd., Connecticut, USA). The
158 main difference between both filters was that the UV-opaque film blocked UV-A
159 transmission (315-400 nm) and the UV-transparent film allowed UV-A transmission, as seen
160 in Figure 1. Lamps were hung at a distance of 1 m above the plant canopy. Irradiance per
161 second was measured daily above cage and at canopy level as well as on the abaxial side of
162 the leaves and through the leaves with clip-cages where insects were monitored with an
163 ALMEMO 25904S radiometer (Ahlborn GmbH, Holzkirchen, Germany). The radiation
164 received by the plants (irradiance) under both treatments is shown in Table 1. The UV daily
165 doses were 71.67 KJ m⁻² d⁻¹ UV-A and 0.55 KJ m⁻² d⁻¹ UV-B for treatment UVA+, and 1.76
166 KJ m⁻² d⁻¹ UV-A and 0.10 KJ m⁻² d⁻¹ UV-B for treatment UVA-. Daily UV-A radiation inside
167 the cage covered by the blocking film was very low (1.76 KJ m⁻² d⁻¹) hence this treatment
168 was called UVA- (near zero UV-A). A forty-fold increase in UV-A transmittance at the
169 plant canopy level inside the regular cage was measured when compared to the cage covered
170 by the UV-absorbing barrier (1.422 vs. 0.035 W m⁻²) (Table 1). Low levels of UV-B radiation
171 inside both experimental treatments were detected although represented less than 1% of the
172 light received by our plants (0.011 W m⁻² in treatment UVA+ and 0.002 W m⁻² in treatment
173 UVA-) (Table 1).

174 It should again be noted that the experimental set up was used to evaluate how supplemental
175 UV-A affects plant-insect interactions and performance in the glasshouse environment. The

176 focus was on crop production and this study was not designed to simulate outdoor
 177 environmental conditions, hence any extrapolation of findings to field conditions should be
 178 done with caution.

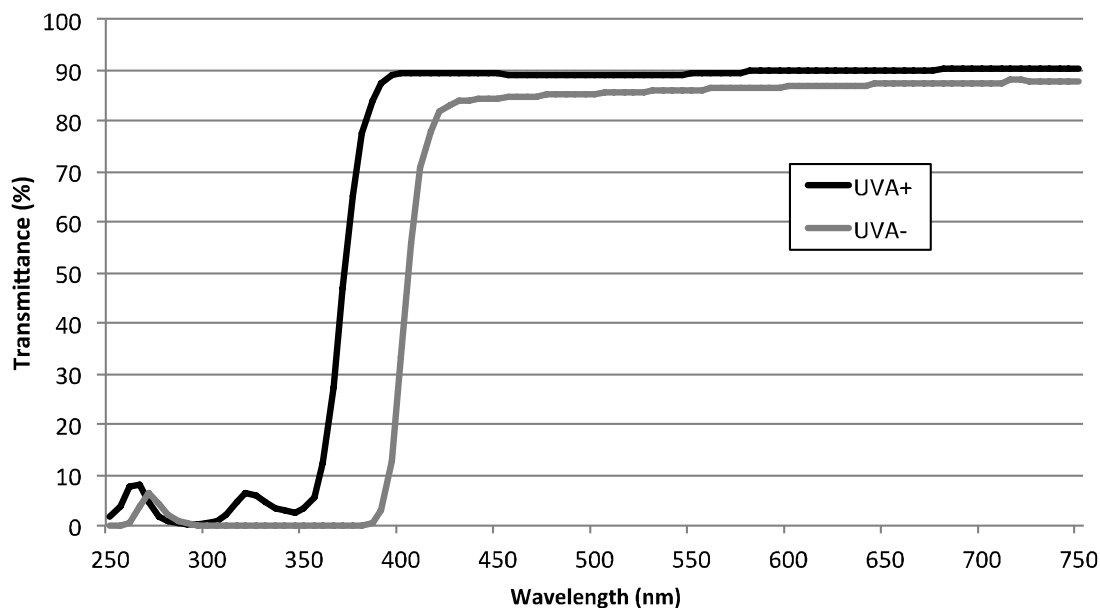
179 Table 1. Radiation conditions at canopy level outside and inside the experimental cages
 180 (UVA+ and UVA- treatments), on the abaxial side of the leaves and through the leaves with
 181 clip-cages where insects were monitored. Transmission percentages represent radiation
 182 transmitted inside both cages in relation to the same level outside cages.
 183

	Treatment UVA+			Treatment UVA-		
	PAR ^a	UV-A ^b	UV-B ^b	PAR	UV-A	UV-B
Canopy level outside cage	515.0 (112.8)	11.722	0.561	505.0 (110.6)	11.290	0.575
Canopy level inside cage	441.8 (96.8)	1.422	0.011	334.6 (73.3)	0.035	0.002
Abaxial side of leaves w/ clip-cage	25.3 (5.5)	0.083	0.002	21.8 (4.8)	0.003	0.002
Through the leaves w/ clip-cage	-	0.030	0.002	-	0.000	0.000
Transmission inside cage (%)	85.79	12.13	1.96	66.26	0.31	0.35

184 ^a $\mu\text{mol m}^{-2} \text{s}^{-1}$ (W m^{-2}), ^b W m^{-2}

185

186 Figure 1. Total transmittance from 250 to 750 nm of the UV-transparent (UVA+) and UV-
 187 opaque (UVA-) plastic films measured by a double monochromator spectrophotometer.



190

191

190 2.3. Insect exposure and maintenance

191 *M. persicae* was continuously reared on pepper plants in a climate chamber at 23:18 °C
 192 (day:night), 60-80% RH, and a photoperiod of 16 h and *B. tabaci* Q biotype was reared on
 193 eggplants in greenhouse facilities at an average temperature of 23:20°C (day:night), 70-80%

194 RH and a photoperiod of 16 h. Both species were synchronised prior to assays to ensure that
195 individuals were the same age.

196 2.3.1. Aphid introduction

197 Pepper plants were infested by *M. persicae* at the 10-true leaf stage. One single wingless
198 aphid adult was placed in a clip-cage on the abaxial side of the youngest fully developed leaf
199 of each pepper plant and allowed to produce nymphs for 24 hours. Surplus nymphs were
200 removed leaving three nymphs per plant, which were monitored until adulthood stage. When
201 the first nymph reached the adult stage, the other two were removed. Offspring from the
202 remaining insect was monitored by removing nymphs daily for an equal number of days to
203 the pre-reproductive period. The parameters pre-reproductive period (d), effective fecundity
204 (Md), intrinsic rate of natural increase ($r_m=0.738*(\log_e Md)/d$), mean relative growth rate
205 ($RGR=r_m/0.86$) and mean generation time ($Td=d/0.738$) were calculated (n=19).

206 2.3.2. Whitefly introduction

207 Eggplants were infested by whiteflies at the 4-true leaf stage. Ten pairs of adult whiteflies
208 were left to produce eggs inside clipcages on the abaxial side of the youngest fully developed
209 leaf of each plant for 24 hours and 10 eggs were monitored until adult emergence. A newborn
210 female and male were placed on a new leaf and their offspring monitored for 30 days. Pre-
211 reproductive period, larvae viability, female fecundity and fertility were studied (n=16).

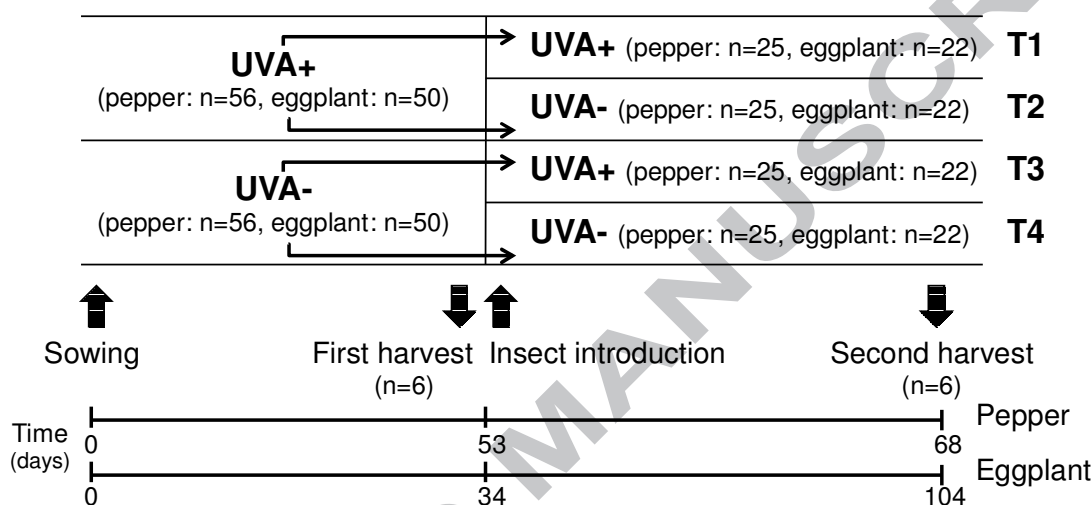
212 2.4. Experimental design

213 Pots with seeds were placed inside cages and plants were grown from seeds under two
214 different radiation regimes, either with supplemental (UVA+) or near zero UV-A radiation
215 (UVA-). At a 10-true leaf stage (53 days) for peppers and 4-true leaf stage (34 days) for
216 eggplants, half of the plants of each cage were moved from the UVA+ to the UVA- treatment
217 and vice versa. Some of the plants were infested by aphids (n=19) or whiteflies (n=16) to
218 study the performance of insects. In this way, we had four UV-A treatments: positive control
219 UVA+/UVA+, plants grown under supplemental UV-A radiation for the entire growth cycle;
220 negative control UVA-/UVA-, plants grown at near zero UV-A radiation for the entire
221 growth cycle; UVA+/UVA-, plants grown under supplemental UV-A radiation before insect
222 introduction and at near zero UV-A after insect introduction; and UVA-/UVA+, plants grown
223 at near zero UV-A radiation before insect introduction and under supplemental UV-A after
224 insect introduction. Figure 2 represents a timeline diagram of the experimental procedure.
225 Stem height, and leaf length and width were monitored weekly using a ruler (n=6). The
226 relationship between our measurements and actual leaf area (cm^2) was calculated by scanning
227 10 leaves of different stages of each plant species and contouring them with Adobe Acrobat
228 software (Pepper: 0.66 ± 0.01 . Eggplant: 0.73 ± 0.01). Experiments were repeated twice over
229 one year. Leaf material harvested throughout the experiment was either snap-frozen and
230 maintained at -80°C or air-dried 70°C as relevant for further analyses.

231 Figure 2. Timeline diagram of the experimental design, showing the four different UV-A
232 treatments (T1: UVA+/UVA+, plants grown under supplemental UV-A radiation for the

233 entire growth cycle; T2: UVA+/UVA-, plants grown under supplemental UV-A radiation
 234 before insect introduction and near zero UV-A after insect introduction; T3: UVA-/UVA+,
 235 plants grown near zero UV-A radiation before insect introduction and under supplemental
 236 UV-A after insect introduction and T4: UVA-/UVA-, plants grown near zero UV-A radiation
 237 for the entire growth cycle), dates of insect infestation to study the performance of aphids and
 238 whiteflies and plant harvests for peppers and eggplants. The arrows refer to the moment when
 239 half of the plants of each treatment were moved from treatment UVA+ to UVA- and vice
 240 versa.

241



243 2.5. Plant harvesting

244 Plants from the two species were harvested at two different growth stages for determining
 245 biomass and content of chemical compounds (Figure 2). Plants were harvested from each of
 246 the treatment cages at the 10-true leaf stage (53 days after sowing) for peppers plants and 4-
 247 true leaf stage (34 days after sowing) for eggplants (n=6). All leaves from each plant were
 248 collected for subsequent chemical analyses. Further plants from the treatments were
 249 harvested at 18-true leaf stage for peppers (68 days after sowing) and at 12-true leaf stage for
 250 eggplants (104 days after sowing). This involved plants from each treatment including those
 251 infested with insects and those not (as above, n=6).

252 2.6. Plant biochemical analysis

253 2.6.1. Secondary metabolites

254 Frozen samples were subsequently freeze-dried for 48 hours and leaf material homogenised
 255 with a pestle and mortar. Samples were analysed for secondary metabolites by extraction in
 256 70% methanol of freeze-dried samples (100 mg), as described by Comont *et al.* (2012).
 257 Supernatants were dried using a Savant SpeedVac SPD121P vacuum centrifuge (Thermo
 258 Scientific, Massachusetts, USA) before re-suspension in 500 μ L 70% methanol. The solid-
 259 phase extraction was performed using a Sep-Pak Vac 500 mg C18 column (Waters Ltd.,
 260 Elstree, UK) before vacuum centrifugation of the sample to complete dryness. Dried pellets

261 were suspended in 500 μL 100% methanol and analysed *via* high pressure liquid
262 chromatography (HPLC) with a system comprising a Waters 515 pump, a Waters 717plus
263 autosampler, a Waters 996 photodiode array detector and a Waters C_{18} Nova-Pak radial
264 compression column (C_{18} 4.0 μm , 8.0x100mm cartridge) (Waters Ltd., Elstree, UK) with an
265 injection volume of 30 μL and a flow rate of 2 mL min^{-1} . The mobile phase consisted of 5%
266 acetic acid (solvent A) and 100% methanol (solvent B) with a linear gradient from 5 to 75%,
267 B in A, over 35 min. Peak integration was performed using the Empower software. Liquid
268 chromatography-mass spectrometry (LC-MS) was performed to identify the major
269 compounds. A Thermo Finnigan LC-MS system (Finnigan Surveyor LC pump plus, PDA
270 plus detector, Finnigan LTQ linear ion trap) (Thermo Scientific, Massachusetts, USA) and a
271 Waters Nova-Pak C_{18} 4.0 μm , 3.9x100 mm column was used with an injection volume of 10
272 μL and a flow rate of 1 mL min^{-1} . The mobile phase consisted of purified water-0.1% formic
273 acid (solvent A) and MeOH-0.1% formic acid (solvent B) with a linear gradient from 5 to
274 65%, B in A, over 60 min. Phenolics were characterised by UV absorption spectra, MS
275 fragmentation patterns in negative ion mode and comparison with standards and previously
276 reported data in the literature (Clifford *et al.*, 2003; Stommel *et al.*, 2003; Marín *et al.*, 2004;
277 Park *et al.*, 2012).

278 2.6.2. Soluble sugars

279 Air dried samples (100 mg) were extracted in 3 mL of distilled water at 80 °C three times.
280 Extracts were centrifuged for 10 min at 10,000 rpm. Supernatants were retained, combined
281 and frozen until the analysis. Then 50 μL of sample were added to 950 μL of a buffer
282 comprising 5 mM H_2SO_4 with a 5 mM crotonic acid internal standard. Samples were
283 analysed *via* HPLC comprising a Jasco LG-980-02 ternary gradient unit, a Jasco PU-1580
284 pump, a Jasco AS-1555 sampler and a Jasco RI-2031 detector (Jasco Ltd., Essex, UK).
285 Injection volume was 25 μL . Sugars were identified by comparison with an internal library of
286 standard compounds (Comont *et al.*, 2012).

287 2.6.3. Free amino acid and proteins

288 Freeze-dried plant material (100 mg) was extracted in 4 mL of boiling distilled water for 25
289 minutes. Extracts were allowed to cool and a 1.5 mL aliquot was centrifuged to clarify the
290 solution, following the methodology described by Winters *et al.* (2002). Amino acid
291 absorbance was measured at 570 nm using an Ultrospec 4000 UV/Vis spectrophotometer (GE
292 Healthcare, Buckinghamshire, England). Histidine was used for the calibration curve as most
293 amino acids have the same response. Total proteins were extracted from 100 mg of freeze-
294 dried sample by grinding in 1.8 mL Mclivaine buffer pH 7 containing 50 mM ascorbic acid,
295 and 0.2 mL 20% lithium dodecyl sulphate. Protein content was analysed by the Lowry
296 protein assay (Lowry *et al.*, 1951) following precipitation of protein in extracts with 20%
297 trichloroacetic acid, 0.4% phosphotungstic acid and resuspension in 0.1 M NaOH. Absorbance
298 was measured at 700 nm with a μQuant microtitre plate reader spectrophotometer (Bio-Tek
299 Instruments Inc., Winooski, USA). Protein contents were determined against a bovine serum
300 albumin calibration curve.

301 2.6.4. Photosynthetic pigments

302 Chlorophyll *a*, chlorophyll *b*, chlorophylls *a+b* and carotenoid contents were analysed in
 303 freeze-dried sample extracts. Leaf material (50 mg) was extracted in 80% acetone and
 304 supernatants were diluted 1:15 in 80% acetone with absorbance measured at 470, 646.6,
 305 663.6 and 750 nm using an Ultrospec 4000 UV/Vis spectrophotometer (GE Healthcare,
 306 Buckinghamshire, England). Pigment contents were determined using equations by
 307 Lichtenthaler (1987) and Porra *et al.* (1989).

308 2.7. Data analysis and statistics

309

310 Data were transformed when necessary with either $\sqrt{(x + 0.5)}$, x^2 , $\ln(x + 1)$ or $2 \cdot \arcsin \sqrt{x}$ in
 311 the case of percentage data to decrease heteroscedasticity and improve normal distribution.
 312 All the parameters were then analysed using IBM Statistics SPSS 21.0 software (SPSS, 2013)
 313 with one-way ANOVA followed by *t*-test ($p \leq 0.05$) to assess differences prior to exchange of
 314 plants or pairwise comparison for least significant differences (LSD) ($p \leq 0.05$) to test
 315 differences after the exchange of plants. If data did not follow a normal distribution, a non-
 316 parametric Kruskal-Wallis *H* or Mann-Whitney *U* test ($p \leq 0.05$) was performed. Stem height
 317 and leaf area over the crop cycle (repeated measures over time) were assessed with ANOVA
 318 univariate repeated measures analysis ($p \leq 0.05$) using SuperANOVA v. 1.11 software for
 319 Macintosh (Abacus Concepts, 1989).

320

321

322 3. Results

323

324 3.1. Plant height and leaf area

325

326 Addition of UV-A to pepper plants over the entire plant growth cycle (UVA+/UVA+) caused
 327 a significant reduction in plant height (Treatment: $F=15.399$, 3 df, $p<0.001$. Time:
 328 $F=137.122$, 6 df, $p<0.001$. Time x Treatment: $F=7.311$, 8 df, $p<0.001$). By 68 days, plants
 329 grown with supplemental UV-A were 57% shorter compared to plants grown at near zero
 330 UV-A (23.9 cm vs. 37.7 cm) (Supplementary Figure 1). Pepper leaf area appeared lower with
 331 UV-A but not significantly different (Treatment: $F=2.618$, 3 df, $p=0.068$. Time: $F=262.928$, 6
 332 df, $p<0.001$. Time x Treatment: $F=1.271$, 8 df, $p=0.267$) when compared to the near zero
 333 UV-A treatment (Supplementary Figure 1).

334

335 Eggplants exposed to UV-A were shorter from 84 days onwards although not significantly
 336 (Treatment: $F=0.018$, 3 df, $p=0.997$. Time: $F=311.450$, 11 df, $p<0.001$. Time x Treatment:
 337 $F=1.575$, 29 df, $p=0.042$). By the end of the experiment, plants exposed to supplemental UV-
 338 A during their entire cycle were 23% shorter than plants that had been grown at near zero
 339 UV-A (50.5 cm vs. 62.2 cm) (Supplementary Figure 1). For leaf area no significant effects
 340 were observed with UV-A (Treatment: $F=0.191$, 3 df, $p=0.901$. Time: $F=262.753$, 11 df,
 341 $p<0.001$. Time x Treatment: $F=1.528$, 29 df, $p=0.054$) (Supplementary Figure 1). Later
 342 addition of UV-A when insects were introduced to plants (53-68 days for aphids and 34-104
 343 days for whiteflies) did not alter the height or leaf area responses observed above.

344

345 3.2. Insect responses

346

347 For aphids, the pre-reproductive period (d) from birth to adult stage was similar in all
 348 treatments ($H=2.656$, 3 df, $p=0.448$) (Table 2). However, effective fecundity (Md) was
 349 significantly higher ($F=2.888$, 70(3) df, $p=0.042$) in early supplemental UV-A treatment
 350 scenario compared to the near zero UV-A treatment (UVA-/UVA-) (Table 2 and Figure 3).
 351 This latter treatment lowered intrinsic rate of natural increase (r_m : $F=2.974$, 70(3) df,
 352 $p=0.037$) as well as mean relative growth rate (RGR : $F=2.974$, 70(3) df, $p=0.037$) when
 353 compared to pepper plants exposed to UV-A during early growth (UVA+/UVA-, Table 2).
 354 UV-A treatment after insect infestation had no effects on aphid fecundity and development
 355 (Figure 3).

356

357 The response of whiteflies to UV-A exposure was different to that of aphids. The pre-
 358 reproductive period (d) from birth to adult stage was significantly shortened by two days
 359 ($H=10.409$, 3 df, $p=0.015$) at near zero UV-A during insect development on plants (UVA-/
 360 UVA- and UVA+/UVA-) (Table 2). Direct exposure of whiteflies to supplemental UV-A on
 361 plants raised at near zero UV-A (UVA-/UVA+) significantly lowered fecundity -egg
 362 numbers- compared to all other treatments ($F=13.256$, 60(3) df, $p<0.001$) (Table 2 and Figure
 363 3). Moreover, egg numbers were significantly lower in treatments UVA+/UVA+ and UVA-/
 364 UVA+, 47% and 123% respectively, when compared to insects maintained on plants raised
 365 at near zero UV-A over the entire experiment (UVA-/UVA-). Supplemental UV-A exposure
 366 also lowered egg fertility ($F=6.254$, 60(3) df, $p=0.001$) (Table 2). This resulted in a
 367 significantly lower ($F=14.380$, 60(3) df, $p<0.001$) number of larvae in the treatments where
 368 insects were exposed to UV-A, regardless of the previous conditions in which eggplants were
 369 raised (treatments UVA+/UVA+ and UVA-/UVA+, Table 2). UV-A treatment after insect
 370 infestation had a negative impact on whitefly fecundity, fertility and development (Figure 3).

371

372 Table 2. Life parameters of *Myzus persicae* and *Bemisia tabaci* raised under four different
 373 UV-A radiation regimes. Different letters stand for statistical differences ($p\leq 0.05$).

374

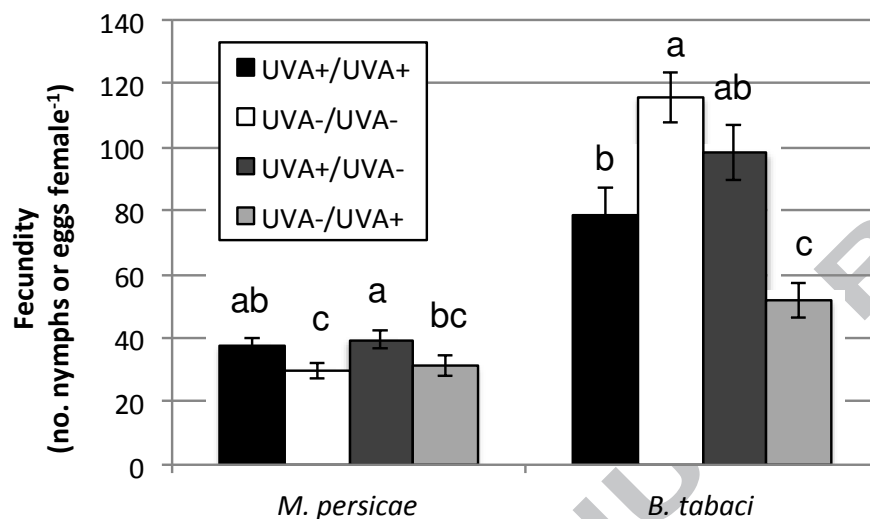
Insect	Parameters	UVA+/UVA+	UVA-/UVA-	UVA+/UVA-	UVA-/UVA+
<i>M. persicae</i>	d^a	8.89±0.15	8.71±0.17	8.63±0.14	8.74±0.15
	Md^b	37.53±2.57 ab	29.71±2.41 c	39.32±2.88 a	31.26±3.18 bc
	Td^c	12.05±0.20	11.80±0.23	11.70±0.19	11.84±0.20
	r_m^d	0.298±0.006 ab	0.284±0.007 b	0.310±0.006 a	0.283±0.010 b
	RGR^e	0.346±0.007 ab	0.330±0.008 b	0.361±0.007 a	0.329±0.011 b
<i>B. tabaci</i>	Viability ^f	72.43±10.48	81.38±8.37	77.86±8.78	75.71±6.61
	d	26.99±0.89 a	24.40±0.48 b	24.66±0.46 b	26.94±0.84 a
	No. eggs	78.69±8.12 b	115.69±7.90 a	98.06±8.72 ab	51.88±5.58 c
	No. larvae	50.69±7.22 b	87.44±8.25 a	73.81±9.54 a	25.94±3.25 c
	Fertility ^f	60.30±4.91 b	73.48±3.51 a	72.12±4.10 a	50.31±4.23 b

375 ^a days, ^b effective fecundity, ^c mean generation time, ^d intrinsic rate of natural increase, ^e mean
 376 relative growth rate, ^f %

377

378 Figure 3. Comparison between *M. persicae* and *B. tabaci* fecundity, showing the number of

379 nymphs and eggs per female on peppers and eggplants, respectively, under four different UV-
 380 A radiation regimes. Bars refer to standard errors and different letters stand for statistical
 381 differences ($p \leq 0.05$).



382

383

384 3.3. Biochemical responses to plant and insect UV-A exposure

385

386 3.3.1. Secondary metabolites

387 HPLC and LC-MS analysis revealed that there were two hydroxycinnamic acids and four
 388 flavonoids identifiable in pepper leaves. Analysis of eggplants revealed phenolics belonging
 389 to three classes (chlorogenic acid isomers, hydroxycinnamic acid amide conjugates and
 390 isochlorogenic acid isomers), as well as 3-*O*-feruloylquinic acid, which were determined
 391 based on HPLC elution times, UV spectra and LC-MS fragmentation data (Supplementary
 392 Table 1). Two kaempferol-hexosides with UV absorption maxima at 265 and 349 nm were
 393 also identified on the basis of their MS₂, however signals were too low to permit effective
 394 quantification of these compounds.

395 Secondary metabolites were increased in peppers by longer term UV-A exposure (68 days)
 396 but this depended on time of harvest and whether plants were simultaneously exposed to
 397 insects. Total content was similar under both UV-A regimes at 53 days ($t=0.947$, 10 df,
 398 $p=0.366$) (Figure 4a). However, when plants were harvested at 68 days, the four main
 399 flavonoid contents of pepper plants previously exposed to UV-A and later moved to a near
 400 zero UV-A regime (UVA+/UVA-) were comparable to levels found in those that had been
 401 grown entirely without UV-A radiation (UVA-/UVA-). This implies that phenolic expression
 402 declined when UV-A radiation was withdrawn. Pepper plants grown initially without UV-A
 403 and subsequently transferred to UV-A (UVA-/UVA+) also showed phenolic levels that were
 404 significantly higher than plants continuously grown under supplemental UV-A
 405 (UVA+/UVA+) (Compound 2: $F=3.987$, 20(3) df, $p=0.022$. Compound 3: $F=5.229$, 20(3) df,
 406 $p=0.008$. Compound 4: $F=11.145$, 20(3) df, $p<0.001$. Compound 5: $F=20.618$, 20(3) df,
 407 $p<0.001$. Compound 6: $F=35.214$, 20(3) df, $p<0.001$. Total: $F=29.945$, 20(3) df, $p<0.001$)
 408 (Figure 4a). Results for pepper suggest rapid acclimation to UV-A with aphid introduction

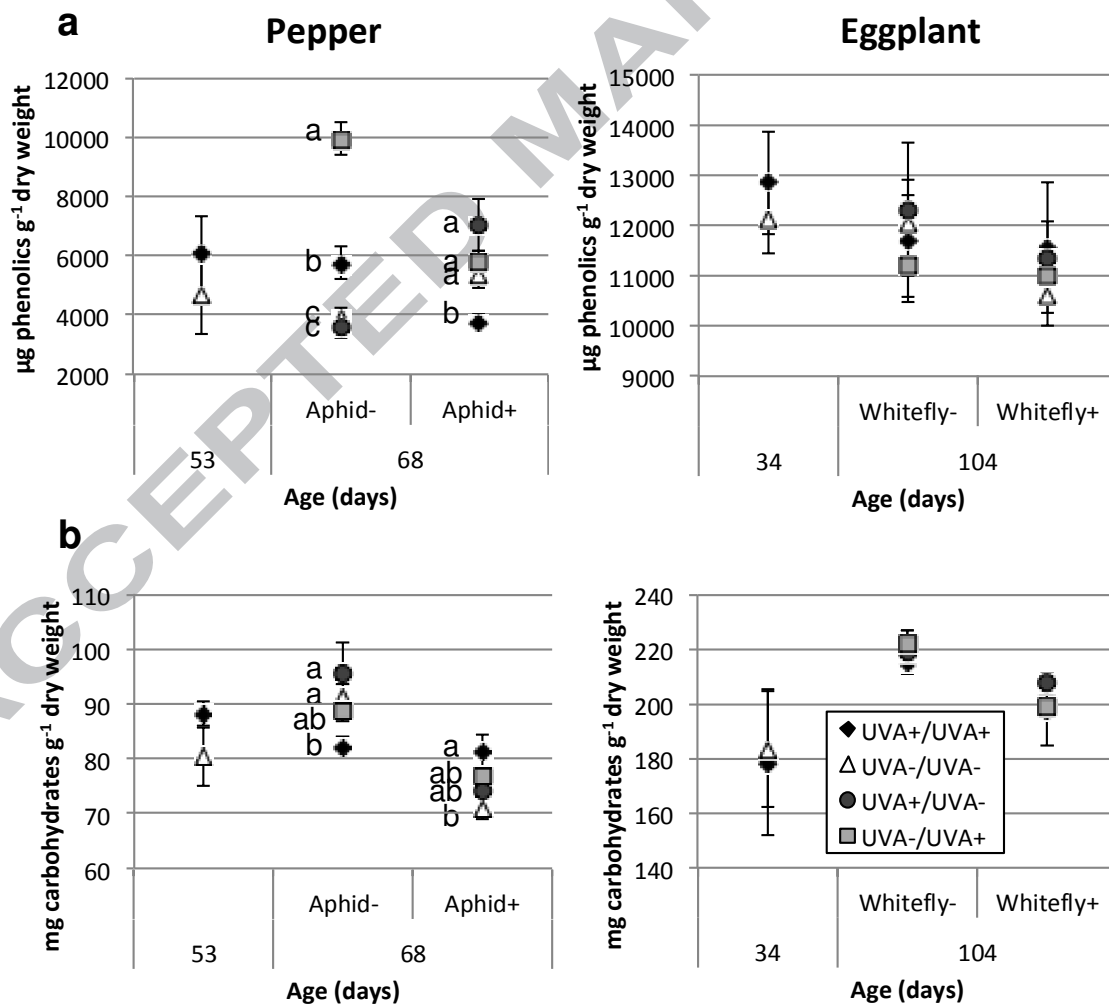
409 and damage influencing flavonoid profiles, as significantly higher levels were found in plants
 410 exposed to supplemental UV-A early but withdrawn from this treatment (UVA+/UVA-)
 411 (Compound 4: $F=4.632$, 20(3) df, $p=0.013$. Compound 5: $F=7.755$, 20(3) df, $p=0.001$.
 412 Compound 6: $F=7.884$, 20(3) df, $p=0.001$. Total: $F=10.546$, 20(3) df, $p<0.001$) (Figure 4a).
 413 N-caffeoylputrescine content in both uninfested and infested plants did not differ
 414 significantly.

415

416 Addition of UV-A radiation did not affect eggplant phenolic expression after the first harvest
 417 (34 days) prior to whitefly infestation ($t=0.697$, 10 df, $p=0.502$) (Figure 4a). In contrast to
 418 pepper plants, eggplant phenolic compounds were unaffected by treatment over the duration
 419 of the experiment ($F=0.306$, 20(3) df, $p=0.821$) (Figure 4a). As seen in Figure 4a, whitefly
 420 infestation did not appear to influence these patterns ($F=0.193$, 20(3) df, $p=0.900$).

421

422 Figure 4. Total phenolic (a) and soluble carbohydrate content (b) of pepper and eggplant
 423 leaves grown under four different UV-A radiation and two herbivore regimes, and harvested
 424 at two dates. Bars refer to standard errors and different letters stand for statistical differences
 425 ($p\leq 0.05$).



426

427

428 3.3.2. Soluble carbohydrates

429

430 Data showed different carbohydrate profiles with species and treatments. Polymer content
431 was similar under all treatments at any harvest time for both species. Polymer content was
432 very high in eggplant leaves. Significantly lower levels of total non-structural sugars
433 (raffinose, sucrose, glucose and fructose) were observed in uninfested pepper plants grown
434 under treatment UVA+/UVA+ at 68 days ($F=3.484$, 20(3) df, $p=0.035$). Raffinose and
435 glucose in particular were significantly higher following treatment UVA-/UVA+ (Raffinose:
436 $F=3.440$, 20(3) df, $p=0.036$. Glucose: $F=5.365$, 20(3) df, $p=0.007$). For infested plants, total
437 non-structural levels were similar ($F=1.205$, 20(3) df, $p=0.334$) although sucrose content was
438 significantly higher in treatments where aphids were grown under supplemental UV-A
439 ($F=3.227$, 20(3) df, $p=0.044$). No differences were found at any date in eggplant non-
440 structural sugars. When total sugar content was analysed, UVA+/UVA+ level was lowest in
441 uninfested peppers ($F=4.622$, 20(3) df, $p=0.013$) but highest in infested plants ($F=3.402$,
442 20(3) df, $p=0.038$) (Figure 4b). Carbohydrate levels under herbivory were lower than those
443 observed in uninfested peppers possibly due to aphid feeding (Figure 4b). Conversely, no
444 differences were found among treatments on eggplants samples both uninfested and infested
445 by whiteflies (Figure 4b).

446

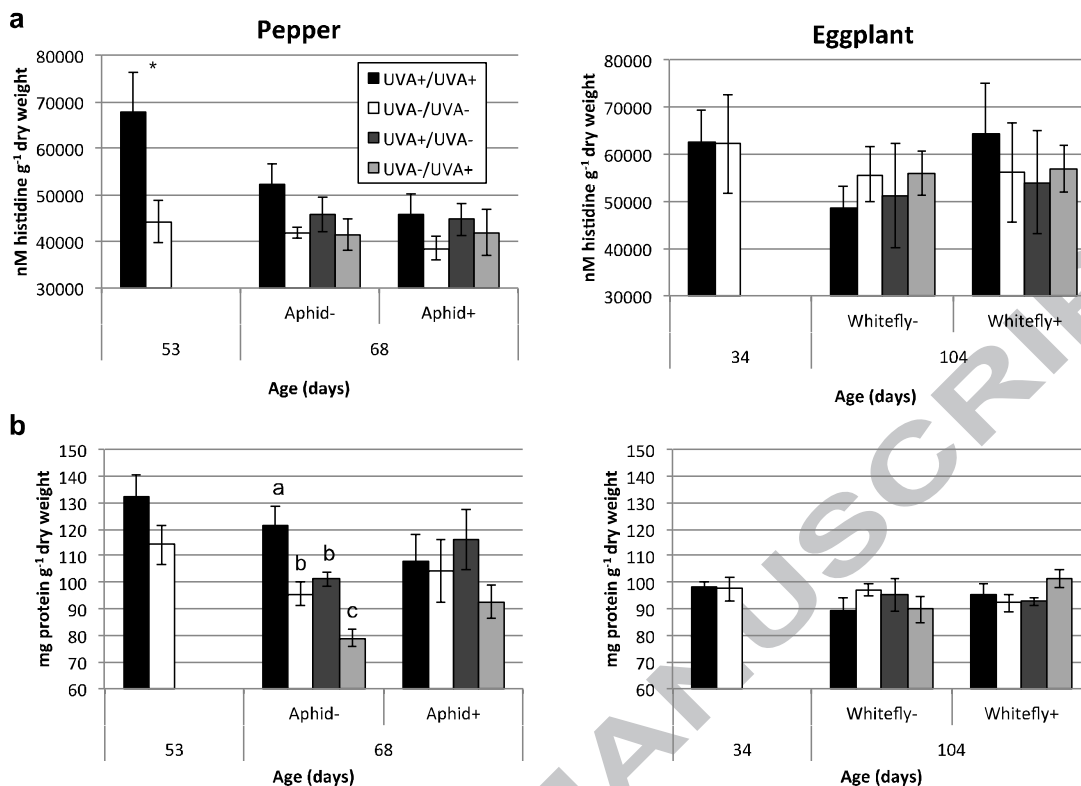
447 3.3.3. Free amino acid and proteins

448

449 At 53 days, pepper plants exposed to supplemental UV-A had significantly higher levels of
450 free amino acids ($t=2.755$, 10 df, $p=0.020$). However, this trend was not significant at 68 days
451 in uninfested peppers ($F=1.871$, 20(3) df, $p=0.167$) (Figure 5a). Infested plants had a lower
452 level compared to uninfested plants possibly due to *in situ* aphid feeding activity but no
453 differences could be found between different radiation regimes ($F=0.609$, 20(3) df, $p=0.617$)
454 (Figure 5a). A similar pattern was observed for total protein content with a significantly
455 higher amount in plants continuously grown under supplemental UV-A at 68 days
456 ($F=15.062$, 20(3) df, $p<0.001$) (Figure 5b). No differences were observed between treatments
457 in eggplants for free amino acids (34 days: $t=0.291$, 10 df, $p=0.777$. 104 days uninfested:
458 $F=0.255$, 20(3) df, $p=0.857$. 104 days infested: $F=0.217$, 20(3) df, $p=0.883$) and total proteins
459 (34 days: $t=0.245$, 10 df, $p=0.812$. 104 days uninfested: $F=0.783$, 20(3) df, $p=0.517$. 104 days
460 infested: $F=1.634$, 20(3) df, $p=0.213$) when exposed to UV-A and/or feeding by whiteflies
461 (Figure 5a and b).

462

463 Figure 5. Free amino acids expressed as histidine (a) and total protein (b) content of pepper
464 and eggplant leaves grown under four different UV-A radiation and two herbivore regimes,
465 and harvested at two dates. Bars refer to standard errors and asterisks stand for statistical
466 differences ($p\leq 0.05$).



467

468

469 3.3.4. Photosynthetic pigments

470

471 There was no significant effect of UV-A exposure on pepper plant photosynthetic pigments
 472 either at any harvest time or under aphid herbivory (Supplemental Table 2). In contrast,
 473 eggplant leaves exposed to supplemental UV-A had lower chlorophyll content radiation at 34
 474 days (Chlorophyll *a*: $t=-2.531$, 10 df, $p=0.030$. Chlorophylls *a+b*: $t=-2.426$, 10df, $p=0.036$)
 475 and under whitefly infestation at 104 days (Chlorophyll *a*: $F=4.613$, 20(3) df, $p=0.013$.
 476 Chlorophyll *b*: $F=3.887$, 20(3) df, $p=0.024$. Chlorophylls *a+b*: $F=4.994$, 20(3) df, $p=0.010$)
 477 (Supplemental Table 2). Carotenoids also showed significant accumulation at near zero UV-
 478 A (34 days: $t=-2.630$, 10 df, $p=0.025$. 104 days uninfested: $F=3.803$, 20(3) df, $p=0.026$. 104
 479 days infested: $F=4.467$, 20(3) df, $p=0.015$). Contents were highest for treatment UVA-/UVA-
 480 and mixed treatments where plants received both radiation regimes had intermediate contents
 481 (Supplemental Table 2). Chl *a/b* ratio was statistically equal in all treatments, ranging from
 482 2.3 to 2.5 in peppers and from 2.7 to 2.9 in eggplants.

483

484

485 4. Discussion

486

487 In the present work we investigated the effects of UV-A radiation on two key global pests,
 488 the aphid *M. persicae* and whitefly *B. tabaci* and their host plants, pepper and eggplant. Our
 489 aim was to determine how UV-A in the glasshouse environment influences plant growth and
 490 chemistry, and insect performance. This work was undertaken in cages placed in a glasshouse

491 facility where plants received UV-A radiation via artificial lamp sources. Although the glass
492 of the facility and filter-covered cages absorbed a considerable amount of radiation we cannot
493 neglect at least some natural UV reaching the plants. In particular a higher UV:PAR ratio
494 may have occurred at the start and end of each day because lamps were already switched on
495 early in the morning and after sunset. These diurnal changes in the UV:PAR ratio might have
496 influenced plant chemistry and insect response. However, UV irradiance reaching the plant
497 canopy was predominantly originating from the lamps (70 %) because sunlight was partially
498 filtered by greenhouse glass. Most (99%) of the UV radiation received by plants and insects
499 in the UVA+ treatment was UV-A. However, we must acknowledge the possibility of a small
500 amount of UV-B irradiance, well below ambient UV-B levels, present during our
501 experiments (Table 1). Considering our 14h photoperiod, our plants received $71.67 \text{ KJ m}^{-2} \text{ d}^{-1}$
502 of UV-A while only $0.55 \text{ KJ m}^{-2} \text{ d}^{-1}$ of UV-B, which is 0.76% of the total UV irradiance.
503 Therefore, we assume that any changes observed in plants and insects under the UVA+
504 treatment were predominantly elicited by UV-A. To our knowledge, this is the first study that
505 has looked at supplemental UV-A effects on plant-insect interactions in the glasshouse
506 environment, as opposed to previous research mainly focused on UV-B impacts (Hunt and
507 McNeil, 1999; Kittas *et al.*, 2006; Kuhlmann and Müller, 2009a, 2010; Paul *et al.*, 2011).

508

509 For both plants species studied, the supplemental UV-A treatment appeared to alter the size
510 and morphology over the entire crop cycle. Although plants had similar numbers of leaves,
511 pepper internodes were significantly shorter, similarly as previously reported in other plant
512 species (Kuhlmann and Müller, 2010; Comont *et al.*, 2012). For eggplants, plant height
513 appeared shortened but there were no significant effects on height or leaf area. This contrasts
514 with previous work focussing on enhanced UV-B impacts on reduced leaf area (Kittas *et al.*
515 2006). In the current study, chlorophyll and carotenoid contents were lowered in eggplant
516 with UV-A treatment at both harvest dates and under whitefly infestation, as found on
517 buckwheat or quinoa with supplemental UV-B (Gaberšcik *et al.*, 2002; González *et al.*,
518 2009). A reduction in chlorophyll has been proposed as an indicator of UV sensitivity (Smith
519 *et al.*, 2000).

520

521 The relevance of components of leaf chemistry was measured in order to try to interpret the
522 insect responses observed. Phenolic patterns in peppers changed in response to UV-A and
523 under herbivory. No secondary metabolite differences were observed during the earlier
524 harvest at 53 days prior to insect introduction but were apparent at 68 days. As expected, 5-
525 *O*-caffeoylquinic acid and flavonoid contents were significantly induced with enhanced UV-
526 A (Gaberšcik *et al.*, 2002, Izaguirre *et al.*, 2007; Mahdavian *et al.*, 2008; Kuhlmann and
527 Müller, 2009a, 2009b, 2010). In the absence of aphids at 68 days, evidence showed how
528 plants grown at near zero UV-A but later moved to a UV-A regime (treatment UVA-/UVA+)
529 had higher level of leaf secondary metabolites, which even exceeded the levels found in UV-
530 A treated plants over the entire crop cycle (UVA+/UVA+). This readiness of peppers to
531 induce 'sunscreen' compounds might be correlated with UV tolerance (Middleton and
532 Teramura, 1993; Harborne and Williams, 2000). Meanwhile, the flavonoid contents of plants
533 grown with supplemented UV-A but subsequently moved to near zero UVA- declined rapidly
534 to levels comparable to the control treatment UVA-/UVA- after stress recovery. Hence the

535 effect of UV-A was not cumulative over time (*cf.* Comont *et al.*, 2012). Besides UV-shielding
536 metabolites, elevated contents of phenolics have been proposed as antifeedants or
537 digestibility reducers (Ballaré *et al.*, 1996; Paul and Gwynn-Jones, 2003). Flavonoid levels
538 are thought to be an important factor in herbivore nutrition and they may be partially induced
539 by the same signaling pathway as UV protection, in which the jasmonic acid plays a key role
540 (Mackerness, 2000; Stratmann, 2003; Demukra *et al.*, 2010; Mewis *et al.*, 2012). Pepper
541 phenolics were affected by aphid feeding as seen previously in tobacco (Izaguirre *et al.*,
542 2007). Whether the flavonoids detected acted also as a defense against *M. persicae* needs
543 further investigation but results suggest aphid damage influencing their accumulation
544 compared to uninfested peppers. Indeed one of the flavonoids present in our samples,
545 luteolin-7-*O*-(2-*apiosyl*)glucoside, has been previously proposed as a deterrent compound
546 against the leafminer fly species *Liriomyza trifolii* Burgess (Diptera: Agromyzidae) in sweet
547 pepper leaves (Kashiwagi *et al.*, 2005). Phenolics found in eggplants were mainly
548 hydroxycinnamic acids, with 5-*trans*caffeoylquinic acid as the major compound (Stommel *et al.*,
549 2003). As opposed to peppers, no significant increases in secondary metabolites were
550 observed with UV-A or whitefly infestation in eggplants. However, induction of several
551 flavonoids has been stated to protect tissues from UV damage in this species (Toguri *et al.*,
552 1993). Past research has shown that eggplants already have high constitutive defences.
553 Exposure to high UV-B irradiances did not influence phenolic accumulation, leaf area and
554 Chl *a*/Chl *b* ratio (Smith *et al.*, 2000; González *et al.*, 2009). These results altogether may
555 indicate a high tolerance to UV irradiance in this species possibly related to its ancestral
556 origin from tropical regions.

557

558 Total non-structural carbohydrates were lowest in uninfested peppers grown under UV-A
559 during the complete duration of the experiment (68 days) compared to all other treatments.
560 Comont *et al.* (2012) also reported reductions in sucrose, glucose and fructose contents on
561 *Arabidopsis thaliana* L. following UV-B treatment although contrasting results have been
562 obtained on maize leaves (Barsig and Malz, 2000). However when insects were introduced,
563 sucrose content was significantly higher in treatments where *M. persicae* was grown under
564 UV-A. This might agree with previous research done under UV-B stress where higher soluble
565 sugar content, mainly sucrose, was observed under addition of UV-B (González *et al.*, 2009).
566 Carbohydrate accumulation may have affected aphid fitness because sucrose is a strong
567 feeding stimulant and the major component of the phloem sap of plants (Mittler *et al.*, 1970;
568 Srivastava and Auclair, 1971). Indeed when UV-A was withdrawn, adults produced less
569 progeny with lower growth rates. By contrast, eggplant soluble sugars were unaffected by
570 UV-A and total levels were similar at every harvest time and under whitefly herbivory,
571 displaying another reliable indicator to UV tolerance (González *et al.*, 2009).

572

573 Amino acids are the major nitrogen source for aphids. In our work, we observed significantly
574 higher free amino acids in pepper leaves exposed to UV-A radiation, suggesting that such
575 plants could be preferred by insects. Amino acids are an essential dietary component for *M.*
576 *persicae* growth (Dadd and Krieger, 1968) that has a mainly nutritive role in aphid feeding
577 (Srivastava and Auclair, 1975; Weibull, 1987). Nitrogen content is thought to act as a feeding
578 stimulant for insects (Schoonhoven *et al.*, 2006), being higher when high radiation intensities

579 are present in the environment (Roberts and Paul, 2006). It is likely that phloem quality under
580 supplemented UV-A conditions had a richer composition that may have triggered a positive
581 plant-mediated effect on *M. persicae* development and fecundity. Moreover, free amino acids
582 levels were unsurprisingly lower under herbivore attack due to aphid feeding. It should be
583 emphasized that here we focussed on the chemical composition of entire pepper leaves and
584 this may not necessary reflect that in the phloem sap (Kehr, 2006). Further studies should be
585 conducted to find out if the observed changes in leaf chemistry due to supplemental UV-A
586 radiation are reflective of the chemical changes in the phloem sap, extracted by stylectomy
587 (Kennedy and Mittler, 1953) or via leaf incisions (Milburn, 1970).

588

589 There were no differences according to UV-A in protein and free amino acid content in
590 eggplants. Very little is known about the impact of UV radiation on the composition of free
591 amino acids in phloem sap, but the same trend has been observed in other species of the
592 family Brassicaceae such as broccoli, where authors reported similar contents except for
593 increased proline under low UV-B compared to high levels of UV-B (Kuhlmann and Müller,
594 2009a, 2010).

595

596 The addition of UV-A to the environment had complex effects on aphids. Mainly, an indirect
597 plant-mediated impact on *M. persicae* effective fecundity was observed. The effective
598 fecundity measured was higher in early UV-A treatment scenarios compared to the near zero
599 UV-A treatment (UVA-/UVA-). This latter treatment also resulted in lowered intrinsic rate of
600 natural increase and mean relative growth rate when compared to the scenario where plants
601 had only been exposed to UV-A during early growth (UVA+/UVA-). This may indicate that
602 alterations in tissue chemistry occurred prior to aphid infestation and contributed to its
603 performance. The reduction in the population growth without UV-A exposure is in agreement
604 with findings previously reported for several aphid species (Antignus *et al.*, 1996; Chyzik *et*
605 *al.*, 2003; Díaz *et al.*, 2006; Kuhlmann and Müller, 2009a; Paul *et al.*, 2011; Legarrea *et al.*,
606 2012). The pre-reproductive period from birth to adult stage was similar for all treatments. In
607 contrast, results provided evidence that supplemental UV-A exposure had an impact on the
608 fitness of whiteflies, this contrasted with aphids. The pre-reproductive period was
609 significantly increased by two days with supplemental UV-A during insect growth on plants
610 regardless of the radiation regime before insect introduction (treatments UVA+/UVA+ and
611 UVA-/UVA+). Exposure of whiteflies to UV-A on plants raised at near zero UV-A (UVA-
612 /UVA+) significantly lowered the number of eggs compared to near zero UV-A for the entire
613 crop cycle (UVA-/UVA-). There was no statistically significant difference in the number of
614 eggs between treatments UVA-/UVA- and UVA+/UVA-, which supports the hypothesis that
615 this effect was not mediated by host cues as it did not depend on the UV-A regime the plants
616 had been grown under before whitefly infestation. This resulted in a significantly lower
617 fertility in the treatments where UV-A was supplemented during insect growth (Table 2).

618

619 When whiteflies were subjected to supplemental UV-A treatments, eggplants received
620 radiation at the same time although the chemical compounds involved in whitefly nutrition
621 that we analysed (free amino acids and sugars) were unaffected by supplemental UV-A. UV-
622 A radiation inside the clip-cages where insects were monitored was 0.00 W m^{-2} in the

623 treatment UVA- vs. 0.03 W m^{-2} in the treatment UVA+, a difference that may not be
624 sufficient to conclude that UV-A had a direct impact on whitefly performance. However, the
625 floor of the cages was aluminium and reflected part of the UV radiation into the clip-cages in
626 the supplemental UV-A treatment. Radiation transmitted through the leaves could reach the
627 ventral part of the whitefly nymphs and the radiation reflected by the floor reaching the
628 abaxial side of the leaves could irradiate the dorsum of whiteflies (Table 1). While results
629 indicate a possible negative effect of UV-A which cannot be explained by changes in plant
630 chemicals measured, we cannot dismiss the possibility of an effect triggered by aspects of
631 host plant chemistry that were not measured. Further work to isolate direct from plant-
632 mediated effects of UV-A radiation on whitefly performance should be conducted in the
633 future by irradiation of insects under a free-plant environment.

634

635 The effect of UV on the life processes of whiteflies has been little studied. Traditionally
636 research has focused on flight behavior in host choice assays, with more whiteflies being
637 trapped under environments with UV radiation (Antignus *et al.*, 1996; Costa and Robb, 1999;
638 Kuhlmann and Müller, 2009a), but to the best of knowledge, for the first time its performance
639 has been tested under different UV-A regimes. In past studies, it is likely that whiteflies were
640 driven by the radiation spectrum rather than by the plant chemistry as they tested orientation
641 and alighting (Kuhlmann and Müller, 2009b), whereas in our work insects were caged and
642 forced to feed on each plant. Whiteflies showed an explicit tendency to grow slower under
643 the UV-A source after insect infestation. This might be explained by the mechanism by
644 which UV radiation triggers a migratory behaviour (Mound, 1962; Coombe, 1982). However,
645 the absence of UV might have extended the mating period so whiteflies fed and laid eggs
646 over a greater period at near zero UV-A radiation.

647

648 Allocation of UV-A-shielding compounds responsible for physicochemical defense involved
649 some constrains on peppers, as plant growth decreased under high UV-A conditions. The
650 UV-induced phenolic pattern in pepper contrasted with lack of changes observed in
651 eggplants. In addition, this latter species also showed other characteristics present in plants
652 tolerant to high UV irradiances, such as no changes in leaf area and content of soluble
653 carbohydrates irrespective of UV-A exposure. We hypothesise that these findings might be
654 related to a high tolerance to UV-A. UV-A radiation altered the chemical composition of
655 pepper plants, with consequences to pest fitness. It is clear that UV-A enriched pepper
656 nutritional quality for aphids. In contrast for whiteflies, there was a direct negative effect of
657 UV-A rather than via tissue quality. As a whole, results reported in the two complexes
658 suggest that UV-mediated changes are highly dependent on the plant and insect studied.
659 Nevertheless, we believe that UV-absorbing nets might be a useful tool against aphids
660 without detrimental effects on crops. Further knowledge is needed to unravel the complete
661 role of UV-A radiation in plant-insect interactions, and to elucidate whether these responses
662 present interactions with effects occurring as a consequence of other fractions of the solar
663 spectrum.

664

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666

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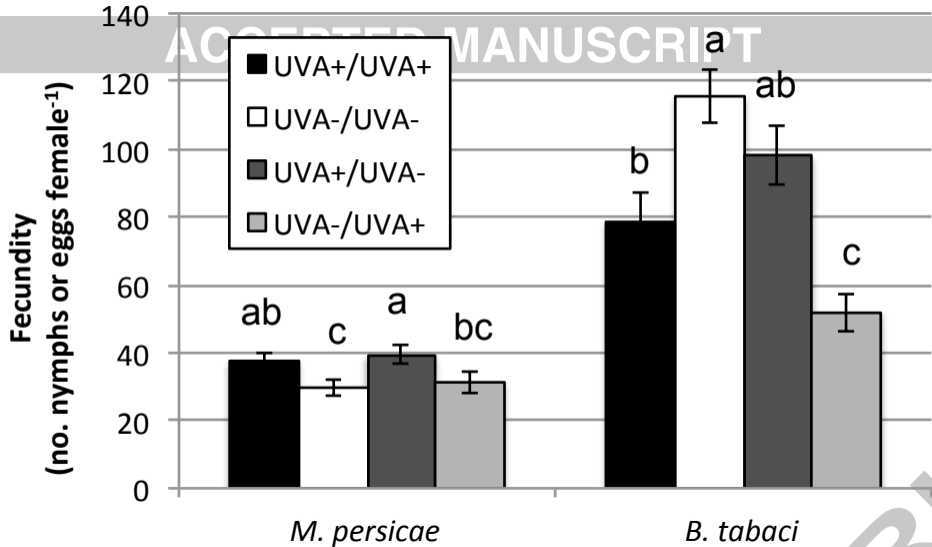
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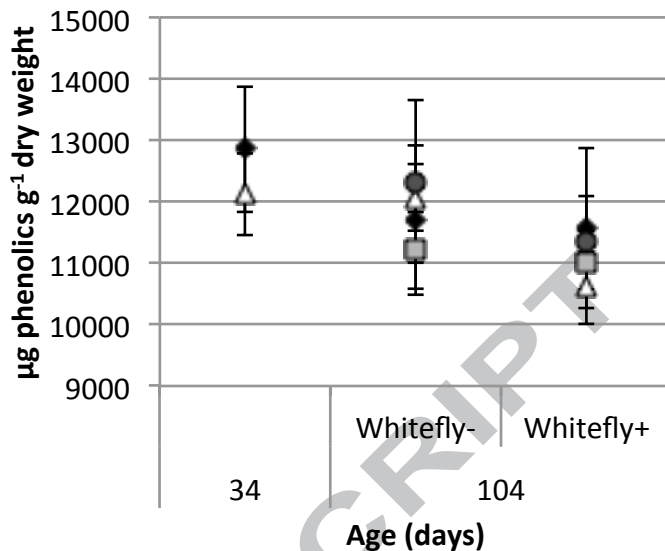
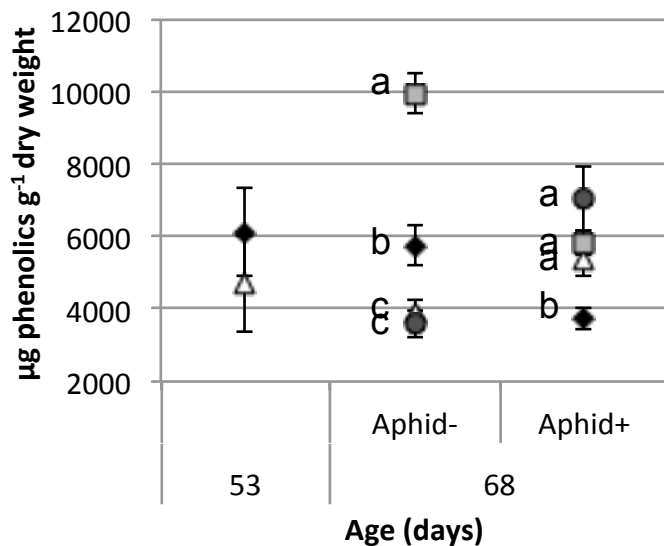
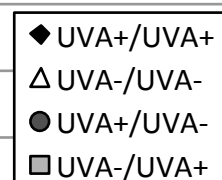
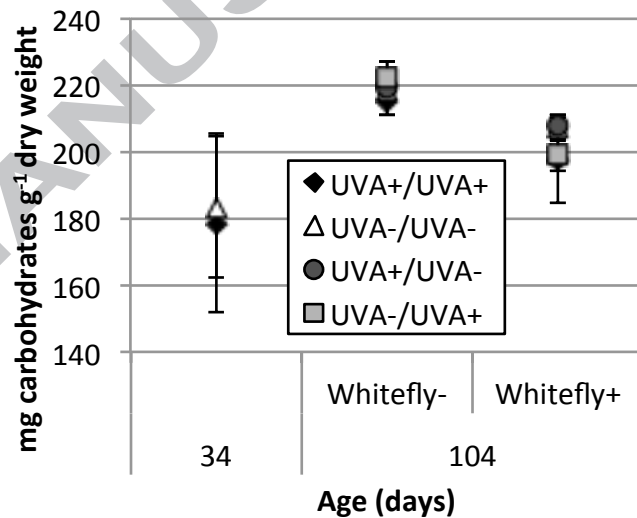
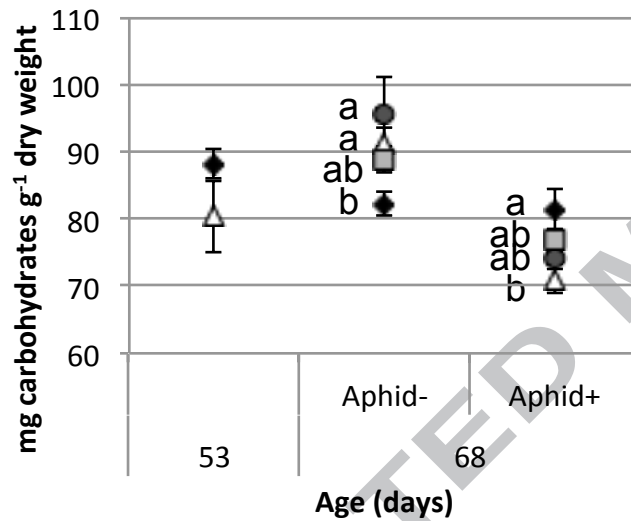
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a**Pepper**

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Eggplant**b**

925 Highlights:

- 926 • Supplemental UV-A causes a reduction in pepper stem height
- 927 • Aphids benefit from changes in pepper metabolites under supplemental UV-A
- 928 • There is a detrimental effect of UV-A radiation on whitefly performance
- 929 • UV-mediated changes appear to be highly dependent on each plant-insect complex

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