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

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## Accepted Manuscript

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

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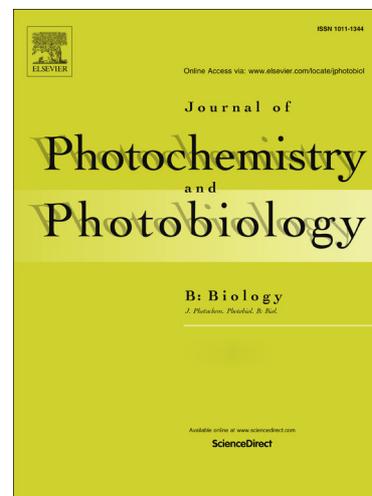
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1 **Impact of UV-A radiation on the performance of aphids and whiteflies and on the leaf**  
2 **chemistry of their host plants**

3

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18

## 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<sup>-1</sup>.

## 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<sup>-2</sup> d<sup>-1</sup> UV-A and 0.55 KJ m<sup>-2</sup> d<sup>-1</sup> UV-B for treatment UVA+, and 1.76  
166 KJ m<sup>-2</sup> d<sup>-1</sup> UV-A and 0.10 KJ m<sup>-2</sup> d<sup>-1</sup> 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<sup>-2</sup> d<sup>-1</sup>) 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<sup>-2</sup>) (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<sup>-2</sup> in treatment UVA+ and 0.002 W m<sup>-2</sup> 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.

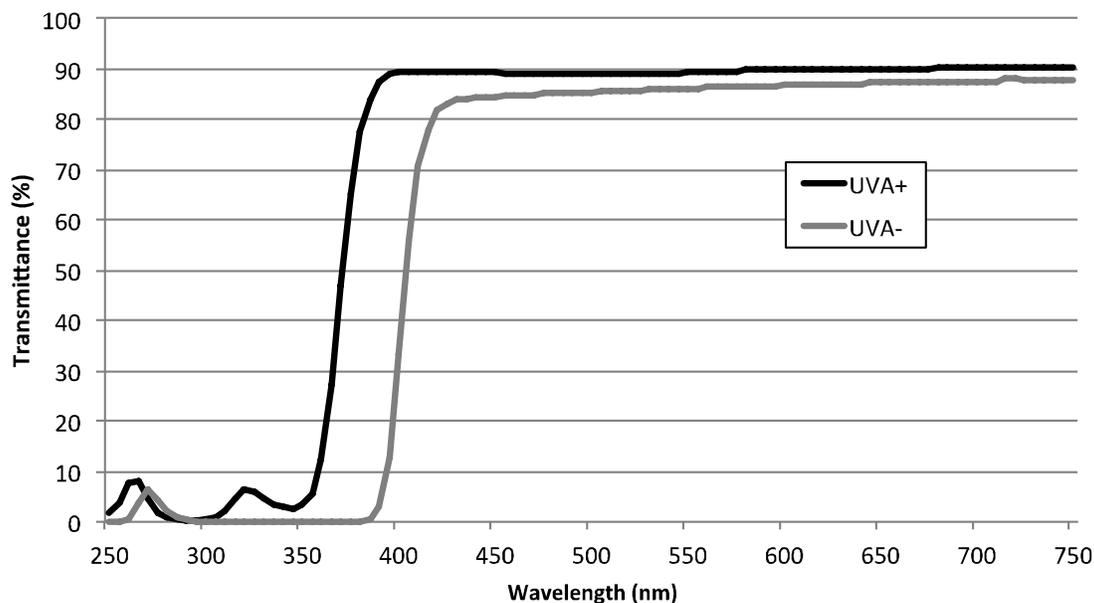
179 Table 1. Radiation conditions at canopy level outside and inside the experimental cages  
 180 (UVA+ and UVA- treatments), on the abaxial side of the leaves and through the leaves with  
 181 clip-cages where insects were monitored. Transmission percentages represent radiation  
 182 transmitted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

	Treatment UVA+			Treatment UVA-		
	PAR <sup>a</sup>	UV-A <sup>b</sup>	UV-B <sup>b</sup>	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 <sup>a</sup>  $\mu\text{mol m}^{-2} \text{s}^{-1}$  ( $\text{W m}^{-2}$ ), <sup>b</sup>  $\text{W m}^{-2}$

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 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).

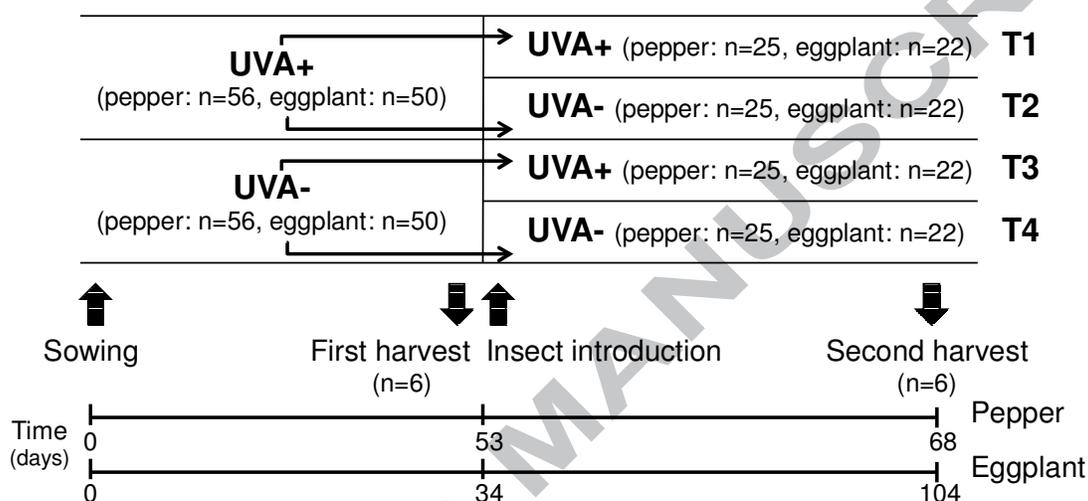
### 212 2.4. Experimental design

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 ( $\text{cm}^2$ ) was calculated by scanning  
227 10 leaves of different stages of each plant species and contouring them with Adobe Acrobat  
228 software (Pepper:  $0.66\pm 0.01$ . Eggplant:  $0.73\pm 0.01$ ). Experiments were repeated twice over  
229 one year. Leaf material harvested throughout the experiment was either snap-frozen and  
230 maintained at  $-80^\circ\text{C}$  or air-dried  $70^\circ\text{C}$  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



242

## 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  $\mu$ 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  $\mu\text{L}$  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  $\text{C}_{18}$  Nova-Pak radial  
264 compression column ( $\text{C}_{18}$  4.0  $\mu\text{m}$ , 8.0x100mm cartridge) (Waters Ltd., Elstree, UK) with an  
265 injection volume of 30  $\mu\text{L}$  and a flow rate of 2  $\text{mL min}^{-1}$ . 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  $\text{C}_{18}$  4.0  $\mu\text{m}$ , 3.9x100 mm column was used with an injection volume of 10  
272  $\mu\text{L}$  and a flow rate of 1  $\text{mL min}^{-1}$ . 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  $\mu\text{L}$  of sample were added to 950  $\mu\text{L}$  of a buffer  
282 comprising 5 mM  $\text{H}_2\text{SO}_4$  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  $\mu\text{L}$ . 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  $\mu\text{Quant}$  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

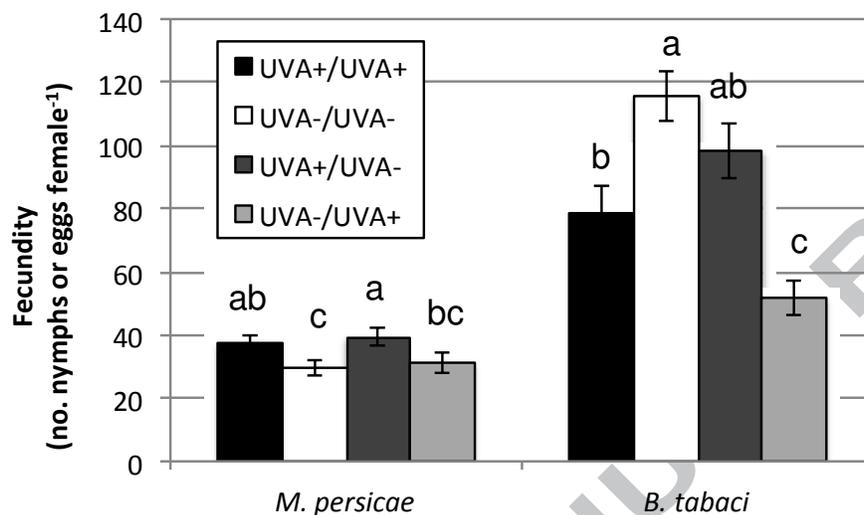
Insect	Parameters	UVA+/UVA+	UVA-/UVA-	UVA+/UVA-	UVA-/UVA+
<i>M. persicae</i>	$d^a$	8.89±0.15	8.71±0.17	8.63±0.14	8.74±0.15
	$Md^b$	37.53±2.57 ab	29.71±2.41 c	39.32±2.88 a	31.26±3.18 bc
	$Td^c$	12.05±0.20	11.80±0.23	11.70±0.19	11.84±0.20
	$r_m^d$	0.298±0.006 ab	0.284±0.007 b	0.310±0.006 a	0.283±0.010 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 <sup>f</sup>	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 <sup>f</sup>	60.30±4.91 b	73.48±3.51 a	72.12±4.10 a	50.31±4.23 b

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

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 MS<sub>2</sub>, 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

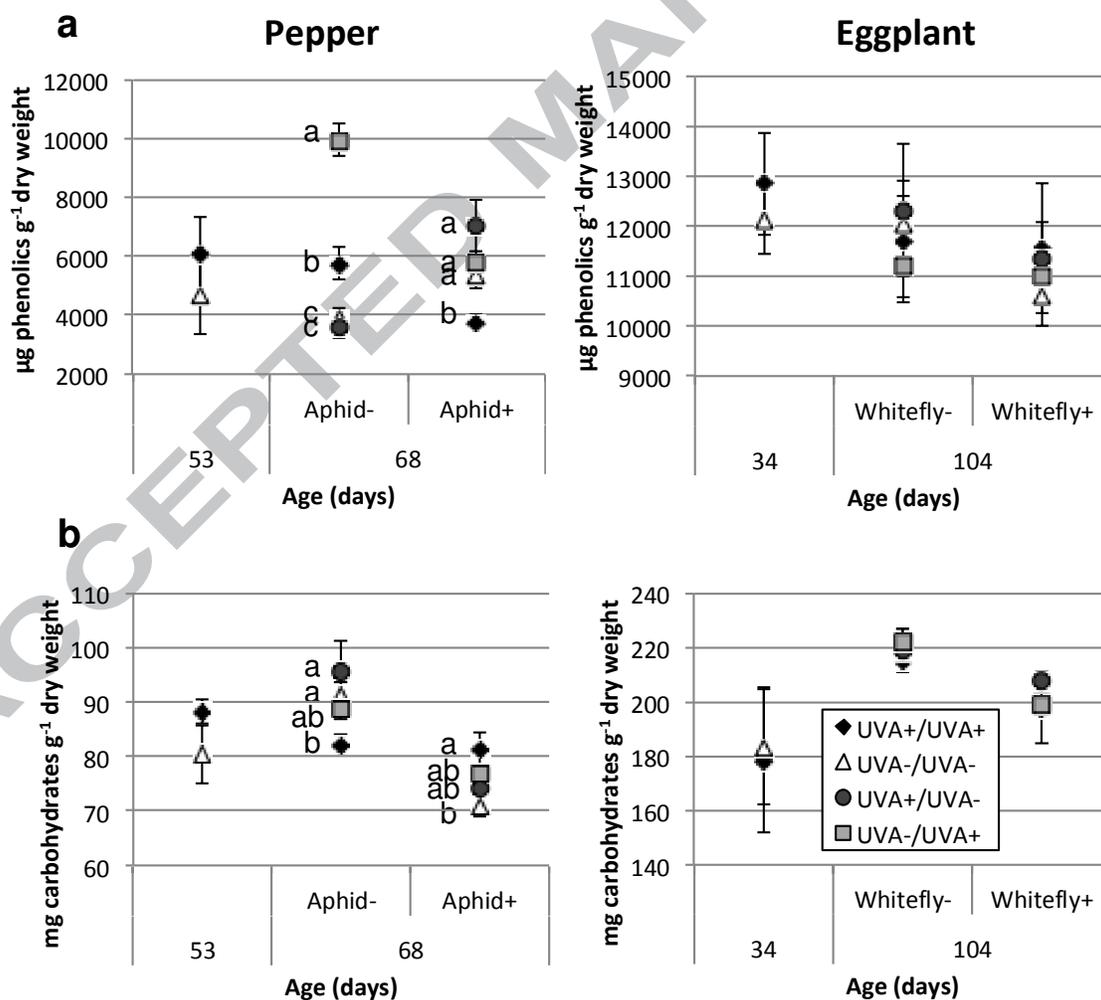
409 and damage influencing flavonoid profiles, as significantly higher levels were found in plants  
 410 exposed to supplemental UV-A early but withdrawn from this treatment (UVA+/UVA-)  
 411 (Compound 4:  $F=4.632$ , 20(3) df,  $p=0.013$ . Compound 5:  $F=7.755$ , 20(3) df,  $p=0.001$ .  
 412 Compound 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

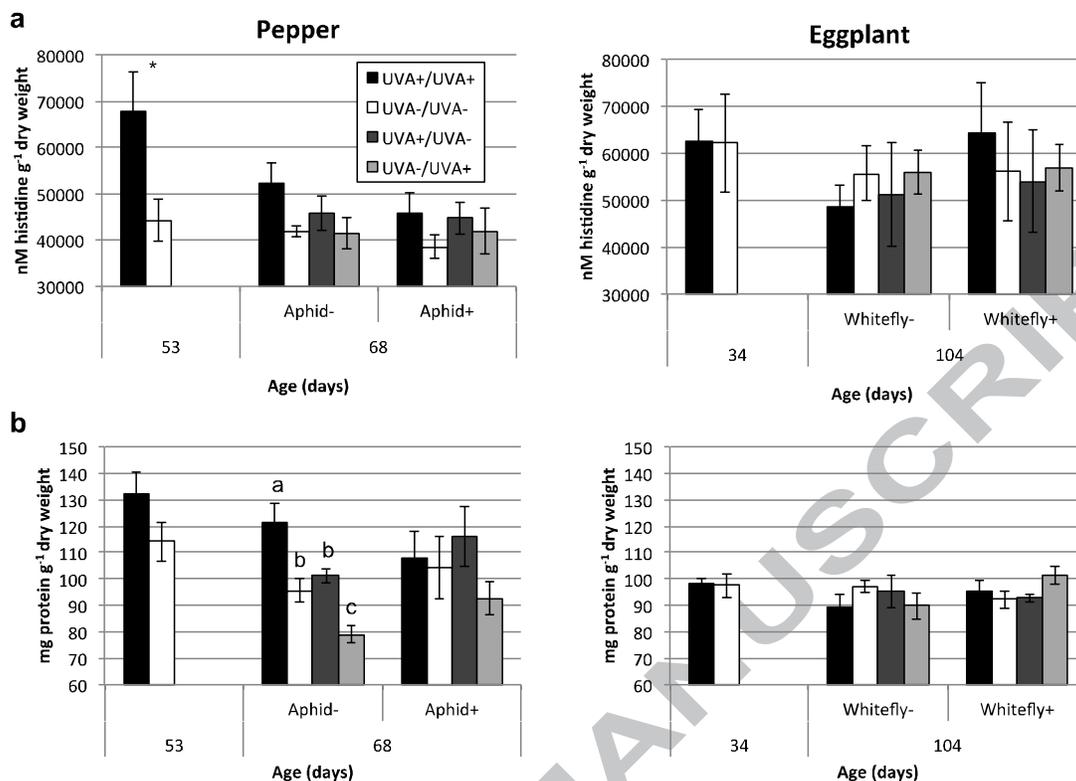
## 447 3.3.3. Free amino acid and proteins

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; Legarra *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  $0.00 \text{ W m}^{-2}$  in the

623 treatment UVA- vs.  $0.03 \text{ W m}^{-2}$  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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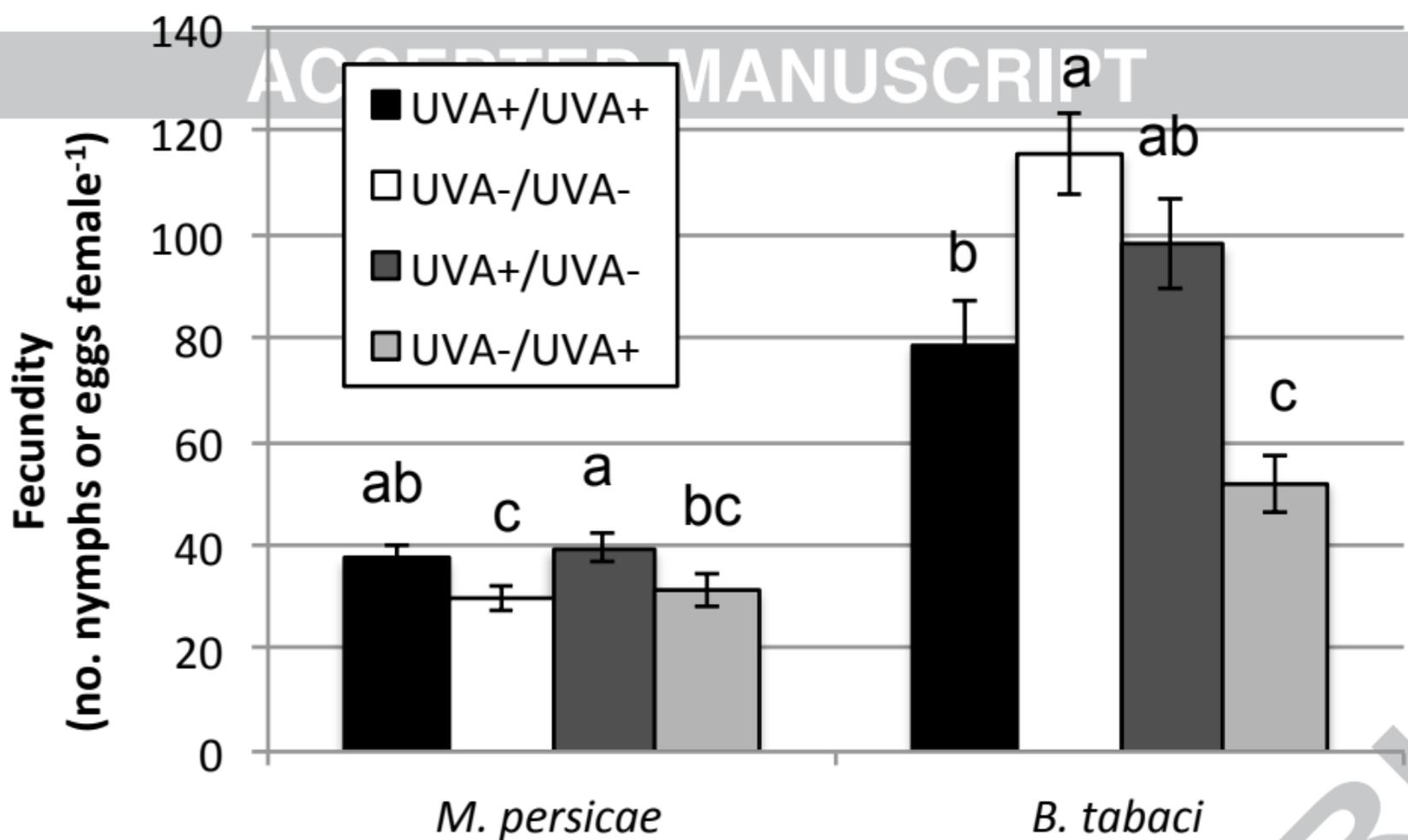
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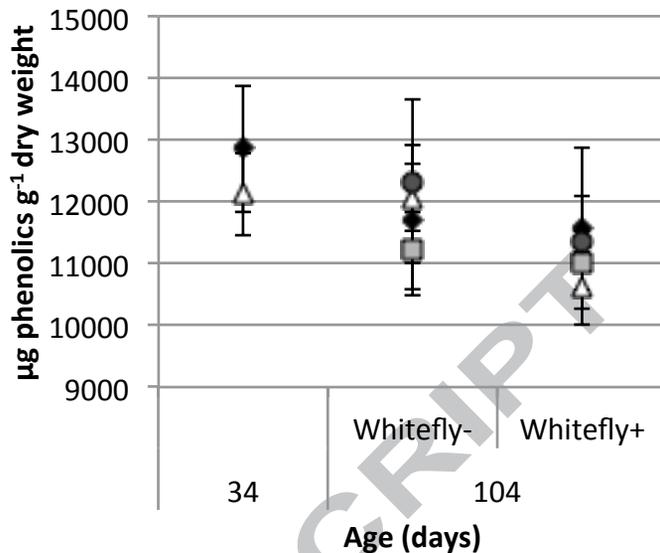
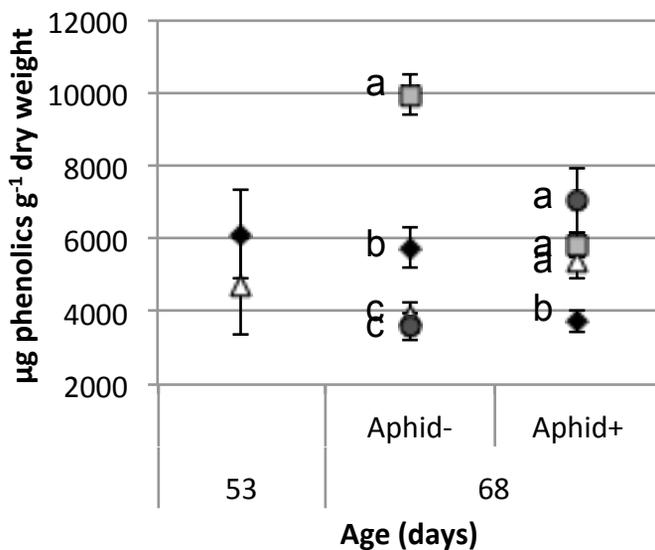
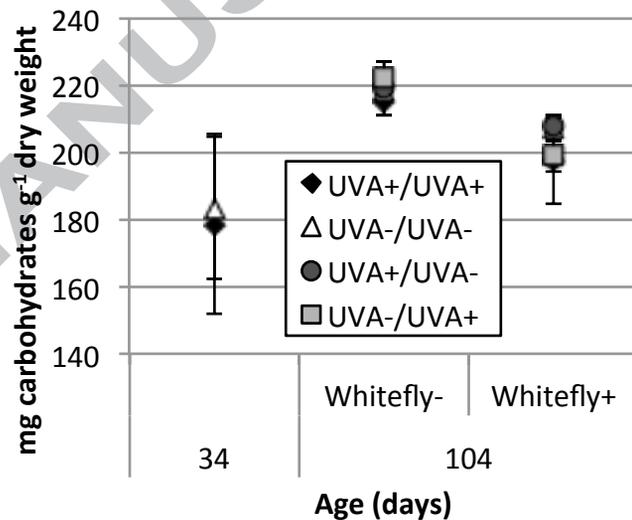
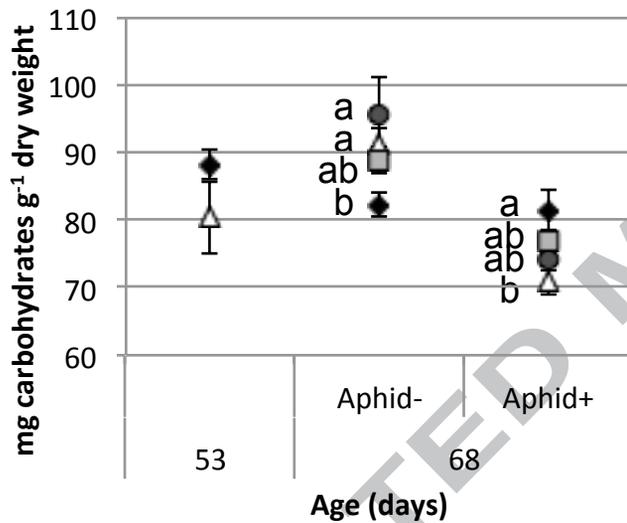
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**a****Pepper**

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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

930

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