

1 **Vulnerability and behavioral response to**  
2 **ultraviolet radiation in the components of a**  
3 **foliar mite prey-predator system**

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15 **Abstract** — Ambient ultraviolet-B (UVB) radiation impacts plant-dwelling arthropods including  
16 herbivorous and predatory mites. However, the effects of UVB on prey-predator systems, such as  
17 that between the herbivorous spider mite and predatory phytoseiid mite, are poorly understood. A  
18 comparative study was conducted to determine the vulnerability and behavioral responses of these  
19 mites to ultraviolet (UV) radiation. First, we analyzed dose-response (cumulative irradiance-  
20 mortality) curves for the eggs of phytoseiid mites (*Neoseiulus californicus*, *Neoseiulus*  
21 *womersleyi*, and *Phytoseiulus persimilis*) and the spider mite (*Tetranychus urticae*) to UVB  
22 radiation from a UV lamp. This indicated that the phytoseiid mites were more vulnerable than the  
23 spider mite, although *P. persimilis* was slightly more tolerant than the other two phytoseiid mites.  
24 Second, we compared the avoidance behavior of adult female *N. californicus* and two spider mite  
25 species (*T. urticae*, a lower leaf surface user; *Panonychus citri*, an upper leaf surface user) in  
26 response to solar UV and visible light. *N. californicus* actively avoided both types of radiation,  
27 whereas *P. citri* showed only minimal avoidance behavior. *T. urticae* actively avoided UV as well  
28 as *N. californicus* but exhibited a slow response to visible light as well as *P. citri*. Such variation in  
29 vulnerability and avoidance behavior accounts for differences in the species adaptations to solar  
30 UVB radiation. This may be the primary factor determining habitat use among these mites on host  
31 plant leaves, subsequently affecting accessibility by predators and also intraguild competition.

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## 33 Introduction

34 Solar ultraviolet (UV) radiation impacts plant-dwelling arthropods in terrestrial  
35 ecosystems (Ballaré et al., 2011). Because of the vulnerability of herbivorous  
36 spider mites and predatory phytoseiid mites to solar UV radiation (Ohtsuka and  
37 Osakabe 2009; Onzo et al. 2010; Sakai et al. 2012a), these impacts may also occur  
38 in foliar mite communities. There is a potential for substantial effects on  
39 interspecific interactions among mite species, e.g., competition (Osakabe et al.  
40 2006) and predation (Onzo et al. 2010).

41 The herbivorous twospotted spider mite, *Tetranychus urticae* Koch (Acari:  
42 Tetranychidae), is a well-known polyphagous, economically important  
43 agricultural pest. Although vulnerable to UV radiation, it can avoid the deleterious  
44 effects of direct exposure by remaining on the lower leaf surfaces (Ohtsuka and  
45 Osakabe 2009). Avoidance of solar UV radiation is likely to be a major selective  
46 force for the preference of *T. urticae* for lower leaf surfaces (Sakai and Osakabe  
47 2010). The component of solar UV radiation that can initiate deleterious effects is  
48 ultraviolet-B (UVB: wavelength 280–315 nm), whereas ultraviolet-A (UVA:  
49 wavelength 315–400 nm) does not affect the survival and fecundity of *T. urticae*  
50 (Barcelo 1981; Suzuki et al. 2009; Ohtsuka and Osakabe 2009; Sakai and  
51 Osakabe 2010).

52 Predatory phytoseiid mites can also increase their survival when exposed to  
53 UVB radiation by remaining on the lower leaf surfaces or more effectively inside  
54 of domatia (Onzo et al. 2010). Interestingly, a phytoseiid mite *Typhlodromalus*  
55 *aripo* De Leon, the predominant natural enemy of an important mite pest of  
56 cassava, the cassava green mite *Mononychellus tanajoa* (Bondar), hides within the  
57 apex of cassava during the day, and moves to leaves and actively forages during  
58 the night (Onzo et al. 2003, 2009). Similar to *T. urticae*, UVA radiation has no  
59 deleterious effects on the survival and fecundity of phytoseiid mites (Onzo et al.  
60 2010). This indicates both the vulnerability of phytoseiid mites and *T. urticae* to  
61 ambient UVB radiation and the absence of negative effects following exposure to  
62 UVA radiation.

63 Weintraub et al. (2007) observed that a phytoseiid mite *Neoseiulus cucumeris*  
64 (Oudemans) avoided both direct and indirect (reflected) sunlight. They used white  
65 paper to reflect sunshine in their study. Because UV of shorter wavelengths is

66 only partly reflected, the reflected radiation is mostly composed of visible light  
67 and some UVA. Therefore, this implies that phytoseiid mites avoid combinations  
68 of UV and visible light radiation or just visible light, but avoidance of UV  
69 radiation alone is not clear. In previous experiments using monochromatic UV  
70 radiation, adult female *T. urticae* avoided 320 and 340 nm wavelengths (not  
71 affected egg hatchability) but not 280 and 300 nm wavelengths (no eggs hatched)  
72 (Sakai and Osakabe 2010). *Tetranychus urticae* females might be incapable of  
73 recognizing UVB and therefore, use the UVA as a source of information for the  
74 avoidance of ambient UVB radiation.

75 In contrast to the majority of plant-dwelling mites, a substantial proportion of  
76 the eggs and adult females of herbivorous *Panonychus* spider mites are present on  
77 the upper leaf surfaces of their host plants, although many juveniles remain on the  
78 lower leaf surfaces (Foott 1963; Jones and Parrella 1984). The eggs are a reddish  
79 color. A previous experiment using artificial UVB radiation revealed that the eggs  
80 of *Panonychus citri* (McGregor) (Acari: Tetranychidae) are not vulnerable to  
81 UVB radiation unlike the whitish eggs of *T. urticae* (Fukaya et al. unpublished  
82 data).

83 If *Panonychus* mites reside together with *Tetranychus* mites on the lower leaf  
84 surface, they may experience amensal effects due to the complicated webs  
85 produced by herbivorous *Tetranychus* species (Morimoto et al. 2006; Osakabe et  
86 al. 2006). These complex webs function as protection against generalist phytoseiid  
87 mite species (McMurtry and Scriven 1964; Osakabe et al. 1987; Osakabe 1988;  
88 Sabelis and Bakker 1992). However, the webs can be exploited as an indicator of  
89 spider mite presence by type I and II phytoseiid mite species, specialized and  
90 selective predators of *Tetranychus* species, respectively (Hoy and Smilanick 1981;  
91 McMurtry and Croft 1997; Furuichi et al. 2005; Yano and Osakabe 2009;  
92 Shinmen et al. 2010). To understand the impact of solar UV radiation on the foliar  
93 mite community, an understanding of the relative impacts of UVB radiation on  
94 competitor, prey, and predator interactions is crucial.

95 We hypothesized that avoidance behavior towards solar radiation would  
96 reflect the UVB tolerance of plant-dwelling mites, which can restrict or expand  
97 their habitat usage on host plant leaves. We conducted a comparative study to  
98 determine the vulnerability and behavioral responses of spider mites and  
99 phytoseiid mites to solar UV and visible light radiation.

## 100 **Materials and methods**

### 101 **Mites**

102 Three species of predatory phytoseiid mite, *Neoseiulus californicus* (McGregor),  
103 *Neoseiulus womersleyi* Schicha, and *Phytoseiulus persimilis* Athias-Henriot  
104 (Acari: Phytoseiidae), were selected for this study. The mites were provided by  
105 the National Institute of Agrobiological Sciences, Japan. *N. californicus* were  
106 originally collected from Japanese pear in Matsukawa, Nagano Prefecture, Japan  
107 (35°36'N, 137°55'E) in September 2000. *N. womersleyi* were originally collected  
108 from roses in Shimoichi, Nara Prefecture, Japan (34°21'N, 135°47'E) in  
109 September 1995. *Phytoseiulus persimilis* was a laboratory strain that had been  
110 established from a population commercially provided by Tomono Agrica Co. Ltd.  
111 (Shizuoka, Japan). The phytoseiid mites were reared on *T. urticae*-infesting  
112 kidney bean leaves on water-soaked cotton in Petri dishes (9 cm diameter).

113 Herbivorous *Panonychus citri* was originally collected from citrus groves at the  
114 National Institute of Fruit Tree Science, Japan (32°36'N, 130°11'E) on 1 June,  
115 2007 and reared on kidney bean (*Phaseolus vulgaris* L.) leaves on water-soaked  
116 cotton in Petri dishes (9 cm diameter). The *T. urticae* population (the yellow-  
117 green type) had been established from several different localities in Japan and  
118 cultured on potted kidney bean plants in the laboratory for at least 6 years. They  
119 were also reared on kidney bean leaves on water-soaked cotton in Petri dishes for  
120 several generations before use in these experiments.

121 All mites were reared in the laboratory at 25°C with a photoperiod of 16 h  
122 light:8 h dark, except during the radiation treatments.

### 123 **Comparative vulnerability to UVB radiation**

124 The vulnerability of eggs to UVB for the three phytoseiid mite species and *T.*  
125 *urticae* was tested as a dose (cumulative irradiance)-response (hatchability)  
126 relationship.

127 To test phytoseiid mite eggs, we prepared five Petri dishes (9 cm in diameter).  
128 Four kidney bean leaf disks (2×2 cm) were placed on water-soaked cotton in each  
129 of the Petri dishes. Ten adult *T. urticae* females were transferred from cultures to  
130 each leaf disk and allowed to oviposit freely for 24 h. The next day, after the *T.*  
131 *urticae* females were removed, five adult females of one phytoseiid mite species

132 were introduced to each leaf disk and allowed to lay eggs for 24 h before being  
133 removed. The phytoseiid mite eggs laid on the leaf disks were counted and each  
134 Petri dish was assigned to one of five treatments: UVB irradiation ( $47 \mu\text{W cm}^{-2}$ )  
135 for 10 min (cumulative irradiance =  $0.282 \text{ kJ m}^{-2}$ ), 20 min ( $0.564 \text{ kJ m}^{-2}$ ), or 30  
136 min ( $0.846 \text{ kJ m}^{-2}$ ); UVA irradiation ( $47 \mu\text{W cm}^{-2}$ ) for 30 min ( $0.846 \text{ kJ m}^{-2}$ ); and  
137 a control ( $0 \text{ kJ m}^{-2}$ : kept in a laboratory without exposure to UV irradiation). To  
138 test the vulnerability of *T. urticae* to the different radiation treatments, we used  
139 eggs within 24 h of oviposition that were prepared in the same manner as  
140 described above, but without the introduction of phytoseiid mites.

141 The lamps used to provide UVB and UVA radiation were the UVL-57 UV  
142 lamp and the UVL-53 UV lamp, respectively (UVP, Cambridge, UK).  
143 Wavelength spectrums of UVB and UVA radiation peaked at 313 and 369 nm,  
144 respectively (Fig. 1). The UVB lamp had tails of emission in both UVA and UVC  
145 ranges. The UV lamps were placed approximately 60 cm above the Petri dishes in  
146 an incubator at  $25^\circ\text{C}$ . UV irradiance on leaf disks was adjusted using a UV Light  
147 Meter UV-340 (UV Light Meter UV-340; Mother Tool Co. Ltd., Ueda city,  
148 Japan), which measured the intensity of UV radiation at a range of wavelengths  
149 ( $290\text{--}390 \text{ nm}$ ; UVA+UVB).

150 After the UV irradiation treatment, the number of hatched and unhatched eggs  
151 was counted every day for 4 and 6 days for the phytoseiid mites and *T. urticae*,  
152 respectively. The experiment was repeated three times for each treatment.

153 The results from the four leaf disks in each Petri dish were combined for  
154 statistical analyses. Differences in the dose-response relationship for UVB  
155 radiation between mite species and the effects of UVA radiation on hatchability  
156 were evaluated separately using a Wald test for model objects produced by a  
157 generalized linear model (GLM: logit-link, binomial error) including mite species  
158 and UVB (UVA) dose as explanatory variables. For the dose-response  
159 relationship for UVB radiation, pairwise comparisons among mite species were  
160 performed by likelihood ratio tests as a post hoc test, and the resulting  
161 probabilities were corrected by a Bonferroni correction method. We used the  
162 “glm” modules in the “MASS” package to construct GLMs, “Anova” in the “car”  
163 package to perform a Wald test, and “anova” to perform likelihood ratio tests  
164 between GLMs, with and without species as explanatory variables, in R software  
165 (version 2.14.0; R Development Core Team 2009).

166 **Avoidance of solar UV and visible light radiation**

167 To test for avoidance of solar UV radiation, we prepared three rectangular  
168 transparent plastic trays (7.5 × 22 cm). A strip of kidney bean leaf strip (1 × 6 cm)  
169 was placed on water-soaked cotton in a dish (Fig. 2a). We placed a strip of wet  
170 paper (0.5 × 3 cm; Kimwipes; Nippon Paper Crexia Co.) across the center of a  
171 leaf disk perpendicular to the longitudinal axis to prevent the movement of mites  
172 between the two sides. Then we introduced 10 adult *N. californicus* females to  
173 one side of the leaf disk divided by the wet paper. Adult females (10 ♀♀) of *T.*  
174 *urticae* and *P. citri* were also separately introduced to one side of the leaf disks in  
175 the remaining two trays. The three plastic trays were kept in the laboratory for at  
176 least 10 min, to allow the mites to settle at one side of the leaf disks.

177 After the strip of wet paper was removed, half of the leaf strip where mites had  
178 settled was covered with a UV transparent film (polyethylene film, 30 µm thick;  
179 Dainichi Sangyo Co., Ltd., Osaka, Japan) and the other half was covered with UV  
180 opaque film (HB3 polyester film, 25 µm thick; Teijin DuPont Films, Japan)  
181 stretched on a plastic frame (8.0 × 22.5 cm; Fig. 2b). The UV opaque film filtered  
182 out more than 90% of UV at wavelengths below 380 nm (UVC, UVB and most of  
183 the UVA) and more than 99% at wavelengths below 363 nm, while allowing the  
184 transmission of 87% of the wavelengths between 388 and 800 nm (some UVA  
185 and visible light; see Sakai and Osakabe 2010). The UV transparent films allowed  
186 the transmission of 84% of 280–800 nm (UVB, UVA and visible light) on average  
187 (Fig. 2d).

188 Then the tray was exposed to solar radiation for 1 h (13:00–14:00) and the  
189 number of individuals on each half of the leaf strips was counted every 10 min on  
190 the roof of a four-story building at Kyoto University in Kyoto City, Japan (35°N,  
191 136°E). The mites were exposed to UV (UVA and UVB) and visible light  
192 radiation (UV+, VIS+) on the half of the leaf strip where they had settled. They  
193 could avoid solar UV radiation by moving to another half of the leaf strip where  
194 they were exposed to visible light radiation (UV-, VIS+).

195 At the same time as the experiment to test UV avoidance described above, we  
196 also prepared mites on the leaf strips for an experiment to test for visible light  
197 avoidance. The preparation and observation procedures were exactly the same as  
198 those used for the UV avoidance experiments. However, half of the leaf strip  
199 where mites had settled was covered with the UV opaque film, and the other half

200 was covered with the UV opaque film and also a visible light opaque film (black  
201 polyethylene film, 30  $\mu\text{m}$  thick; Dainichi Sangyo Co., Ltd., Osaka, Japan; Fig.  
202 2c). The mites were exposed to visible light radiation without UV radiation (UV–,  
203 VIS+) on the half of the leaf strip where they had settled. They could avoid visible  
204 light radiation by moving to the other half of the leaf strip where both UV and  
205 visible light radiation were attenuated (UV–, VIS–; Fig. 2d).

206 The experiments for both UV and visible light avoidance were performed on 7  
207 September (air temperature: 29.2°C [13:00], weather: clear), 10 September  
208 (32.6°C, clear), 24 September (23.2°C, clear), 29 September (27.2°C, clear), and 8  
209 October (22.7°C, clear), 2011. The average temperature and weather reported in  
210 parentheses above were obtained from the Kyoto Local Meteorological  
211 Observatory (35°N, 136°E) of the Japan Meteorological Agency  
212 (<http://www.jma.go.jp/jp/amedas/>).

213 For the statistical analysis, the data from all dates was combined and analyzed  
214 as an experiment without replication. This was because the number of females  
215 used in each treatment (10 ♀♀ each) was too small to evaluate the difference in  
216 ratios. Instead, the series of experiments was performed on clear days within a 1-  
217 month period. Individuals which escaped from leaf strips to water-soaked cotton  
218 (0–2 ♀♀ in *N. californicus*, 0–1 ♀♀ in *T. urticae*, and 0–10 ♀♀ in *P. citri* in total  
219 of all dishes at the each observation time) were excluded from the following data  
220 analyses.

221 The differences in mite ratios remaining on the half of leaf strip where they  
222 originally settled were evaluated using GLMs for repeated measures of UV and  
223 visible light avoidance separately. Then, multiple comparisons were performed  
224 using Tukey contrasts. We used “glmer” modules in the “lme4” package to  
225 construct GLMs for repeated measures, and “glht” in the “multcomp” package for  
226 multiple comparisons, using R software (version 2.14.0; R Development Core  
227 Team 2009).

228 To test for an avoidance response, the departure of values from 50% (the  
229 expected random distribution for the “no choice” situation) was tested on the  
230 number of individuals on each half after 60 min for each species by an exact  
231 binomial test using “binom.test” modules in the R software.



## 232 Results

### 233 Comparative vulnerability to UVB radiation

234 Most phytoseiid mites had hatched within 3 days following the UV treatment, and  
235 a few eggs exposed to UVB radiation hatched on day 6. Only the *N. womersleyi*  
236 eggs exposed to UVA (and some in the control) had hatched by day 6. All of the  
237 *T. urticae* eggs in the control and those exposed to UVA radiation had hatched  
238 within 5 days following the treatment, and some eggs exposed to UVB radiation  
239 had hatched by day 6. In the control ( $0 \text{ kJ m}^{-2}$ ), most eggs of all mite species  
240 successfully hatched. The hatchability from all three replications combined in the  
241 control condition was 99.4% ( $n = 164$ ) in *P. persimilis*, 96.0% ( $n = 124$ ) in *N.*  
242 *californicus*, 98.8% ( $n = 169$ ) in *N. womersleyi*, and 97.3% ( $n = 224$ ) in *T. urticae*.

243 In the UVB treatments, egg hatchability decreased with increased cumulative  
244 UVB irradiance (Fig. 3: Wald test,  $df = 1$ ,  $\chi^2 = 745.7$ ,  $P < 2.2 \times 10^{-16}$ ). The effect  
245 of UVB radiation on egg hatchability varied among the different mite species  
246 (Wald test,  $df = 3$ ,  $\chi^2 = 165.38$ ,  $P < 2.2 \times 10^{-16}$ ). The highest hatchability was  
247 found in the spider mite, *T. urticae* (likelihood ratio tests, corrected  $P < 0.001$ ).  
248 Phytoseiid mites were more vulnerable to UVB radiation. Among phytoseiid  
249 mites, the egg hatchability of *P. persimilis* was higher than that of *N. californicus*  
250 (likelihood ratio tests, corrected  $P < 0.001$ ) and *N. womersleyi* (likelihood ratio  
251 tests, corrected  $P < 0.001$ ). The dose-response relationship for *N. californicus* and  
252 *N. womersleyi* was broadly similar, and no significant was between them  
253 (likelihood ratio tests,  $P = 0.8333$ ).

254 Exposure to UVA radiation ( $0.846 \text{ kJ m}^{-2}$ ) had no deleterious effects on the  
255 egg hatchability of either phytoseiid mite or spider mite species. The hatchability  
256 of eggs exposed to UVA radiation was 98.3% (for all eggs from the three  
257 replications combined,  $n = 177$ ) in *P. persimilis*, 98.5% ( $n = 136$ ) in *N.*  
258 *californicus*, 100% ( $n = 154$ ) in *N. womersleyi*, and 94.1% ( $n = 270$ ) in *T. urticae*.  
259 Although egg hatchability varied between mite species (Wald test,  $df = 3$ ,  $\chi^2 =$   
260  $12.1268$ ,  $P = 0.006961$ ), it did not differ significantly between the two UVA doses  
261 ( $0$  and  $0.846 \text{ kJ m}^{-2}$ ; Wald test,  $df = 1$ ,  $\chi^2 = 0.6183$ ,  $P = 0.431672$ ; Data not  
262 shown).

## 263 **Avoidance of solar UV and visible light radiation**

264 In the experiments to test for the avoidance of solar UV radiation, female *N.*  
265 *californicus* and *T. urticae* moved rapidly from the UV+ area where they had  
266 settled to the UV- area, resulting that more than half females of both species were  
267 in the UV- area (exact binomial test, *N. californicus*:  $P = 2.465 \times 10^{-10}$ , *T.*  
268 *urticae*:  $P = 1.522 \times 10^{-5}$ ). Therefore, the number of females of these mites on the  
269 UV+ half of the leaf decreased substantially after 10 min (Fig. 4a). The response  
270 tended to be more sensitive in *N. californicus* than *T. urticae*, although no  
271 significant difference between species was detected (Tukey method,  $P = 0.122$ ). In  
272 contrast, the response of *P. citri* was clearly slower than those of *N. californicus*  
273 (Tukey method,  $P < 0.001$ ) and *T. urticae* (Tukey method,  $P < 0.001$ ). More than  
274 half of the *P. citri* females remained on the UV+ half of the leaf for 60 min (exact  
275 binomial test,  $P = 0.04703$ ).

276 When the avoidance of visible light radiation was tested, female *P. citri* and *T.*  
277 *urticae* displayed similar slow responses (Tukey method,  $P = 0.585$ ). They  
278 gradually moved and after 60 min were almost evenly distributed between the  
279 VIS+ and VIS- regions of the leaf (Fig. 4b; exact binomial test, *P. citri*:  $P =$   
280  $0.5682$ , *T. urticae*:  $P = 0.1439$ ). Therefore, it is not clear whether the spider mite  
281 females actively avoided visible light. In contrast, *N. californicus* responded more  
282 rapidly to visible light radiation than *T. urticae* (Tukey method,  $P < 0.0001$ ) and  
283 *P. citri* (Tukey method,  $P < 0.0001$ ). The females remaining in the VIS+ region of  
284 the leaf had decreased by approximately 25% of the number initially settled after  
285 20 min, resulting that more than half of *N. californicus* females were in the VIS-  
286 area (exact binomial test,  $P = 3.846 \times 10^{-5}$ ).

## 287 **Discussion**

288 Most plant-dwelling mites prefer to remain on lower leaf surfaces (Sudo and  
289 Osakabe 2011). Many abiotic factors such as temperature, humidity, wind, rain,  
290 and gravity may determine the resource accessibility and exploitation patterns of  
291 both herbivorous (Mori 1961; Ferro and Chapman 1979; Boyne and Hain 1983; Li  
292 and Margolies 1991; Bounfour and Tanigoshi 2001; Sakai et al. 2012b) and  
293 predacious (Shipp et al. 1996; Schausberger 1998; Rowles and O'Dowd 2009)  
294 species in foliar mite communities. Of the abiotic factors, Sakai and Osakabe  
295 (2010) considered that avoiding UV damage was the primary reason why *T.*

296 *urticae* shows a preference for lower leaf surfaces. The mites suffered damage  
297 from UVB radiation but not from UVA, and would exploited UVA of a shorter  
298 wavelength, e.g., 320 and 340 nm, as a cue to avoid UVB radiation (Sakai and  
299 Osakabe 2010).

300 Our previous experiments using a UV lamp revealed that *P. citri* eggs were less  
301 vulnerable than *T. urticae* eggs. The hatchability of *P. citri* eggs was 35–55%  
302 higher than *T. urticae* eggs following exposure to UVB radiation (Fukaya et al.  
303 unpublished). The dose-response relationships determined in this study revealed  
304 that the eggs of phytoseiid mites, especially *N. californicus* and *N. womersleyi*,  
305 were much more vulnerable to UVB radiation. We also found variation in UVB  
306 vulnerability among phytoseiid mite species. The hatchability of *P. persimilis*  
307 eggs was intermediate between that of *T. urticae* and other phytoseiid mite species  
308 of the genus *Neoseulus*. Onzo et al. (2010) also reported variation in UVB  
309 vulnerability between *T. aripo* and other phytoseiid mite species. *Amblydromalus*  
310 (= *Typhlodromalus*) *manihoti* (Moraes) and *Euseius fustis* (Pritchard and Baker)  
311 avoided UV damage by locating to lower leaf surfaces, whereas the survival and  
312 egg production of *T. aripo* adult females declined when they were irradiated with  
313 UVB. *T. aripo* prevented UV damage by sheltering within domatia at the apices  
314 of cassava (Onzo et al. 2010).

315 These differences in UVB vulnerability among mite species might be reflected  
316 in the behavioral responses of adult females towards exposure to UV and visible  
317 light radiation and affect niche exploitation, because oviposition site selection is  
318 likely to depend on the preference of females (Sudo and Osakabe 2011).  
319 However, we found that the upper leaf surface user, *P. citri*, did not show a clear  
320 response to either UV or visible light irradiation. In contrast, *T. urticae*, a lower  
321 leaf surface user, was sensitive to UV irradiation. Moreover, *N. californicus*, a  
322 plant domatia user (e.g., Palevsky et al. 2008), was sensitive to both UV and  
323 visible light irradiation. Generally, plant domatia are exploited by predaceous  
324 mites but not by spider mites (Walter 1996). Despite the fact that many phytoseiid  
325 mites prefer to lay eggs inside domatia (Walter 1996), *P. persimilis* is reported to  
326 only rarely lay eggs within plant domatia (Palevsky et al. 2008). There is some  
327 evidence that leaf hairs and trichomes protect underlying tissues against UVB  
328 radiation (Karabourniotis et al. 1993; Skaltsa et al. 1994; Liakoura et al. 1997;

329 Semerdjieva et al. 2003), implying that eggs laid inside leaf domatia are protected  
330 from not only predators and desiccation (Walter 1996) but also UVB damage.

331 The incidence of UV avoidance of *T. urticae* was equivalent to that of *N.*  
332 *californicus*. The incidence of visible light avoidance of *T. urticae* was also  
333 similar to that of *P. citri*. *T. urticae* does not avoid UV radiation with a  
334 wavelength longer than 350 nm and may not perceive deleterious UVB radiation  
335 (Sakai and Osakabe 2010; but see Suzuki et al. 2009). However, positive  
336 phototaxis occurs at wavelength of 375 nm (Naegele et al. 1966). Although  
337 McEnroe (1966) described the absence of a response to UV below a wavelength  
338 of 360 nm from the phototaxis viewpoint, our results regarding changes in  
339 behavioral response suggest that *T. urticae* can perceive and avoid UV radiation  
340 around the 320–340 nm wavelengths (Sakai and Osakabe 2010) in solar radiation.  
341 Spider mites have two pairs of eyes (anterior and posterior) and an UV receptor is  
342 present in the unshielded posterior eye (McEnroe 1969; McEnroe and Dronka  
343 1969).

344 Negative phototaxis of eyeless phytoseiid mites away from visible light has  
345 been recorded in several studies (Auger et al. 1999; Weintraub et al. 2007). *N.*  
346 *californicus* negatively and rapidly responded to not only visible light but also  
347 solar UV radiation. It has been well documented for this species that vitamin A or  
348  $\beta$ -carotene (a precursor of vitamin A) are required to induce diapause (Veerman et  
349 al. 1983; Veerman 2001). Although photoreceptors and mechanisms concerned  
350 with phototactic behavior are not known for *N. californicus*, the response to  
351 visible light radiation was gradual compared to the response to UV radiation.  
352 Therefore, *N. californicus* might also perceive wavelength differences in the  
353 components of the radiation spectrum.

354 Some studies have assumed that the direct effects of solar radiation on the  
355 distribution of mites result from heating and a lower humidity in the outer canopy  
356 compared to the inner canopy (Villanueva and Childers 2005). In this context, the  
357 negative phototaxis of mites might be considered an escape from high  
358 temperatures and desiccation during daylight hours (Villanueva and Childers  
359 2005) rather than direct UV damage. Air temperatures during the experimental  
360 periods for determining avoidance behavior (22.7–32.6°C) were acceptable for  
361 mites. Although solar radiation potentially generates a harsh microenvironment  
362 for mites, high temperatures and desiccation may not be the principal effect on

363 plant-dwelling mites over all seasons. Weintraub et al. (2007) pointed out that the  
364 temperature on a leaf surface is substantially cooler than the ambient temperature  
365 due to evapotranspiration and that the internal environment of domatia is humid.

366 Many mite species may be able to escape from solar UV damage by moving to  
367 the lower leaf surfaces even in the outer canopy. However, highly sensitive  
368 species such as some phytoseiid mites might move to the inner canopy or inside  
369 domatia during daylight periods. In contrast, some species that can limit UV  
370 damage via physical or physiological protection, such as *Panonychus* mites, can  
371 exploit both lower and upper leaf surfaces in the outer canopy, on which they may  
372 encounter fewer competitors and natural enemies. Our findings, incorporating  
373 with a previous study (Fukaya et al. unpublished), suggest the possibility some  
374 herbivorous mites may have evolved tolerance of solar UV radiation as a predator  
375 avoidance strategy.

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## 380 **References**

- 381 Auger P, Tixier MS, Kreiter S, Fauvel G (1999) Factors affecting ambulatory dispersal in the  
382 predaceous mite *Neoseiulus californicus* (Acari: Phytoseiidae). *Exp Appl Acarol* 23: 235–  
383 250
- 384 Ballaré CL, Caldwell MM, Flint SD, Robinson SA, Bornman JF (2011) Effects of solar ultraviolet  
385 radiation on terrestrial ecosystems. Patterns, mechanisms, and interactions with climate  
386 change. *Photoch Photobio Sci* 10: 226–241
- 387 Barcelo JA (1981) Photoeffects of visible and ultraviolet radiation on the two-spotted spider mite,  
388 *Tetranychus urticae*. *Photochem Photobiol* 33: 703–706
- 389 Bounfour M, Tanigoshi LK (2001) Effect of temperature on development and demographic  
390 parameters of *Tetranychus urticae* and *Eotetranychus carpini borealis* (Acari:  
391 Tetranychidae). *Ann Entomol Soc Am* 94: 400–404
- 392 Boyne JV, Hain FP (1983) Effects of constant temperature, relative humidity, and simulated  
393 rainfall on development and survival of the spruce spider mite (*Oligonychus ununguis*). *Can*  
394 *Ent* 115: 93–105.
- 395 Ferro DN, Chapman RB (1979) Effects of different constant humidities and temperatures on  
396 twospotted spider mite egg hatch. *Environ Entomol* 8: 701–705

- 397 Foott WH (1963) Competition between two species of mites. II. Factors influencing intensity. Can  
398 Entomol 95: 45–57
- 399 Furuichi H, Yano S, Takafuji A, Osakabe M (2005) Prey preference of the predatory mite  
400 *Neoseiulus womersleyi* Schicha is determined by spider mite webs. J Appl Entomol 129:  
401 336–339
- 402 Hoy MA, Smilanick JM (1981) Non-random prey location by the phytoseiid predator *Metaseiulus*  
403 *occidentalis*: Differential responses to several spider mite species. Enomol Exp Appl 29:  
404 241–253
- 405 Jones VP, Parrella MP (1984) Intratree regression sampling plans for the citrus red mite (Acari:  
406 Tetranychidae) on lemons in southern California. J Econ Entomol 77: 810–813
- 407 Karabourniotis G, Kyparissis A, Manetas Y (1993) Leaf hairs of *Olea europaea* protect underlying  
408 tissues against ultraviolet-B radiation damage. Environ Exp Bot 33: 341–345
- 409 Li J, Margolies DC (1991) Factors affecting location of Banks grass mite, *Oligonychus pratensis*  
410 (Acari: Tetranychidae), on corn leaves. Exp Appl Acarol 12: 27–34
- 411 Liakoura V, Stefanou M, Manetas Y, Cholevas C, Karabourniotis G (1997) Trichome density and  
412 its UV-B protective potential are affected by shading and leaf position on the canopy.  
413 Environ Exp Bot 38: 223–229
- 414 McEnroe WD (1966) Color vision in the adult female two-spotted spider mite. Science 154: 782–  
415 784
- 416 McEnroe WD (1969) Eyes of the female two-spotted spider mite, *Tetranychus urticae*. I.  
417 Morphology. Ann Entomol Soc Am 62: 461–466
- 418 McEnroe WD and Dronka K (1969) Eyes of the female two-spotted spider mite, *Tetranychus*  
419 *urticae*. II. Behavioral analysis of the photoreceptors. Ann Entomol Soc Am 62: 466–469
- 420 McMurtry JA, Croft BA (1997) Life-styles of phytoseiid mites and their roles in biological  
421 control. Annu Rev Entomol 62: 291–321
- 422 McMurtry JA, Scriven GT (1964) Studies on the feeding, reproduction, and development of  
423 *Amblyseius hibisci* (Acarina: Phytoseiidae) on various food substances. Ann Entomol Soc  
424 Am 57: 649–655
- 425 Mori H (1961) Comparative studies of thermal reaction in four species of spider mites (Acarina  
426 Tetranychidae). J Fac Agric Hokkaido Univ 51: 574–591
- 427 Morimoto K, Furuichi H, Yano S, Osakabe M (2006) Web mediated interspecific competition  
428 among spider mites. J Econ Entomol 99: 678–684
- 429 Naegele JA, McEnroe WD, Soans AB (1966) Spectral sensitivity and orientation response of the  
430 two-spotted spider mite, *Tetranychus urticae* Koch, from 350 m $\mu$  to 700 m $\mu$ . J Insect Physiol  
431 12: 1187–1195
- 432 Ohtsuka K, Osakabe Mh (2009) Deleterious effects of UV-B radiation on herbivorous spider  
433 mites: they can avoid it by remaining on lower leaf surfaces. Environ Entomol 38: 920–929
- 434 Onzo A, Hanna R, Zannou I, Sabelis MW, Yaninek JS (2003) Dynamics of refuge use: Diurnal,  
435 vertical migration by predatory and herbivorous mites within cassava plants. Oikos 101:59–  
436 69

- 437 Onzo A, Hanna R, Sabelis MW (2009) Within-plant migration of the predatory mite  
438 *Typhlodromalus aripo* from the apex to the leaves of cassava: Response to day–night cycle,  
439 prey location and prey density. *J Insect Behav* 22: 186–195
- 440 Onzo A, Sabelis MW, Hanna R (2010) Effects of ultraviolet radiation on predatory mites and the  
441 role of refuges in plant structures. *Environ Entomol* 39: 695–701
- 442 Osakabe M (1988) Relationships between food substances and developmental success in  
443 *Amblyseius sojaensis* Ehara (Acarina: Phytoseiidae). *Appl Entomol Zool* 23:45–51
- 444 Osakabe Mh, Inoue K, Ashihara W (1987) Effect of *Amblyseius sojaensis* Ehara (Acarina:  
445 Phytoseiidae) as a predator of *Panonychus citri* (McGregor) and *Tetranychus kanzawai*  
446 Kishida (Acarina: Tetranychidae). *Appl Entomol Zool* 22: 594–599
- 447 Osakabe Mh, Hongo K, Funayama K, Osumi S (2006) Amensalism via webs causes unidirectional  
448 shifts of dominance in spider mite communities. *Oecologia* 150: 496–505
- 449 Palevsky E, Walzer A, Gal S, Schausberger P (2008) Evaluation of dry-adapted strains of the  
450 predatory mite *Neoseiulus californicus* for spider mite control on cucumber, strawberry and  
451 pepper. *Exp Appl Acarol* 45: 15–27
- 452 R Development Core Team (2009) R: A Language and Environment for Statistical Computing,  
453 Version 2.10.1. R Foundation for Statistical Computing, Vienna, Austria.
- 454 Rowles AD, O’Dowd DJ (2009) Leaf domatia and protection of a predatory mite *Typhlodromus*  
455 *doreenae* Schicha (Acari: Phytoseiidae) from drying humidity. *Aust J Entomol* 48: 276–281
- 456 Sabelis MW, Bakker FM (1992) How predatory mites cope with the web of their tetranychid prey:  
457 a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp Appl Acarol* 16: 203–225
- 458 Sakai Y, Osakabe Mh (2010) Spectrum-specific damage and solar ultraviolet radiation avoidance  
459 in the two-spotted spider mite. *Photochem Photobiol* 86: 925–932
- 460 Sakai Y, Sudo M, Osakabe M (2012a) Seasonal changes in the deleterious effects of solar  
461 ultraviolet-B radiation on eggs of the twospotted spider mite, *Tetranychus urticae* (Acari:  
462 Tetranychidae). *Appl Entomol Zool* 47: 67–73
- 463 Sakai Y, Sudo M, Osakabe Mh (2012b) A comparison of the effects of gravity and the nutritional  
464 advantage of leaf surfaces on fecundity in the two-spotted spider mite (Acari: Tetranychidae).  
465 *J Acarol Soc Jpn* 21: 1–6
- 466 Schausberger P (1998) The influence of relative humidity on egg hatch in *Euseius finlandicus*,  
467 *Typhlodromus pyri* and *Kampimodromus aberrans* (Acari, Phytoseiidae). *J Appl Entomol*  
468 122: 497–500
- 469 Semerdjieva SI, Phoenix GK, Hares D, Gwynn-Jones D, Callaghan TV, Sheffield E (2003)  
470 Surface morphology, leaf and cuticle thickness of four dwarf shrubs from a sub-Arctic heath  
471 following long-term exposure to enhanced levels of UV-B. *Physiol Plant* 117: 289–294
- 472 Shinmen T, Yano S, Osakabe Mh (2010) The predatory mite *Neoseiulus womersleyi* (Acari:  
473 Phytoseiidae) follows extracts of trails left by the two-spotted spider mite *Tetranychus*  
474 *urticae* (Acari: Tetranychidae). *Exp Appl Acarol* 52: 111–118
- 475 Shipp JL, Ward KI, Gillespie TJ (1996) Influence of temperature and vapor pressure deficit on the  
476 rate of predation by the predatory mite, *Amblyseius cucumeris*, on *Frankliniella occidentalis*.  
477 *Entomol Exp Appl* 78: 31–38

- 478 Skaltsa H, Verykokidou E, Harvala C, Karabourniotis G, Manetas Y (1994) UV-B protective  
479 potential and flavonoid content of leaf hairs of *Quercus ilex*. *Phytochem* 37: 987–990
- 480 Sudo M, Osakabe M (2011) Do plant mites commonly prefer the underside of leaves? *Exp Appl*  
481 *Acarol* 55: 25–38
- 482 Suzuki T, Watanabe M, Takeda M (2009) UV tolerance in the two-spotted spider mite. *J Insect*  
483 *Physiol* 55: 649–654
- 484 Veerman A (2001) Photoperiodic time measurement in insects and mites: a critical evaluation of  
485 the oscillator-clock hypothesis. *J Insect Physiol* 47: 1097–1109
- 486 Veerman A, Overmeer WPJ, van Zon AQ, de Boer JM, de Waard ER, Huisman HO (1983)  
487 Vitamin A is essential for photoperiodic induction of diapause in an eyeless mite. *Nature*  
488 302: 248–249
- 489 Villanueva RT, Childers CC (2005) Diurnal and spatial patterns of Phytoseiidae in the citrus  
490 canopy. *Exp Appl Acarol* 35: 269–280
- 491 Walter DE (1996) Living on leaves: mites, tomenta, and leaf domatia. *Annu Rev Entomol* 41:  
492 101–114
- 493 Weintraub PG, Kleitman S, Alchanatis V, Palevsky E (2007) Factors affecting the distribution of a  
494 predatory mite on greenhouse sweet pepper. *Exp Appl Acarol* 42: 23–35
- 495 Yano S, Osakabe M (2009) Do spider mite-infested plants and spider mite trails attract predatory  
496 mites? *Ecol Res* 24: 1173–1178
- 497
- 498



499 **Figure legends**

500

501 Fig. 1 Wavelength spectrums of ultraviolet radiation emitted by UVA (broken line) and UVB  
502 (solid line) lamps.

503

504 Fig. 2 Experimental design for the test to determine avoidance of solar UV and visible light  
505 (VIS) radiation by *N. californicus*, *T. urticae* and *P. citri*. (a) Kidney bean leaf strip on  
506 water-soaked cotton in a plastic dish, (b) a lid with UV-transparent (UV+, VIS+) and UV-  
507 opaque film (UV-, VIS+), and (c) a lid with UV-opaque film (UV-, VIS+) on one half of  
508 a leaf and a combined UV-opaque and black film (UV-, VIS-) on the other half, (d)  
509 wavelength spectrum of transmittance through the different films. UV-transparent film:  
510 chain line, UV-opaque film: broken line, UV-opaque and black film: solid line.

511

512 Fig. 3 Dose-response relationship following UVB exposure for eggs of *T. urticae* (open circles),  
513 *P. persimilis* (solid triangles), *N. californicus* (solid circles), and *N. womersleyi* (open  
514 triangles). Vertical lines above and below each plot indicate the 95% confidence interval.  
515 Different letters represent the significance in pairwise comparisons by a likelihood ratio  
516 test ( $P < 0.05$ ). The probabilities were corrected by a Bonferroni correction method.

517

518 Fig.4 Avoidance of solar UV (a) and visible light (VIS) (b) radiation by *P. citri* (solid triangle),  
519 *T. urticae* (open circles) and *N. californicus* (gray diamond). Species with different letters  
520 are significantly different from each other according to the Tukey method ( $P < 0.001$ ).

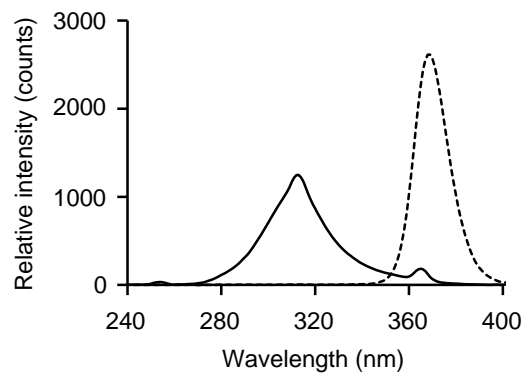


Fig. 1

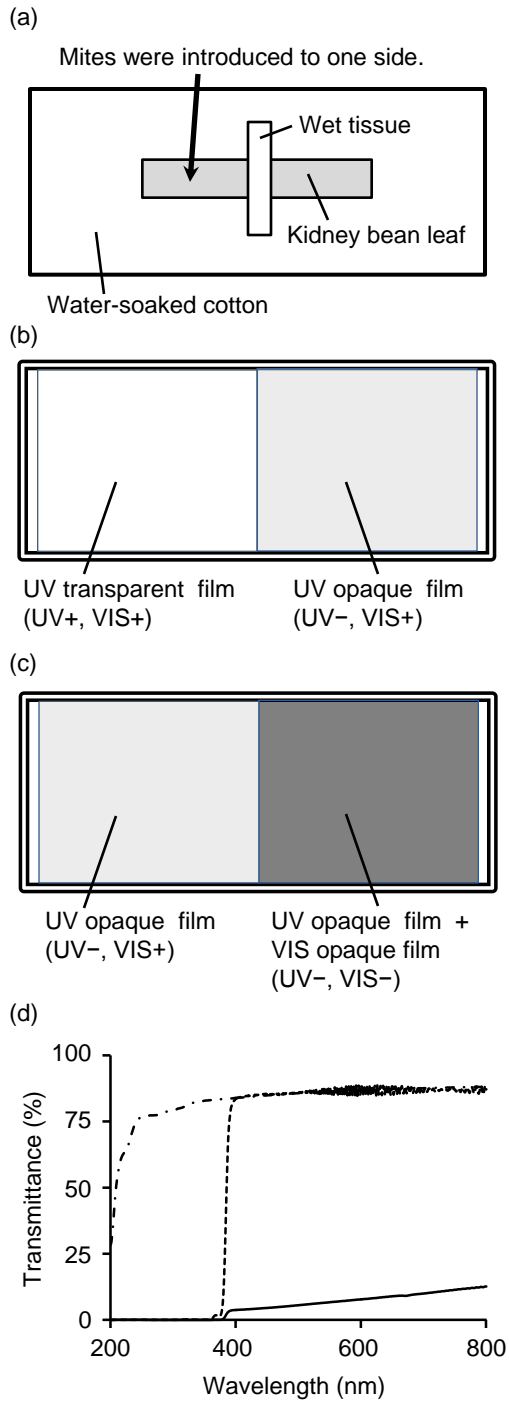


Fig. 2

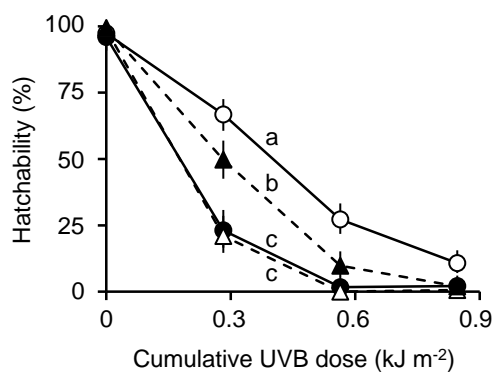


Fig. 3

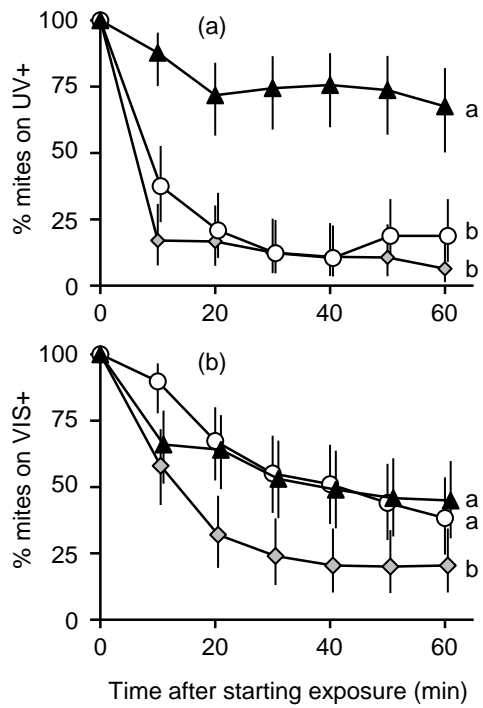


Fig. 4