

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

4

5

6 Fuyuki Tachi and Masahiro Osakabe

7 *Laboratory of Ecological Information, Graduate School of Agriculture, Kyoto*
8 *University, Kyoto 606-8502, Japan*

9 Phone: +81757532267

10 Fax: +81757532267

11 E-mail: mhosaka@kais.kyoto-u.ac.jp (Masahiro Osakabe)

12

13

14

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.

32

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 kJ m^{-2}), 20 min (0.564 kJ m^{-2}), or 30
136 min (0.846 kJ m^{-2}); UVA irradiation ($47 \mu\text{W cm}^{-2}$) for 30 min (0.846 kJ m^{-2}); and
137 a control (0 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°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 (290–390 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 μm 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 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 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 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 *Neoseiulus*. 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 β -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.

376 Acknowledgements

377 We thank Dr. N. Hinomoto who provided phytoseiid mites and Dr. H. Kishimoto who collected *P.*
 378 *citri*. This study was supported by a Grant-in-Aid for Scientific Research from the Ministry of
 379 Education, Culture, Sports, Science, and Technology of Japan (18580053).

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 mμ to 700 mμ. 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 ($P < 0.001$).

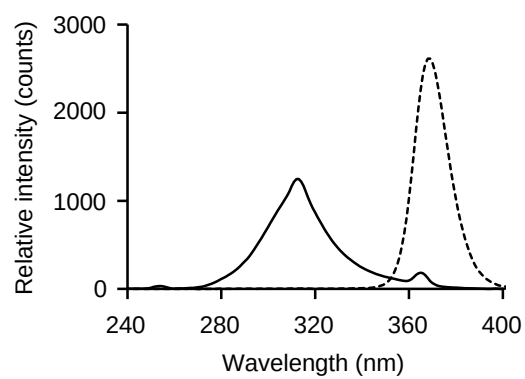


Fig. 1

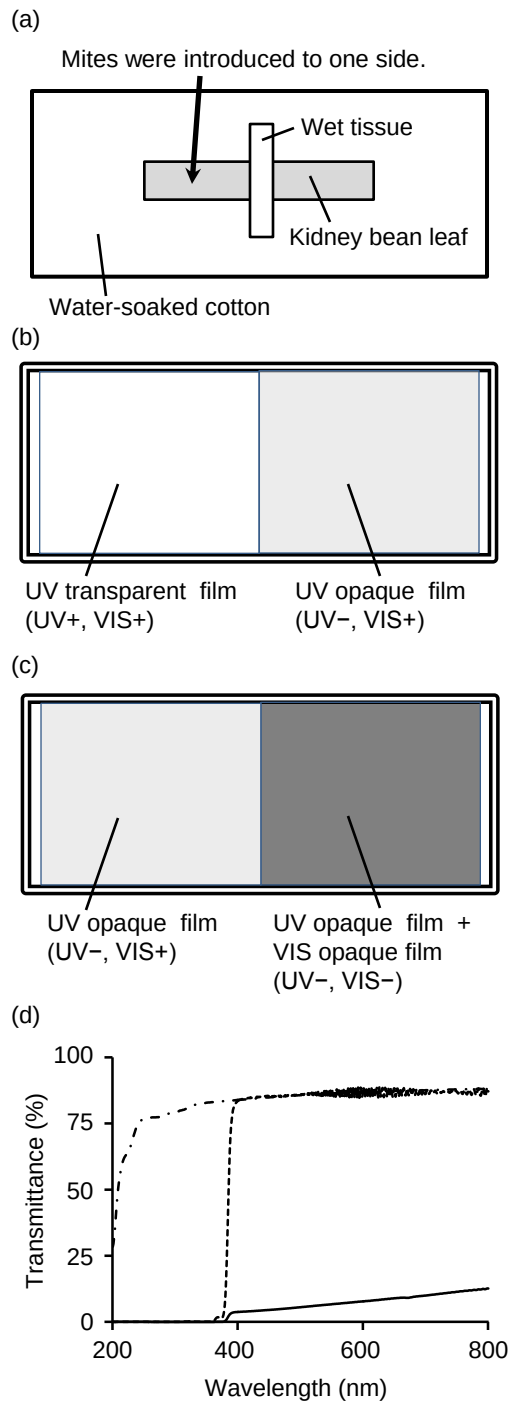


Fig. 2

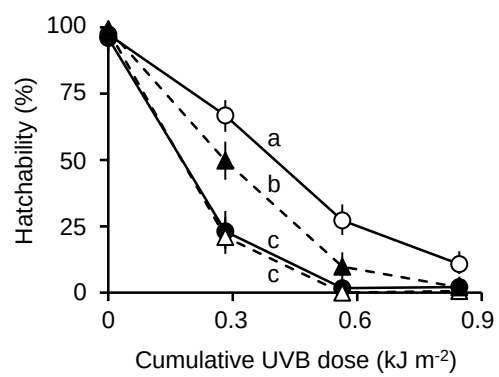


Fig. 3

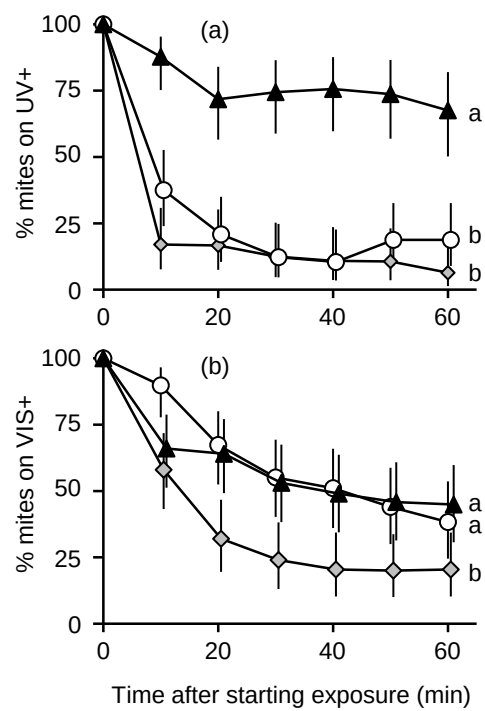


Fig. 4