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

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

Introduction

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

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

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

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

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

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

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

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

Materials and methods

Mites

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

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

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

Comparative vulnerability to UVB radiation

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

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

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

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

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

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

Avoidance of solar UV and visible light radiation

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

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

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

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

was covered with the UV opaque film and also a visible light opaque film (black polyethylene film, 30 μm thick; Dainichi Sangyo Co., Ltd., Osaka, Japan; Fig. 2c). The mites were exposed to visible light radiation without UV radiation (UV−, VIS+) on the half of the leaf strip where they had settled. They could avoid visible light radiation by moving to the other half of the leaf strip where both UV and visible light radiation were attenuated (UV−, VIS−; Fig. 2d).

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

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

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

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

Results

Comparative vulnerability to UVB radiation

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

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

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

Avoidance of solar UV and visible light radiation

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

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

Discussion

Most plant-dwelling mites prefer to remain on lower leaf surfaces (Sudo and Osakabe 2011). Many abiotic factors such as temperature, humidity, wind, rain, and gravity may determine the resource accessibility and exploitation patterns of both herbivorous (Mori 1961; Ferro and Chapman 1979; Boyne and Hain 1983; Li and Margolies 1991; Bounfour and Tanigoshi 2001; Sakai et al. 2012b) and predacious (Shipp et al. 1996; Schausberger 1998; Rowles and O'Dowd 2009) species in foliar mite communities. Of the abiotic factors, Sakai and Osakabe (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 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

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

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

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Figure legends

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

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

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

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

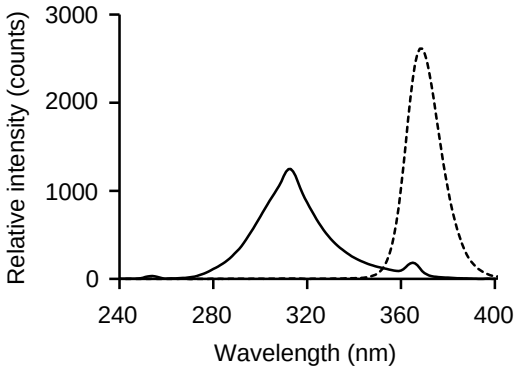
Relative intensity (counts)
3000
2000
1000
0
240
280
320
360
400
Wavelength (nm)

Fig. 1

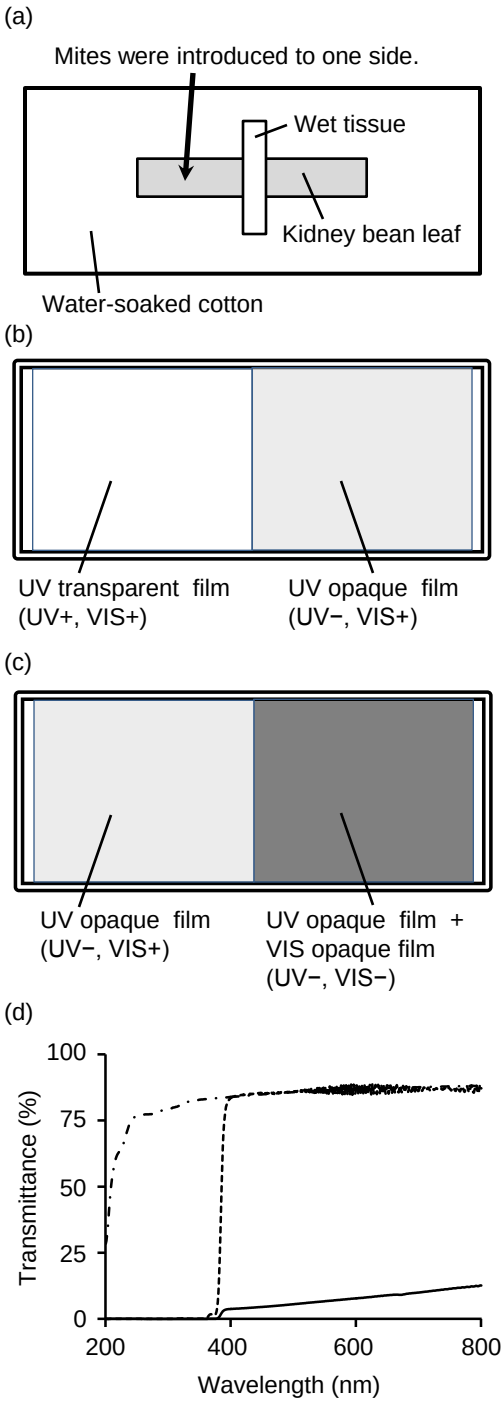
(a)
Mites were introduced to one side.
Wet tissue
Kidney bean leaf
Water-soaked cotton
(b)
UV transparent film
(UV+, VIS+)
UV opaque film
(UV−, VIS+)
(c)
UV opaque film
(UV−, VIS+)
UV opaque film +
VIS opaque film
(UV−, VIS−)
(d)
Transmittance (%)
100
75
50
25
0
200
400
600
800
Wavelength (nm)

Fig. 2

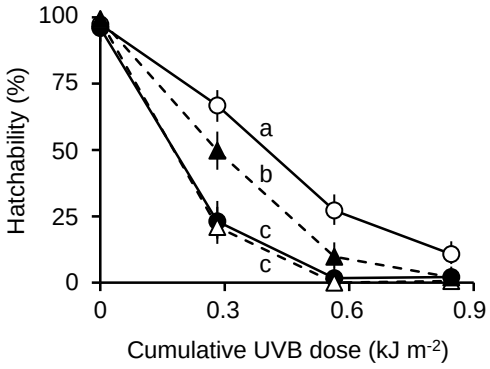
100
75
50
25
0
Hatchability (%)
a
b
c
c
0
0.3
0.6
0.9
Cumulative UVB dose (kJ m-2)

Fig. 3

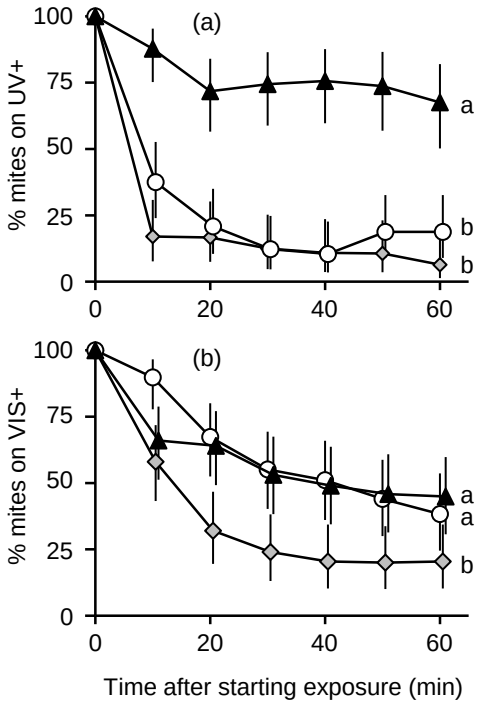
(a)
100
75
50
25
0
% mites on UV+
a
b
b
0
20
40
60
(b)
100
75
50
25
0
% mites on VIS+
a
a
b
0
20
40
60
Time after starting exposure (min)

Fig. 4