

## RESEARCH ARTICLE

# Photo-orientation regulates seasonal habitat selection in the two-spotted spider mite, *Tetranychus urticae*

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### SUMMARY

**Non-diapausing spider mites (*Tetranychus urticae*) live on the undersurface of host leaves during summer, but diapausing mites overwinter in dark hibernacula. The light environments of these habitats differ: visible radiation (VIS) but not ultraviolet radiation (UV) reaches the undersurface of leaves, but neither enters dark hibernacula. Thus, mites of either seasonal form could locate their preferred habitat by photo-orientation responses to UV and VIS. To investigate this possibility, we analysed the mites' locomotion behaviour on a virtual field with a programmed chequered pattern of light and dark patches in a micro-locomotion compensator. Both non-diapausing and diapausing mites moved away from UV-illuminated patches into dark patches. Non-diapausing mites moved towards VIS-illuminated patches, whereas diapausing mites did not show a preference. Our results show that non-diapausing mites avoid UV and are attracted to VIS, suggesting that this can guide them beneath a leaf. Diapausing mites simply avoid UV. The lack of a preference for VIS during diapause could be due to changes in carotenoid metabolism, which also involve orange pigmentation of diapausing mites. We consider that a diapause-mediated switch of the response to VIS, together with regular avoidance of UV, plays a key role in the seasonal change of habitat selection in this species. This seasonal polyphenism involves alterations in not only reproductive state and pigmentation, but also in photo-spectral responses.**

Key words: diapause, locomotion compensator, seasonal change, ultraviolet radiation, virtual field, visible radiation.

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### INTRODUCTION

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), stays predominantly beneath host leaves, where it feeds, spins webs and reproduces. Researchers have proposed that this location protects mites from fluctuations of air temperature (Gutierrez and Helle, 1985), rain (Gutierrez and Helle, 1985; Jeppson et al., 1975) and the deleterious effects of ultraviolet radiation (UV) (Barcelo, 1981; Ohtsuka and Osakabe, 2009; Sakai and Osakabe, 2010; Suzuki et al., 2009), which leaves absorb and reflect (Smith, 1986).

Avoidance of UV has been observed in bacteria (Bebout and Garcia-Pichel, 1995; Häder, 1987; Kruschel and Castenholz, 1998), protozoans (Barcelo and Calkins, 1979), nematodes (Edwards et al., 2008), echinoderms (Adams, 2001; Pennington and Emler, 1986), amphibians (Han et al., 2007; Nagl and Hofer, 1997; van de Mortel and Buttemer, 1998), fish (Fukunishi et al., 2006; Holtby and Bothwell, 2008; Kelly and Bothwell, 2002), crustaceans (Barcelo and Calkins, 1979; Barcelo and Calkins, 1980; Storz and Paul, 1998), insects (Bothwell et al., 1994; Mazza et al., 1999; Mazza et al., 2002) and mites (Barcelo, 1981; Barcelo and Calkins, 1980; Onzo et al., 2010; Sakai and Osakabe, 2010; Suzuki et al., 2009). In addition, mites are attracted to visible radiation (VIS) (Dimock and Davids, 1985; Hussey and Parr, 1963; McEnroe and Dronka, 1966; McEnroe and Dronka, 1969; Mori, 1962; Naegele et al., 1966; Suski and Naegele, 1963a; Suski and Naegele, 1963b). As leaves transmit some VIS (Smith, 1986),

the undersurface provides an attractive environment characterised by a dominance of VIS over UV. Therefore, the localization of mites beneath leaves may be regulated by photo-orientation responses to both UV and VIS.

However, mites lose their attraction towards light during winter. Hussey and Parr (Hussey and Parr, 1963) showed that the avoidance of light was induced upon diapause in *T. urticae*, although they did not present light spectra. Diapause is defined as a hormonally mediated metabolic arrest with an increase in resistance to environmental stresses, a change in behaviour, and suppression of morphogenesis (Tauber and Tauber, 1981). In *T. urticae*, only adult females enter diapause to overwinter when nights lengthen and low air temperatures prevail (Veerman, 1985). Diapausing females overwinter in dark hibernacula in clods of soil, litter on the ground surface, cracks in trees, and under bark (Veerman, 1985). They remain slowly mobile, so the choice of these dark hibernacula may be explained by negative photo-orientation responses to UV, VIS or both.

To obtain behavioural evidence, we used a micro-locomotion compensator (Kojima et al., 2003) newly equipped with an LED lighting apparatus, which allows light-cue control in real time to simulate mosaic illumination in the environment, as well as precise acquisition of locomotion data. Here, we examined the photo-orientation behaviour in non-diapausing and diapausing females of *T. urticae* towards UV and VIS to identify possible cues responsible for their seasonal habitat selection.

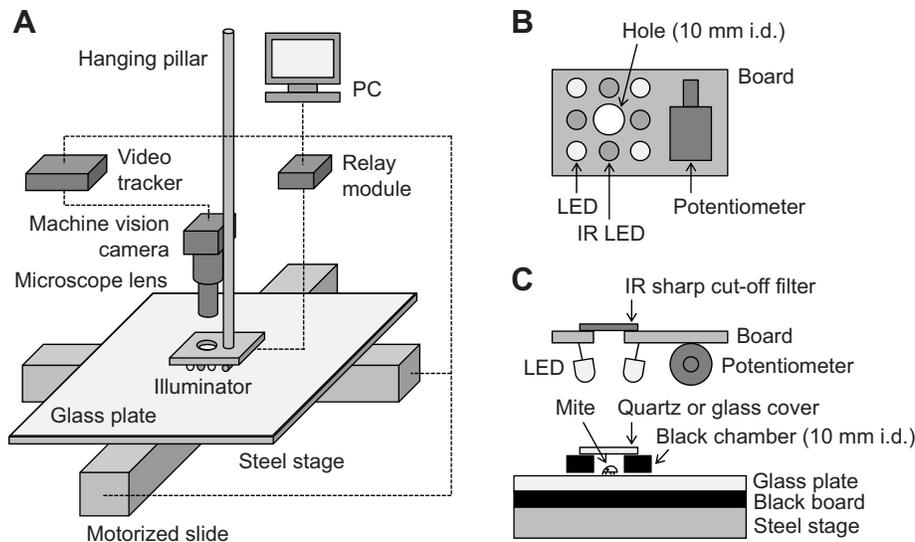


Fig. 1. Schematic diagrams of (A) the micro-locomotion compensator (MLC) and the (B) bottom and (C) side views of the illuminator. Broken lines represent signal lines. The MLC keeps a walking mite centred beneath the video camera by the use of micro-stepping motors. The mite is retained within a black acrylic test chamber, which is suspended just above the sliding stage. A PC switches ultraviolet (UV) or visible (VIS) LEDs on and off according to the mite's movement on a virtual light-and-dark field. Continuous infrared (IR) LEDs illuminate the mite for video tracking. See Materials and methods for details.

## MATERIALS AND METHODS

### Mites

We collected a *T. urticae* population from an apple orchard in Akita, Japan (39°N), and subsequently maintained this population on kidney bean (*Phaseolus vulgaris*) leaves under a 16h:8h light:dark photoperiod at an air temperature of 25°C and a relative humidity of 50%. Adult females of random ages were introduced onto a fresh *P. vulgaris* leaf placed on water-soaked cotton in a Petri dish and allowed to lay eggs for 24h in the dark at 25°C. The adult females were then removed and the eggs were maintained for 5 days under the same conditions. Newly hatched larvae were reared until adulthood in photoperiod chambers (Suzuki and Takeda, 2009) under 16h:8h light:dark at 25°C or 8h:16h light:dark at 18°C, producing non-diapausing and diapausing females, respectively. Adult females were considered to be in diapause if their body colour turned from yellowish-green to uniform orange, owing to the accumulation of carotenoids (Veerman, 1985).

### Instrumentation

We used a locomotion compensator (LC) designed for submillimetre-sized animals, specifically, a micro-locomotion compensator (MLC; Fig. 1) that our group developed for studies of olfactory behaviour in mould mites (Kojima et al., 2003). The function of an LC, or servosphere, first developed by Kramer and Heinecke, is 'to keep a walking animal in a small experimental field and to precisely record the intended movements' of the animal (Kramer, 1975). The Kramer–Heinecke-type LC, with a rotating sphere, has been extensively used with various ambulatory arthropods from tiny predatory mites *Phytoseiulus persimilis* (van Tilborg et al., 2003) to American cockroaches, *Periplaneta americana* (Bell and Kramer, 1979), mainly to analyse their olfactory (Kramer, 1975; Kramer, 1976; Bell and Kramer, 1979; Thiery and Visser, 1986; Visser and Taanman, 1987; Vet and Papaj, 1992; Taneja and Guerin, 1995; McMahon and Guerin, 2000; Sakuma, 2002; van Tilborg et al., 2003) and auditory behaviours (Weber et al., 1981; Verburt et al., 2008).

In addition to the automated observation of a walking animal, an LC enables the analysis of its orientation mechanisms through the closed-loop control of sensory cues with reference to the location or kinematics of the animal (Kramer, 1976; Weber et al., 1981; Sorensen and Bell, 1986; Sakuma, 2002; Kojima et al., 2003). We

used an integrated system of motor and stimulator controls, which makes the feedback cue control more precise and reliable without extra position encoding for the stimulation (Sakuma, 2002). This is particularly advantageous for the cue control of a micro-scaled LC (Kojima et al., 2003). Here, we examined fine-scale localization of mites in programmed illumination fields by using the MLC driven by the control system.

The MLC uses a sliding glass plate, in place of a rotating sphere, to compensate for the locomotion of a test animal. This planar structure ensures very tight clearance of a test chamber above the moving floor, which helps to insulate the interior of the test chamber from the environment. The MLC comprises two major parts: a mobile stage system set on the floor, and a video system with a test chamber suspended from a hanging pillar. The mobile stage system consists of a steel stage (600×600×3 mm) fully covered with a glass plate on a black acrylic board, and a pair of orthogonal motorized slides (SPF86B10-8P, Oriental Motor, Tokyo, Japan), which move the stage to compensate for the locomotion of a test animal. The video system captures the test animal's image with a machine vision camera (CV-M30E, JAI, Yokohama, Japan) equipped with a microscopic lens (TMS-740, HOGA, Kyoto, Japan). A video tracker (G-280, OKK, Tokyo, Japan) processes the image and calculates its location relative to the centre of the frame in real time to transmit the (x, y) coordinates every 1/120s to a computer, which controls the motors by generating pulses with a motor control board (PCPG-46, Cosmotechs, Kanagawa, Japan) to carry the animal back to the centre. A black acrylic test chamber (10 mm i.d.) is suspended from the hanging pillar just above the sliding glass plate, together with the LED illuminator. A clear quartz or glass cover was placed on the top of the chamber. The MLC keeps the mite inside the chamber directly beneath the camera as the mite walks about freely on the glass plate.

The computer logs the signed number of generated pulses every 100 ms to calculate positional shifts in later path analysis. The software also processes the shifts in real time to obtain the mite's location within a programmed chequered pattern of light and dark patches (30×30 mm) that forms a virtual field as described below. The device-control program was modified from the original version created and compiled in Turbo C++ v. 4.0 (Embarcadero Technologies, Tokyo, Japan) to run under PC DOS 2000 (IBM, Tokyo, Japan) (Sakuma, 2002).

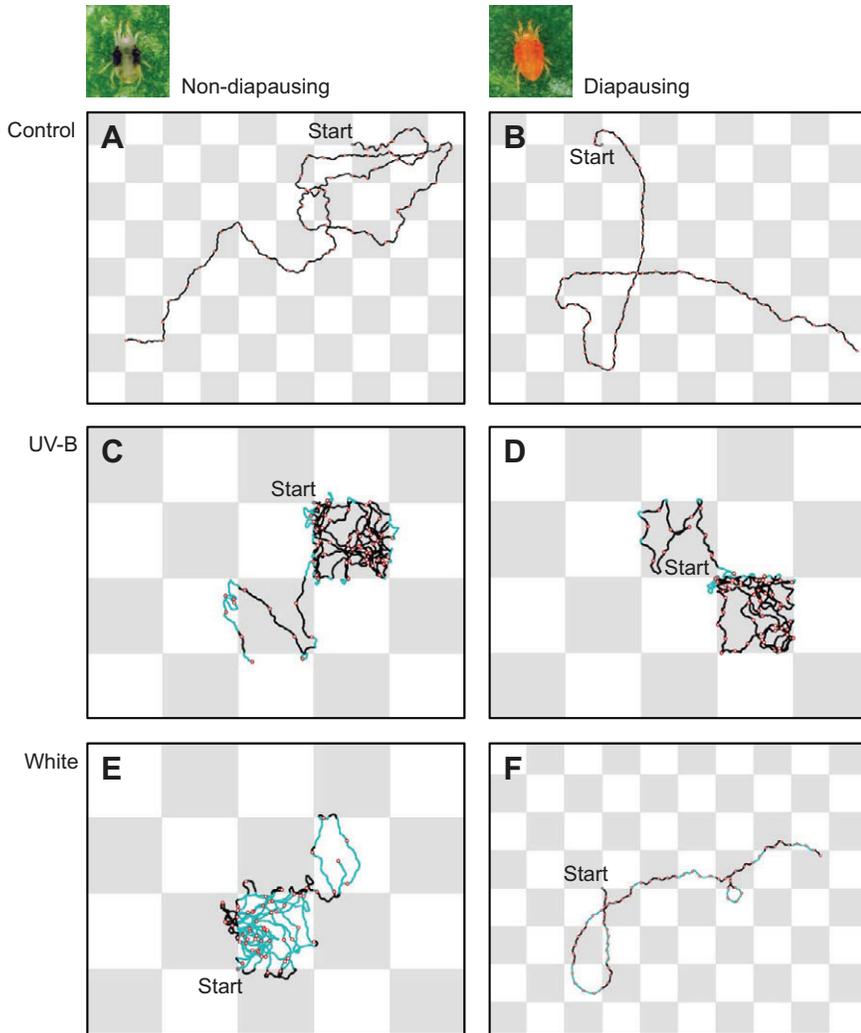


Fig. 2. Walk paths of *Tetranychus urticae* in a virtual field. (A,C,E) Non-diapausing and (B,D,F) diapausing females walked for 10 min in a chequered pattern of light and dark patches (30×30 mm) programmed on the virtual field. White and grey squares indicate light and dark patches, respectively (except in the control treatments). (A,B) Mites walked under continuous dark. (C,D) Mites avoided UV-B ( $\lambda_{\max}=307$  nm,  $2 \text{ W m}^{-2}$ ). (E,F) Only non-diapausing mites sought out white light ( $20 \text{ W m}^{-2}$ ). Colours of path portions indicate the actual illumination status. Red circles plot the mite's location every 10 s.

The illuminator consists of four each of the following LEDs, denoted by the colour and peak wavelength ( $\lambda_{\max}$ ) of their light: UV-B ( $\lambda_{\max}=307$  nm; T9B31, Seoul Optodevice, Kyunggi-do, Korea), UV-A ( $\lambda_{\max}=370$  nm; NSHU590B, Nichia, Tokushima, Japan), white (NSPL500S, Nichia), blue ( $\lambda_{\max}=466$  nm; NSPB500S, Nichia), green ( $\lambda_{\max}=536$  nm; NSPG500S, Nichia) and red ( $\lambda_{\max}=653$  nm; GL5UR3K1, Sharp, Osaka, Japan). These LEDs create light patches under the control of a relay module board (RRY-32, Contec, Osaka, Japan) that switches them on or off when a mite enters or leaves a predefined light patch within the virtual field. An analogue potentiometer (model 7274, BI Technologies, Fullerton, CA, USA) controls the irradiance provided by the LEDs. In addition, four infrared (IR) LEDs ( $\lambda_{\max}=953$  nm; OSIR5113A, OptoSupply, Hong Kong, China) were installed to highlight the mite's image during video tracking, while an IR sharp cut-off filter (IR-80, Fujifilm, Tokyo, Japan) passes only IR to the camera. The irradiance provided by the UV LEDs was measured with a UV meter (UV-340, Custom, Tokyo, Japan) calibrated by a spectroradiometer (USR-45D, Ushio, Tokyo, Japan), and that provided by the VIS LEDs was measured with a spectroradiometer (MS-720, EKO Instruments, Tokyo, Japan).

#### Treatments

Only one colour of light was supplied in each test, and only the illuminator provided light during each test. The irradiance inside

the chamber under the quartz cover was set at 0.02, 0.2 or  $2.0 \text{ W m}^{-2}$  for UV-B and UV-A, and that inside the chamber under the glass cover was set at 0.2, 2.0 or  $20 \text{ W m}^{-2}$  for white, blue, green and red light. As a control, a uniformly continuous dark field was maintained. All treatments were performed for 10 min in a dark room at  $25^\circ\text{C}$  and 50% relative humidity.

#### Data analysis

The acquired positional data were analysed using data analysis software written in Visual C++ with the Microsoft Foundation Class Library (Microsoft, Redmond, WA, USA) (Sakuma, 2002). To evaluate the localization of mites in light patches, we calculated an 'excess proportion index' (EPI) (Sakuma and Fukami, 1985) as:

$$\text{EPI} = (F_L - F_D) / (F_L + F_D), \quad (1)$$

where  $F_L$  and  $F_D$  are the frequencies of the stays in light and dark patches, respectively. The total number of data points ( $F_L + F_D$ ) is 6000 because the computer logs the positional data every 100 ms for 10 min. EPI ranges from  $-1$  (complete localization in dark patches) to  $+1$  (complete localization in light patches). We tested for significant differences in the mean EPIs between each treatment and the control using the Mann-Whitney  $U$ -test.

The sensitivities to UV and VIS relative to those to a reference light were computed by parallel line assay (Finney, 1978) with a probit analysis program (PriProbit) designed for preference testing

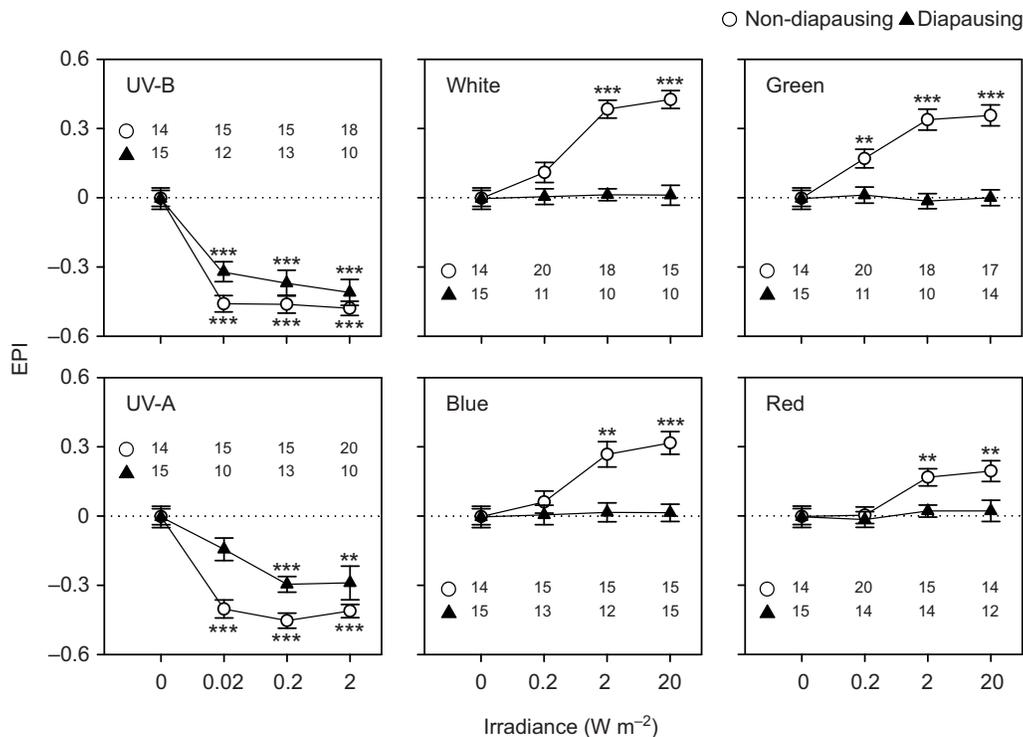


Fig. 3. Photo-orientation responses of *Tetranychus urticae*. The effect of illumination on localization in the light or dark patches is indicated by the excess proportion index (EPI; means  $\pm$  s.e.m.). Values of  $-1$  indicate complete localization in dark patches, values of  $0$  indicate no bias and values of  $1$  indicate complete localization in light patches. EPI was obtained from the frequencies of stays in dark and light patches for each individual, which were incremented every 100 ms for 10 min, i.e. 6000 points in total. Numbers of non-diapausing (open circles) and diapausing (closed triangles) individuals tested are shown for each corresponding irradiance. Values labelled with asterisks differ significantly from the control: \*\* $P < 0.01$ ; \*\*\* $P < 0.001$  (Mann-Whitney  $U$ -test).

(Sakuma, 1998). The program iteratively maximizes the log-likelihood function of probit transformation of EPI on a log dose metameter, in which members are substituted with data points of light and dark patches in a graded series of irradiance, and estimates intercepts and a common slope of the log(dose)-probit equations. The relative sensitivities were calculated with the equations and plotted against the  $\lambda_{\max}$  values of the LEDs to construct an action spectrum for photo-orientation responses of mites.

Analyses were performed in Microsoft Excel 2010, SPSS 11.5J (IBM, Armonk, NY, USA), SigmaPlot 12.0 (Systat Software, Chicago, IL, USA) or PriProbit 1.64 (programmed by M.S.).

## RESULTS

### Walk paths

Both non-diapausing and diapausing females walked with gentle turns in the control (dark) treatment (Fig. 2A,B). However, they remained within the dark patches in the UV-B treatment (Fig. 2C,D) and the UV-A treatment (data not shown): whenever they entered a light patch, they abruptly turned back, even when the irradiance was as low as  $0.02 \text{ W m}^{-2}$ .

In the white light treatment, non-diapausing females exhibited the opposite responses to those in the UV treatments: when they entered a dark patch, they abruptly turned back (Fig. 2E), and subsequently remained within the light patch. Similar behaviour was observed in the blue, green and red light treatments (data not shown). This behaviour was clearly observed in the green light treatment at  $\geq 0.2 \text{ W m}^{-2}$  and in the other VIS treatments at  $\geq 2.0 \text{ W m}^{-2}$ . However, diapausing females failed to show any attraction towards VIS; they walked with gentle turns similar to those in the control treatment

even when the white light irradiance was as high as  $20 \text{ W m}^{-2}$  (Fig. 2F). No attraction towards VIS was observed in the blue, green and red light treatments even at  $20 \text{ W m}^{-2}$  (data not shown).

### Photo-orientation responses

In the UV treatments, EPI values for the non-diapausing and diapausing females were negative and were significantly lower than those ( $\approx 0$ ) in the control treatment, except for diapausing females at a UV-A of  $0.02 \text{ W m}^{-2}$  (Fig. 3). In the VIS treatments, in contrast, EPIs of non-diapausing females were positive and significantly higher than those in the control treatment at  $\geq 0.2 \text{ W m}^{-2}$  (green) and  $\geq 2 \text{ W m}^{-2}$  (white, blue and red). In contrast, EPIs of diapausing females were not significantly different from the control even at  $20 \text{ W m}^{-2}$ .

### Action spectra for photo-orientation responses

In non-diapausing females, the principal peak wavelength of the action spectrum was in the UV region, with a minor peak in the green region (Fig. 4). Within the VIS region, the sensitivity to light decreased in the order of white=green>blue>red light. In diapausing females, the action spectrum was fitted only in the UV region, because  $\text{EPI} \approx 0$  in the VIS treatments (Fig. 3). The sensitivities to UV-B and UV-A were lower than those in non-diapausing females but were still higher than the sensitivities to VIS in non-diapausing females.

## DISCUSSION

Both non-diapausing and diapausing females clearly avoided UV (Fig. 2C,D, Fig. 3). In contrast, only non-diapausing females were

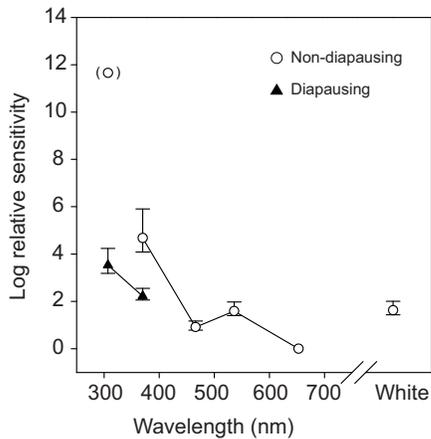


Fig. 4. Action spectra for photo-orientation responses of *Tetranychus urticae*. The spectra are shown as relative sensitivities plotted against  $\lambda_{\max}$  of the LEDs. The sensitivity to red light is set as zero. Sensitivities (symbols with 95% fiducial intervals) were obtained by probit analysis of localization data used in Fig. 3. Although non-diapausing females showed very high sensitivity to UV-B (Fig. 3), the value is shown in parentheses because of difficulties in calculating the fiducial interval.

clearly attracted to VIS (Fig. 2E, Fig. 3). Our study is the first to investigate the negative and positive photo-orientation responses of terrestrial arthropods to UV and VIS in the same experimental system. Storz and Paul (Storz and Paul, 1998) showed similar opposite responses to UV and VIS in the water flea *Daphnia magna* (an aquatic arthropod), and suggested that the distribution of UV and VIS in different water layers was one of the factors that controlled the vertical position of *D. magna* in water.

Plant leaves filter out UV from sunlight before it reaches the chloroplasts, while at the same time passing some photosynthetically active radiation (PAR; 400–700 nm), which almost overlaps the range of wavelengths in VIS (Caldwell et al., 1983). Less than 5% of UV is reflected by the upper surface of a typical leaf, whereas 75 to 95% is absorbed by the epidermis, and the rest by the mesophyll, leading to little or no transmittance of UV through the leaf (Caldwell et al., 1983). Between 85 and 90% of PAR is absorbed by the leaf; the rest (particularly green light) is either reflected at the leaf's upper surface or is transmitted through the leaf (Smith, 1986). Because non-diapausing *T. urticae* females were sensitive to UV in particular as well as to green light (Fig. 4), they may be able to sense differences in the distributions of these wavelengths between the two sides of a leaf and use them as a cue to locate the undersurface of the leaf, like the vertical positioning of *D. magna* (Storz and Paul, 1998). If non-diapausing females only avoid UV, it would be difficult for them to find the undersurface of leaves, and they might move into dark sites with increased risk of starvation. If mites were only attracted to VIS, they would have a high risk of UV damage (Barcelo, 1981; Ohtsuka and Osakabe, 2009; Sakai and Osakabe, 2010; Suzuki et al., 2009). Therefore, non-diapausing females need both UV avoidance and VIS attraction to successfully locate the undersurface of leaves.

Surprisingly, however, diapausing females showed no preference for VIS (Fig. 2F, Fig. 3). To our knowledge, ours is the first report of a lack of response to specific wavelengths during diapause. Although Hussey and Parr (Hussey and Parr, 1963) showed light avoidance in diapausing females of *T. urticae*, the light source (which they did not describe) would have included some UV if they used sunlight or

fluorescent tubes; thus, avoidance of UV would have been induced, as we observed here (Fig. 2D). Mori (Mori, 1962) showed that *T. urticae* females collected in late October (autumn) were less sensitive to light than those collected in summer in Sapporo, Japan (43°N). Although it is unclear whether the less sensitive females were true diapause forms, the result is comparable to the lack of response to VIS by our diapausing females (Fig. 2F), because Mori passed light from an incandescent bulb through a water bath and frosted glass, which would result in VIS alone. However, Mori did not take the result further to consider the winter habitat selection of *T. urticae*. Diapausing females overwinter in dark hibernacula (Veerman, 1985), which probably offer a refuge from UV as well; thus, avoidance of UV is also an adaptive response for diapausing females. Moreover, if diapausing females were attracted to VIS, as in the case of non-diapausing females, they would risk exposure to the abundant UV in leafless trees in winter. Furthermore, a lack of preference for VIS may save energy that can be used to maintain the photoreceptors during diapause. Therefore, the absence of attraction to VIS is also a reasonable adaptation for diapausing females.

The mites showed much higher sensitivity to UV than to VIS (Fig. 4), as did *D. magna* (Storz and Paul, 1998). This difference and the lack of preference for VIS during diapause suggest that *T. urticae* has at least two types of photoreceptors. This mite has adjacent pairs of anterior and posterior eyes, on each side of the propodosoma (McEnroe, 1969; Mills, 1974), and both sets of eyes act as photoreceptors (Suski and Naegele, 1963b). McEnroe and Dronka (McEnroe and Dronka, 1969) suggested that the anterior eyes have photoreceptors for UV and VIS but the posterior eyes have photoreceptors only for UV. The hypothesis that photoreceptors for UV and VIS are independent was also proposed on the basis of electroretinogram analyses of the eyes of spiders (DeVoe, 1967) and scorpions (Machan, 1968).

In animals, the VIS-sensitive molecule rhodopsin and its relatives consist of an opsin and the chromophore retinal (Terakita, 2005).  $\beta$ -carotene, which is the precursor of retinal, is essential for the photoreception involved in the photoperiodic induction of diapause in the predacious mite *Amblyseius potentillae* (Van Zon et al., 1981), suggesting that opsin-based photoreceptors also function in mites. Diapausing *T. urticae* females feed only a little (Veerman, 1985), so the intake of plant carotenoids (e.g.  $\beta$ -carotene) likely decreases. Moreover, hydroxy-keto-carotenoids, which are not found in leaves but are converted from  $\beta$ -carotene, are present in greater quantities in diapausing females than in non-diapausing females, possibly because of the dissolution of these carotenoids in lipids or the lipid moiety of lipoproteins, which are present in increased amount in diapausing females, and consequently the mite's body is orange during diapause (Veerman, 1985) (see inset in Fig. 2). These facts suggest that  $\beta$ -carotene is insufficiently converted into retinal for use in opsin-based photoreceptors in diapausing females, which therefore become blind to VIS. However, sensitivity to UV was preserved even during diapause (Fig. 2D, Figs 3, 4), thus UV photoreceptors might be a non-opsin-based type such as cryptochrome, which is sensitive to short wavelengths, possesses the flavin chromophore, and acts as a photoreceptor in the circadian clock of plants and animals (Cashmore et al., 1999).

Further investigations will be needed to verify the hypotheses that non-diapausing females discriminate between the two sides of a leaf by sensing spatial differences in the distribution of UV and VIS; that diapausing females select dark hibernacula by sensing spatial differences in the distribution of UV; that *T. urticae* has independent UV and VIS photoreceptors; and that the VIS photoreceptor ceases to function during diapause, probably owing

to insufficient conversion of  $\beta$ -carotene to retinal. We anticipate that our findings will provide a basis for examining the role of light in the mites' habitat selection and the effect of seasonal changes in carotenoid metabolism on the photoreception systems.

Furthermore, *T. urticae* is a hard-to-control agricultural pest because of the rapid development of pesticide resistance. Our findings may contribute to the development of a lighting method that disturbs its behaviour using artificial light sources or reflective materials. To incorporate the lighting method into integrated pest management, further investigations of the photo-orientation behaviour of natural enemies will be needed. Interestingly, the predatory mite *Typhlodromalus aripo* hides in the apex of cassava during the day and emerges at night to forage for the herbivorous mite *Mononychellus tanajoa* on young leaves (Onzo et al., 2003; Onzo et al., 2009). Hiding in the apex during the day protects *T. aripo* against the deleterious effects of UV (Onzo et al., 2010). Therefore, providing UV cut-off materials to shelter UV-susceptible natural enemies may reinforce biological control measures.

This paper focuses exclusively on the seasonal change of photo-orientation responses of mites. Our results suggest that the mites compare the light intensities before and after they cross the boundary between light and dark patches because they cannot detect the direction of light in the horizontal plane with only overhead illumination. The abrupt self-steered turn triggered by the onset or cessation of light cues is likely to be the same response seen in klinokinesis and klinotaxis (Kennedy, 1978). Further path analysis (to be published elsewhere) will help to reveal the photo-orientation mechanisms causing localization of the mites under illumination.

#### LIST OF SYMBOLS AND ABBREVIATIONS

EPI	excess proportion index
$F_D$	frequency of the stays in dark patches
$F_L$	frequency of the stays in light patches
LC	locomotion compensator
LED	light-emitting diode
MLC	micro-locomotion compensator
PAR	photosynthetically active radiation
UV	ultraviolet radiation
VIS	visible radiation
$\lambda_{max}$	peak wavelength

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