THE RED PHOTORESPONSE OF THE SPIDER MITE *TETRANYCHUS URTICAE* (ACARINA : TETRANYCHIDAE) [1]

BY

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ABSTRACT.

On the basis of behavioral responses, it was postulated that far red light, but not near IR, has a generalized excitatory effect on motor response. The photoreceptor for this spectral region is not in the eyes.

The directional photoresponse of the summer form of the adult female spider mite *Tetranychus urticae* K. is based on color vision in the near UV and green region (McEnroe and Dronka, 1966). On the basis of behavioral response, separate green and UV receptors were assigned to the anterior eyes and UV receptors were assigned to the posterior eyes (McEnroe and Dronka, 1969). Two photobehavioral classes were separated by their negative or positive photoresponses to green illumination and differences in levels of response to UV illumination. These classes have been referred to as the green + and green — class. The control of these physiological states has been described (McEnroe in press). Teneral females show a phototactic response to green but not UV illumination (McEnroe, 1969 a). The response of mites to skyshine indicated that the photoresponse to the total spectrum is greater than the responses to individual spectral bands (McEnroe, 1969 b).

In studies on the spectral response of this spider mite, the small negative response at 700 mμ was not considered significant (Soans, 1963). However, the negative response index was more than 1 standard deviation away from the positive response index at 650 mμ. As the response index is based on a one minute time constant, the far red spectral region was reinvestigated for a slow kinesis type of photoresponse. The test used in this work included a long time constant to determine if there was a slow behavioral response in the far red region as a long time constant was required to find the slow photonegative response of the green — class.

METHODS.

In general the behavioral test conditions have been previously described (McEnroe and Dronka, 1966). The tests were run at 25° and 20 — 25 % RH in a room with all flat black surfaces. The test arena, 15 × 50 cm, was painted flat black and outlined with Tangelfoot[R]. The green + and green — photobehavioral classes were separated by their responses to green illumi-

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nation. The horizontal illumination was presented at 15° to the surface of the test arena. The vertical illumination was presented at 90° to the surface. The intensity measurements were made with a thermistor type radiometer (bandwidth flat 250-3300 mμ). The spectral regions were isolated as follows : — Klett # 40 near UV ; Wratten # 54 green ; # 660, high pass, far red and IR ; Wratten # 88A, high pass for IR. Both the # 660 and 88A had approximately the same transmission in the near IR (Fig. 1). The difference in transmission of these two filters was a narrow region of the far red centered around 670 mμ (Fig. 1). The intensity of this band, the 670 mμ region (Fig. 1), was measured by taking the IR passed by the 88A filter as the dark current and setting the intensity scale at zero. The 88A filter was then replaced by the # 660 filter and the intensity measured was taken as the 670 mμ band. The intensity levels used were as follows : # 660, positive end 10 mw/cm², center 2.0 mw/cm², negative end 0.2 mw/cm² ; 88A, 9 mw/cm², 1.8 mw/cm², 0.18 mw/cm² by difference for the 670 mμ band, 1.0 mw/cm², 0.2 mw/cm², and 0,02 mw/cm². These levels were held constant during the tests with horizontal illumination. In the tests where vertical red illumination was used, a uniform intensity level of 1,0 mw/cm² (670 mμ) was maintained.

The response index (RI) and RI versus intensity for the behavioral classes has been described (McEnroe and Dronka, 1966).

Results.

About 200 adult female mites were placed in the center of the test arena and exposed to the horizontal red (# 660) illumination. Within two hours all the mites were at the negative end away from the light source. The # 660 filter was then replaced by the 88A filter, which maintained the same IR intensity level. After 2 hours the mites appeared to be randomly distributed in the test arena. These paired tests were repeated 4 times with the same results. Therefore, the negative photoresponse was due to the far visible red region passed by the 660 filter rather than the IR component passed by the 88A filter. This is the 670 mμ spectral region show in Fig. 1.

The slow accumulation of mites at the end of the arena away from the light source, appeared to be the result of descreasing random activity along the intensity gradient, rather than a directional orientated response away from the light source. There was a qualitative difference in the negative response to green and red illumination. The green — mites, in response to green illumination, piled up on the Tangelfoot barrier. In contrast, the mites, in response to red illumination, accumulate at the negative end but were not driven onto the Tangelfoot barrier. This qualitative difference in a crude measure of the difference in level of negative photoresponse.

The initial tests for the response to red light were made with mixed green + and green — classes of mites. The mites for the next series were separated into the green + and green — photobehavioral classes. The mites were placed in the center of the arena and the mites were scored as negative in the last 2 cm area away from the light source. The results of the photoresponse to # 660 and 88A illumination are shown for the green + and green — mites in Fig. 2. The rates of accumulation of negative mites from # 660 illumination, green + 4 %/min. versus green — 1.5 %/min., shows the increased sensitivity of the green + class to this stimulus. The response of these classes to 88A illumination showed only a small negative reaction which indicates that the photoreceptor is centered in the 670 mμ region (Fig. 2).

In the next test, green + mites were illuminated with horizontal UV illumination at an intensity to stimulate the maximum response index. The response of the green + class to hori-

RELATIVE TRANSMITTANCE (%)

660 670 88A

600 700 800

λ mμ

1

PHOTONEGATIVE MITES (%)

GREEN   +   660 88a
             ⊙   ●
         —   △   ▲

15   .30

TIME (MINUTES)

2

NUMBER OF MITES

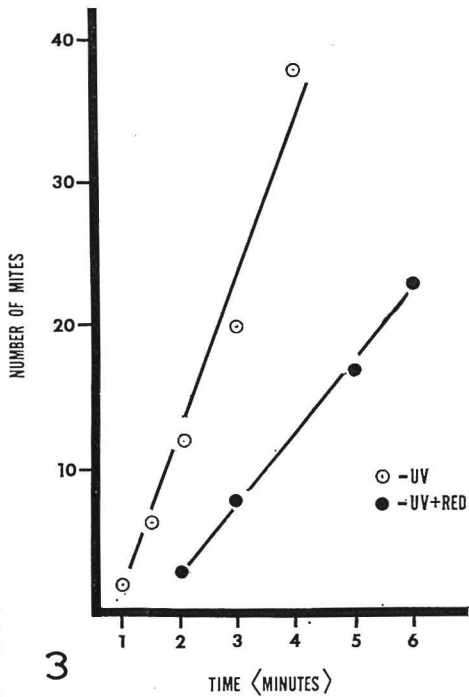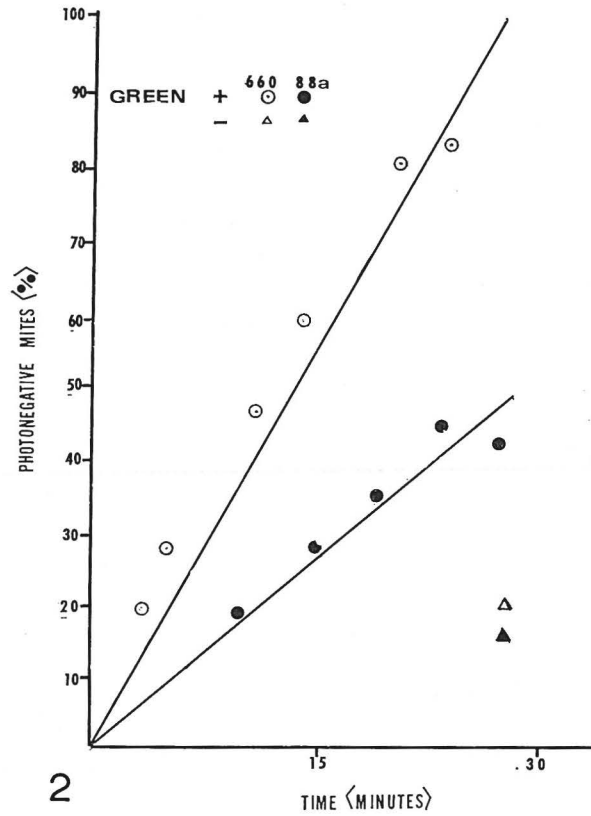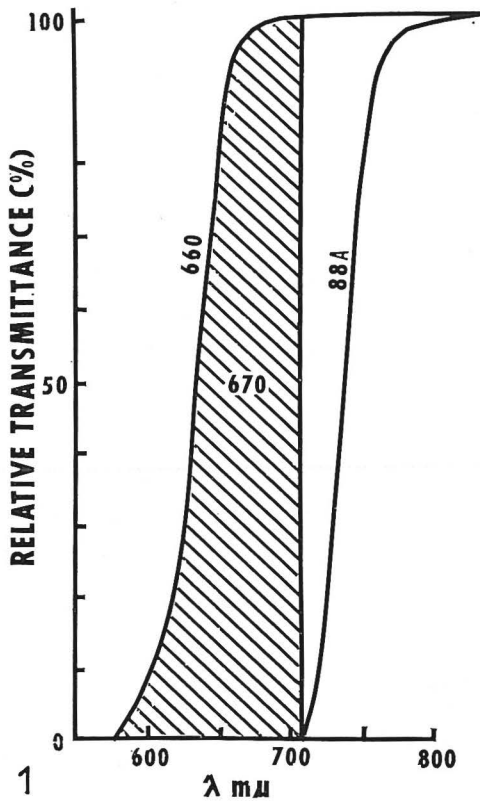⊙ −UV
● −UV+RED

1 2 3 4 5 6

TIME (MINUTES)

3

FIG. 1 : Relative transmission of # 600 filter (far red and IR) and Wratten # 88A filter (IR). The difference in spectrum, 670, is shown by the shaded area.

FIG. 2 : Photonegative response of green + and green — classes to 660 (far red + IR) and 88A (IR) illumination. 100 mites per test.

FIG. 3 : Positive response to UV illumination showing the additive effect of red illumination. Each test based on 100 mites.

zontal UV illumination has been shown to involve the anterior and posterior pair of eyes and is a directional response. Paired tests were run with and without the test arena uniformly illuminated from above by red light with the 670 mμ band at an intensity of 1.0 mw/cm². The positive photoresponse to the combined sources of illumination was scored as the cumulative number of mites moving more than 12 cm toward the UV source versus time (Fig. 3). The added red illumination had the effect of increasing the proportion of the test population which moved > 12 cm per unit time. This increase was not due to an increase in net speed along the axis of the UV source. The average speed of 10 mites which traveled the 12 cm without pause was 42.7 mm/min. with the red light and 41.3 mm/min. without the red light. The effect of the red illumination was to maintain a constant directional response to the UV source. The overall average speed (Fig. 3) for the mites under red illumination was 40 mm/min. and without red illumination was 30 mm/min. This apparent change in speed reflects the maintenance of a constant directional response.

The next series of tests were designed to see if red illumination would lower the threshold of photoresponse to UV stimulation. Green + mites were tested with horizontal UV illumination with and without added red illumination. A level of UV illumination which gave a submaximal response index of + 27 was used. This response was based on a test of 200 animals. The red illumination was added with a second source parallel to the UV source. The response index with added red light was increased to + 58, a change equal to doubling the intensity of the UV source.

The next series of tests were designed to study the interaction of red and green light on photoresponse. The mites continued to separate into green + and green — behavioral classes in response to green illumination when the test arena was illuminated at + 90° with red light at 1.0 mw/cm². Horizontal green illumination was adjusted to give response index of + 8 for 200 green + mites. A second source in parallel was used to add red illumination as previously described. The effect of the added red illumination was to raise the response index to + 47. The effect of the added red illumination was again the same as doubling the intensity level of the green illumination.

The negative photoresponses resulting from green or red illumination show opposite interactions with UV illumination. Although red illumination alone results in a negative response in green + mites, it lowers the threshold of positive response to a UV or green stimulus. In contrast, the photonegative response of green — mites to green illumination can override and decrease the positive response to UV stimulus (McENROE, 1969). Moreover the green photoresponse can be demonstrated at an intensity level of one order of magnitude lower than that required for the red photonegative response.

The red guard oil, which surrounds the eyes is transparent in the far red region. Red light therefore can enter through the side of the eye and penetrate into the receptor area (McENROE, 1969 c). Overhead (+ 90°) red illumination does not abolish the UV or green + phototaxis. The failure of overhead red illumination to block the photoresponse to green or UV supports ; (1) the absence of response of photopigments in the eye to far red light and ; (2) the location of the red light receptors outside the eyes. Furthermore, the constant negative response to red light, in contrast to the positive response to both green and UV illumination, lends further support for the independence of the red receptors. The different behavioral responses to red illumination can be caused by a lowering of the threshold for motor response. The negative photo response along an intensity gradient of red illumination would thus result from a decrease in random activity at the lowest intensity. The additive effect on positive photoresponse with green or UV illumination also would be due to the lowered threshold for stimulus. On the basis

of the above behavioral responses, it is postulated (1) that the red spectral region around 670 mμ lowers the threshold for motor activity, and (2) the photoreceptor(s) is not located in the eyes.

DISCUSSION.

The far red spectrum has little or no effect on the photobehavior of insects. (Review by GOLDSMITH, 1961). The apparent peak in spectral effectiveness (measured by ERG) in the far red found in the eye of *Calliphora erythrocephala* has been attributed to light scattered through the shielding pigment (GOLDSMITH, 1965). Electrophysiological measurements showed no red receptors in the eyes of a spider or scorpion (DEVOE et al 1969, MACHIAN 1968). In these groups, related to the Acarina, there is apparently no photoreceptor in the eye which shows a response centered in the far red spectral region. In the crustaceans, Daphnia has a photobehavioral response which extends into the red spectral region (KOEHLER, 1924) and the water flea, Cladocera, has a behavioral response, the 'red response' specific for the red region (SMITH and BAYLOR, 1953). In eyeless mites behavioral responses have been found in the red spectral region (STERNLICHT 1969, WOODRING 1966). As these animals are small and semi-transparent, the receptor area may be in the central nervous system. The direct stimulation of photoreceptor neurons has been reviewed by KENNEDY (1964) and carotenoids are believed to serve as a photopigment in specialized neurons. In the mollusc Spisula, red light was found to have a direct effect on the excitatory process (KENNEDY 1960). The red light may stimulate the CNS directly in this mite. The photobehavior of ticks can be accounted for by direct stimulation of the CNS (GEORGE 1963). A photosensitive region has been found on the front legs of the snake mite (CAMIN 1953), however, the removal of the front legs of the spider mite had little effect on their photobehavior (SUSKI and NAEGELE 1963).

Under field conditions, the effect of the red stimulus would be to reinforce the phototaxis of the mites in their migratory activities. The migratory phase of SUSKI and NAEGELE (1963) is the equivalent of the green + class (McENROE in press). The decreased effect of red light on the green — class and the cutoff of response in the IR, a region of high leaf reflectance, raises the threshold for photostimulation during the feeding period.

The overwintering stage of the adult female is negatively phototropic (PARR and HUSSEY 1963). This negative photoresponse is not based on the response to red or green light alone. The overwintering female also shows a negative photoresponse in the UV region (McENROE unpublished). In the overwintering female, the fat deposits in the midgut are opaque in the far red region (McENROE 1970) and would shield the CNS from red light during this quiescent stage.

REFERENCES CITED

1. CAMIN (J. H.), 1953. — Observations on the life history and sensory behavior of the snake mite, *Ophionyssus natricis* (Gervais) (Acarina : Macronyssidae). — Chicago Acad. Sci. Spec. Publ., **10**, 75 p.

2. DEVOE (R. D.), SMALL (R. J. W.) and ZVARGULIS, 1969. — Spectral sensitivities of wolf spider eyes. — J. Gen. Physiol., **54** : 1-32.

3. GEORGE (J. E.), 1963. — Responses of *Haemaphysalis leporispalustris* to light. — Adv. Acarology, **1** : 425-434.

4. GOLDSMITH (T. H.), 1961. — Color vision of insects. — *In* Light and Life The Johns Hopkins Press, Baltimore, Md. pp. 771-94.

5. GOLDSMITH (T. H.), 1965. — Do flies have a red receptor ?. — J. Gen. Physiology, **49** : 265-7.

6. KENNEDY (D.), 1960. — Neural Photoreception in a Lamellibranch mollusc. — J. Gen. Physiol., **44** : 277-99.

7. KENNEDY (D.), 1964. — The photoreceptor process in lower animals. — *In* Photophysiology II ed. A. C. Giese Academic Press, N. Y., N. Y.

8. KOEHLER (O.), 1942. — Uber das Farbensehen von *Daphnia magna*. — Z. vergl. Physiol., **1** : 84-174.

9. MACHAN (L.), 1968. — Spectral sensitivities of scorpion eyes and the possible role of shielding pigment effect. — J. Exp. Biol., **49** : 95-105.

10. McENROE, (W. D.), in press. — Photobehavioral classes of the spider mite *Tetranychus urticae* Koch.

11. McENROE (W. D.), 1969 *a*. — Spreading and inbreeding in the spider mite. — J. Heredity, **60** : 343-5.

12. McENROE (W. D.), 1969 *b*. — The photoresponse to skyshine of the two-spotted spider mite, *Tetranychus urticae* K. — Acarologia, **11** : 281-3.

13. McENROE (W. D.), 1969 *c*. — Eyes of the female two-spotted spider mite, *Tetranychus urticae* K. I. — Morphology Ann. Entomol. Soc. America, **62** : 461-66.

14. McENROE (W. D.), 1970. — Fat in the midgut walls of the overwintering two-spotted spider mite *Tetranychus urticae*. — Ann. Entomol. Soc. America, **63** : 000-000.

15. McENROE (W. D.), and DRONKA (K.), 1966. — Color vision in the adult female two-spotted spider mite. — Science, **154** : 782-4.

16. McENROE (W. D.), and DRONKA (K.), 1969. — Eyes of the female two-spotted spider mite, *Tetranychus urticae*. II Behavioral analysis of the photoreceptors. — Ann. Entomol. Soc. America, **62** : 466-9.

17. PARR (W. J.) and HUSSEY (N. W.), 1966. — Diapause in the glasshouse red spider mite (*Tetranychus urticae* Koch). A synthesis of present knowledge. — Hort. Res., **6** : 1-21.

18. SMITH (F. E.), and BAYLOR (E. R.), 1953. — Color responses in the Cladocera and their ecological significance. — Amer. Nat., **87** : 49-55.

19. SOANS (A. B.), 1963. — Response of the two-spotted spider mite *Tetranychus urticae* Koch. to limited regions of the spectrum. — Ph. D. thesis Cornell Univ., Ithaca, N. Y.

20. STERNLICHT (M.), 1970. — Effect of different wave lengths of light on the behavior of an eriophyid mite *Aceria sheldoni*. — Ent. exp. & app., **12** : 377-82.

21. SUSKI (Z. W.) and NAEGELE (J. A.), 1963. — Light response in the two-spotted spider mite II Behavior of the " Sedentary and Dispersal " phases. — Advan. Acarology, **1** : 445-53.

22. WOODRING (J. P.), 1966. — Color phototactic responses of an eyeless oribatid mite. — Acarologia, **8** : 382-8.

Note added in proof.

R. MILLS (personal communication) in his survey of the fine structure of the central nervous system of this mite has found structures in the optic lobe which appear to be morphologically identical to rhabdomeres. These structures would serve as the postulated light receptors in the CNS.