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VISUAL ORIENTATION OF CERTAIN TROPICAL INSECT SPECIES

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The visual sense of insects has been studied from many points of view, from studies on the extent of the sensitivity of the insect eye (AUTRUM, 1957; CAMERON, 1938; WEISS, 1943) through those determining colour discrimination, especially in bees (DAUMER, 1956; VON FRISCH, 1915) and other insect species (BERTHOLF, 1940; BURKHARDT, 1964; ILSE, 1929, 1949; NOLTE, 1959), to studies checking these capacities by physical (MAZOCHIN-PORSCHNIAKOV, 1959; BOWNES & WOLKEN, 1958) and electro-physiological methods (AUTRUM, 1958). These problems, however, are closely related to those of orientation of insects in their environment. The problems involved here pertain, on one hand, to orientation according to the direction, source and wave lengths of incident light and, on the other hand, to orientation according to the colour of the substrate, the two aspects being closely related (HECHT, 1964). While insects are capable of perceiving a fairly wide range of the light spectrum, from ultraviolet (wave length shorter than 300 nm) to yellow (wave length shorter than 600 nm), various wave lengths are not of equal importance for the orientation of various insects in their environment. We concentrated our attention towards this facts in our previous studies. On the basis of the available data in the above-cited papers as well as from our own experiments, we are inclined to believe that ultraviolet light is of major importance, while a minor part is also played by green-yellow light. Aphids provide an exception where green-yellow light is of major importance (POSPÍŠIL, 1962, 1963; POSPÍŠIL & ŽĎÁREK, 1965; ŽĎÁREK & POSPÍŠIL, 1966; HARAGSIM & POSPÍŠIL, 1969). Similarly, in the orientation of insects on alighting on some substrate either in the search for food or for oviposition, the capacity of the substrate to reflect light of a certain wave length (ultraviolet light according to some authors, but also green-yellow light) is essential.

Previous studies on visual orientation of alate aphids of the temperate zone tend to indicate that these aphids are most strongly attracted by green-yellow light of wave length around 550 nm (KENNEDY & BOOTH, 1961; MOERICKE, 1952, 1956; ŽĎÁREK & POSPÍŠIL, 1966). Throughout their life alate forms of aphids are not attracted by light wave lengths from 350 to 450 nm or 600 nm and over, i.e., by ultraviolet, violet, blue and orange to red light. Moreover, aphids searching for a substrate to alight upon have been found to be attracted by yellow. Based on these observations, the so-called Moericke's dishes have been widely used to trap alate aphids of the temperate zone under natural conditions throughout the period of their occurrence. First attempts at applying this method to trap alate aphids in the tropics (Cuba), have met with no success. This, too, stimulated the necessity of examining the visual orientation of alate aphids in that region.

The visual orientation of *Coleoptera* and *Diptera* in the temperate zone has also been investigated by a number of the above-mentioned authors. Flies and beetles were found to be most strongly attracted by light of shorter wave lengths, i.e., by ultraviolet light. It was also found that green-yellow light plays an important part in this respect particularly in insetcs damaging cultivated plants. Some authors, however, do not consider this to be of importance, and connect even this with the capacity of the substrate to reflect ultraviolet light.

As mentioned above, most of the experiments have been carried out in the temperate zone. The fact that in this region the sunlight spectrum contains mostly light with wave lengths between 450 and 550 nm, i.e., green-yellow, can explain the increased importance of this colour for the visual orientation of insects. Since in the tropics the contents of wave lengths of the ultraviolet range in the sunlight spectrum is about 1/3 higher than in the temperate zone, this light may be assumed to be of still greater importance for the visual orientation of insects in the tropics than in the temperate zone. I based my experiments in Cuba in 1968 on this assumption.

MATERIAL AND METHODS

Due to their being easily accessible in large numbers, the following insect species were selected for the experiments described below:

Aphis gossypii GLOWER *(Homoptera)*
Peregrinus maidis ASHMEAD *(Homoptera)*
Lixophaga diatraeae TOWNSEND *(Diptera)*
Macroaltica jamaicensis FABRICIUS *(Coleoptera)*

The aphid *Aphis gossypii* occurs in Cuba in large numbers on various plants; it is mainly a pest of cucumbers. Aphids used in the experiments were collected in the field and kept in the laboratory on cucumbers *(Cucurbita pepo)* and tradescantias *(Comelina elegans)* for one to three days until the development of alate forms. For experiments on orientation to light of different wave lingths, newly winged aphids were collected each morning after dawn from the walls of the cages, and used in experiments immediately or at most within two hours after being collected.

In experiments on orientation to coloured substrates, the aphids collected from the cage walls in the morning were placed in an empty cage 25 by 25 by 40 cms and kept there until the next day. The cage was rotated at times against incident light to induce movements of the aphids within the cage. On the next day, the aphids were used for the above experiments. Experiments on both the above types were conducted at ambient temperature around 30° C.

The leafhopper *Peregrinus maidis* is one of the major pests of maize, both directly and indirectly as a vector of a virus disease. It is very vagrant although it spends most of its life on one plant, especially in the nymphal stage. Visual orientation in leafhoppers has not been studied as yet. The leafhopper was selected because it is an insect whose environmental requirements and movements are similar to those of aphids. Our experiments involved leafhoppers bred for a complete generation on young maize plants in a nylon cage under natural conditions of tropival summer, i.e., at ambient temperatures around 30° C., maximum relative air humidity and sunshine. The experiments were carried out under the same temperature and humidity conditions.

Lixophaga diatraeae is a tachinid fly whose larvae parasitize the larvae of the sugarcane borer, *Diatraea saccharalis* F. In our experiments, we used adult flies which emerged within a span of two days, 3 to 5 days old, male and female, and starved for one day. The ambient temperature during our experiments varied between 25 and 30° C.

Macroaltica jamaicensis is a phytophagous beetle feeding on leaves of various swamp plants, above all, *Jussiaea suffruticosa*, and is easy to collect and keep in large numbers. Our experiments involved beetles two weeks after emergence, kept in a nylon cage under natural conditions of that area and season, at ambient temperatures of 20 to 30° C., relative air humidity around 50% and thirteen hours of daylight, in sunlight, so that no adaptation to artificial light could have occurred. Young plants of *Jussiaea suffruticosa* were daily available to the beetles to feed on; on the days of experiments, no food was available to them since the early morning, so that the beetles were very lively. The experiments were conducted at ambient temperatures between 25 and 30° C. as then the beetles showed maximum activity.

In experiments with orientation to light of different wave lengths, we used a phototropometer of the same type as that used in our earlier studies. Substantially, it is a T-shaped tube, the lower arm of which serves to let the insect in. Into each of its two opposite horizontal arms, a system of aluminium mirrors throws non-polarized, monochromatic light of equal quality, with intensity varying around 4,000 1 × . The light enters the tube directly from both opposite sides. The source of light was a xenon fluorescent tube, 150 W, 220 V. The light, coming from a point source, is transformed by a lens to form a bundle of parallel rays more than 50 mm in diameter. Monochromatic light was obtained by using interference filters (Tab. 1). A recent modification of this apparatus has been described by HARAGSIM & POSPÍŠIL (1969).

TABLE 1

Technical data of metal interference filters used in the phototropometer

Light colour	max A	D max %	HwBr A
ultraviolet	357	24.0	23.0
ultraviolet	379	27.0	14.0
violet	417	33.3	9.8
blue	461.3	43.1	8.3
green	517	37.8	9.0
green-yellow	547	31.1	7.4
yellow	562	47.6	12.6
orange	583.3	38.5	10.6
red	638.3	29.6	10.1
infra-red	800	28.0	8.0

In the range of green-yellow light, several filters were used, providing light with shorter intervals of wave lengths, as in this range the insects show altered orientation to light. Filters producing monochromatic light with wave length shorter than 357 nm were not used as they decrease the intensity of light sources including sunlight.

The wave lengths were tested in pairs against each other. The percentages of beetles showing response to individual wave lengths were added and the sums plotted in a diagram. The diagram also indicates how many times each of the light colours used was significantly more attractive.

In experiments with the orientation of aphids to substrates of different colours, we used a cage, 15 by 15 by 15 cms in size, with plexiglass walls, a nylon gauze top, and the bottom covered with brown paper. On the bottom was placed a thin plexiglass plate, 6 by 15 cms, coated with a colourless, transparent, nondrying glue; beneath this plate were placed two paper discs 5 cms in diameter, painted various colours. We tested yellow colour in combination with blue, blue-green, green and red.

EXPERIMENTAL RESULTS

1. Orientation to light of different wave length

The results given in Table 2 indicate that immediately after getting winged, the aphid *A. gossypii* shows a significant photopositive response to ultraviolet light, i.e., light with wave length between 357 and 379 nm, preferring it to all other colours of the light spectrum, including green and yellow. The winged aphids still show a positive response to light with wave length between 400 and 562 nm and can distinguish between these two wave length ranges, preferring these ranges, i.e., blue, green and yellow light to light with longer wave lengths, i.e., orange and red. In addition, they show an insignificant preference for green-yellow and yellow light to blue

TABLE 2

wave length in nm	*Aphis gossypii* attracted	*Aphis gossypii* per cent	*Aphis gossypii* did not fly	*Aphis gossypii* statistical significance	*Lixophaga diatraeae* attracted	*Lixophaga diatraeae* per cent	*Lixophaga diatraeae* did not fly	*Lixophaga diatraeae* statistical significance	*Macroaltica jamaicensis* attracted	*Macroaltica jamaicensis* per cent	*Macroaltica jamaicensis* did not fly	*Macroaltica jamaicensis* statistical significance	*Peregrinus maidis* attracted	*Peregrinus maidis* per cent	*Peregrinus maidis* did not fly	*Peregrinus maidis* statistical significance
357	29	64	5	—	16	70	11	+	19	100	14	+	21	66	10	—
379	19	36			7	30			—	—			11	34		
357	51	100	2	+	28	100	9	+	35	95	2	+	36	97	5	+
419	—	—			—	—			2	5			1	3		
357	52	100	—	+	21	100	7	+	34	100	2	+	38	100	2	+
461	—	—			—	—			—	—			—	—		
357	52	100	—	+	22	100	19	+	36	100	6	+	32	91	5	+
517	—	—			—	—			—	—			3	9		
357	52	100	—	+	21	100	18	+	34	100	12	+	37	92	—	+
547	—	—			—	—			—	—			3	8		
357	47	98	3	+	27	100	21	+	30	100	3	+	38	98	1	+
562	1	2			—	—			—	—			1	2		
357	49	96	—	+	16	100	15	+	19	100	15	+	28	80	5	+
583	2	4			—	—			—	—			7	20		
357	50	100	—	+	26	100	14	+	30	100	—	+	29	83	5	+
638	—	—			—	—			—	—			6	17		
357	50	100	—	+	21	100	16	+	25	100	16	+	37	100	3	+
800	—	—			—	—							—	—		
379	48	96	—	+	22	100	14	+	32	94	4	+	31	97	4	+
418	2	4			—	—			1	6			1	3		

379 461	47 3	94 6	—	+	*x*	17 —	100 —	12	+		23 1	96 4	21	+	35 2	95 5	2	+
379 517	45 3	94 6	2	+		25 —	100 —	18	+		27 —	100 —	11	+	37 —	100 —	4	+
379 547	46 2	96 4	2	+		27 —	100 —	16	+		30 1	97 3	15	+	37 3	92 8	1	+
379 562	36 3	92 8	2	+		22 —	100 —	18	+		27 4	87 13	7	+	31 6	84 16	4	+
379 583	47 3	94 6	1	+		22 —	100 —	16	+		17 3	85 15	21	+	32 6	84 16	3	+
379 638	49 2	96 4	—	+		23 —	100 —	17	+		24 1	96 4	26	+	35 4	90 10	2	+
379 800	50 —	100 —	1	+		25 —	100 —	14	+		26 —	100 —	38	+	36 1	97 3	4	+
419 461	42 7	86 14	2	+		11 6	69 31	17	—		17 1	94 6	16	+	14 3	82 18	10	+
419 517	34 14	71 29	2	+		10 —	100 —	31	+		12 —	100 —	32	+	11 4	73 27	12	+
419 547	24 25	49 51	4	—		9 —	100 —	28	+		14 1	93 7	68	+	16 4	80 20	7	+
419 562	26 21	55 45	5	—		16 —	100 —	24	+		15 2	88 12	52	+	16 4	80 20	7	+
419 583	32 6	84 16	6	+		10 —	100 —	27	+		15 —	100 —	28	+	22 2	92 8	3	+
419 638	39 1	97 3	1	+		19 —	100 —	25	+		14 1	93 7	46	+	22 3	88 12	2	+
419 800	41 —	100 —	—	+		29 —	100 —	14	+	*x*	32 —	100 —	18	+	24 2	92 8	1	+

TABLE 2 (cont.)

wave length in nm	*Aphis gossypii* attracted	per cent	did not fly	statistical significance	*Lixophaga diatraeae* attracted	per cent	did not fly	statistical significance	*Macroaltica jamaicensis* attracted	per cent	did not fly	statistical significance	*Peregrinus maidis* attracted	per cent	did not fly	statistical significance
461	31	61	5	—	10	100	28	+	17	78	48	+	18	72	2	+
517	20	39			—	—			5	22			7	28		
461	16	41	6	—	15	100	38	+	8	44	34	—	20	80	2	+
547	28	59			—	—			10	56			5	20		
461	11	26	5	+	18	95	12	+	20	77	28	+	20	80	2	+
562	32	74			1	5			6	23			5	20		
461	29	67	5	+	14	100	16	+	17	65	56	—	22	88	2	+
583	14	33			—	—			9	35			3	12		
461	41	91	3	+	24	100	12	+	17	81	24	+	22	92	3	+
638	4	9			—	—			4	19			2	8		
461	43	93	1	+	18	100	15	+	16	100	18	+	24	96	2	+
800	3	7			—	—			—	—			1	4		
517	14	38	6	—	3	17	18	+	8	44	22	—	14	64	8	—
547	23	62			15	83			11	58			8	36		
517	8	23	8	—	3	19	12	+	14	54	15	—	23	92	5	+
562	27	77			13	81			12	46			2	8		
517	31	76	6	+	19	100	11	+	22	76	16	+	24	86	2	+
583	10	24			—	—			7	24			4	14		
517	38	90	5	+	16	94	14	+	24	86	11	+	26	96	3	+
638	4	10			1	6			4	14			1	4		

517	39	89	4	+	21	95	11	+	32	100	22	+	25	89	2	+
800	1	2			1	5			—	—			3	11		
547	19	61	5	—	5	36	17	—	16	64	17	—	28	100	1	+
562	12	39			9	64			9	36			—	—		
547	21	75	4	+	19	100	11	+	15	65	14	—	27	100	2	+
583	7	25			—	—			8	35			—	—		
547	26	93	2	+	23	100	19	+	29	85	11	+	26	93	—	+
638	2	7			—	—			5	15			2	7		
547	28	97	1	+	21	95	18	+	28	74	6	+	22	92	2	+
800	1	3			1	5			10	26			2	8		
562	21	73	2	+	17	81	16	+	15	68	8	—	21	87	2	+
583	8	27			4	19			7	32			3	13		
562	26	87	1	+	23	88	17	+	18	60	11	—	22	88	1	+
638	4	13			3	12			12	40			3	12		
562	27	96	2	+	24	96	15	+	24	60	3	—	23	92	1	+
800	1	4			1	4			16	40			2	8		
583	26	90	1	+	17	90	18	+	12	57	8	—	22	100	1	+
638	3	10			2	10			9	43			—	—		
583	29	97	—	+	19	90	17	+	16	48	3	—	20	95	2	+
800	1	3			2	10			17	52			1	5		
638	27	93	1	+	4	80	34	—	19	68	8	+	14	87	6	+
800	2	7			1	20			9	32			2	13		

and blue-green light, i.e., they prefer wave lengths around 550 nm to those between 400 and 540 nm.

The diagram in Fig. 1 indicates that alate forms of *A. gossypii*, like other insects, can percieve and distinguish colours of the whole range visible to them, i.e., wave lengths from 562 nm down to the range of ultraviolet light, i.e., wave lengths shorter than 400 nm. Hence, they perceive ultraviolet, violet, blue, green and yellow light but do not perceive or respond

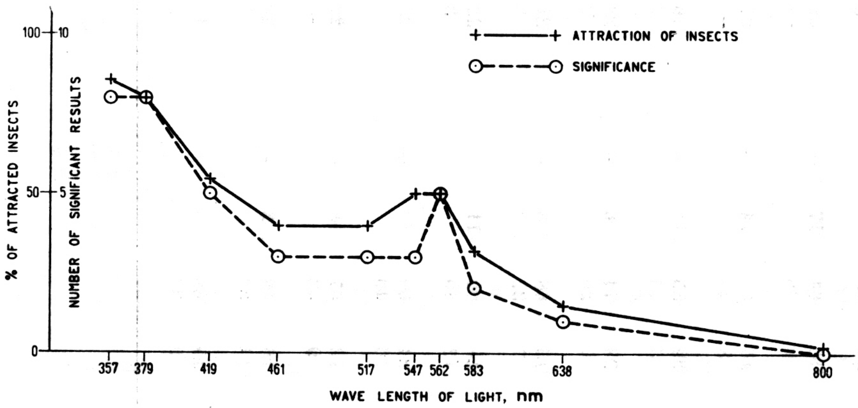

Fig. 1: Orientation of *Aphis gossypii*

to orange and red light. At the same time, the decisive part in their orientation is played by ultraviolet light, the remaining colours of the light spectrum being of inferior importance.

Much the same results, just slightly different in the green and yellow range of the spectrum, have been obtained with the leafhopper *P. maidis*. The results given in Tab. 2 indicate that in choosing between two light

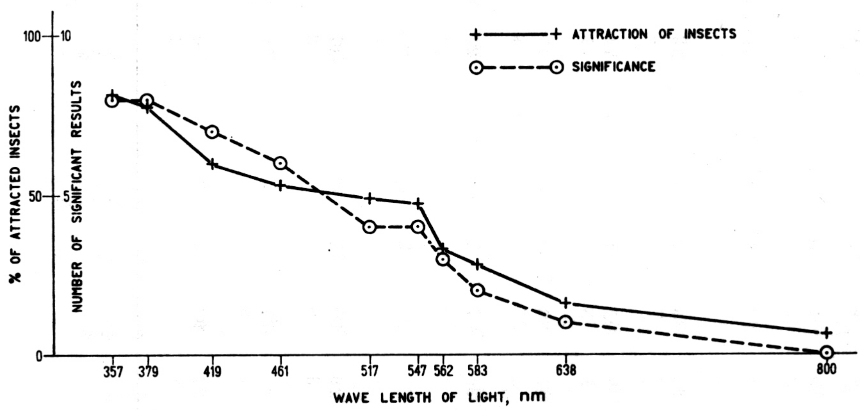

Fig. 2: Orientation of *Peregrinus maidis*

colours, the leafhopper significantly prefers that of shorter wave length even if the wave lengths are very close to one another. Only in the range of ultraviolet and green light, is its capability of distinguishing between two wave lengths impaired. As seen in Fig. 2, the lights most important for the orientation of *P. maidis* are those with wave lengths shorter than 550 nm, i.e., green-yellow, green, blue, violet and ultraviolet light. The leafhopper shows no response to lights of longer wave lengths, i.e., to yellow, orange, red and infra-red light, and invariably prefers all other colours of the light spectrum. No difference in orientation to light has been found, between adults and nymphs of *P. maidis*. For this reason, adults were used in our experiments; some of the results were checked with nymphs but the results there of are not stated here.

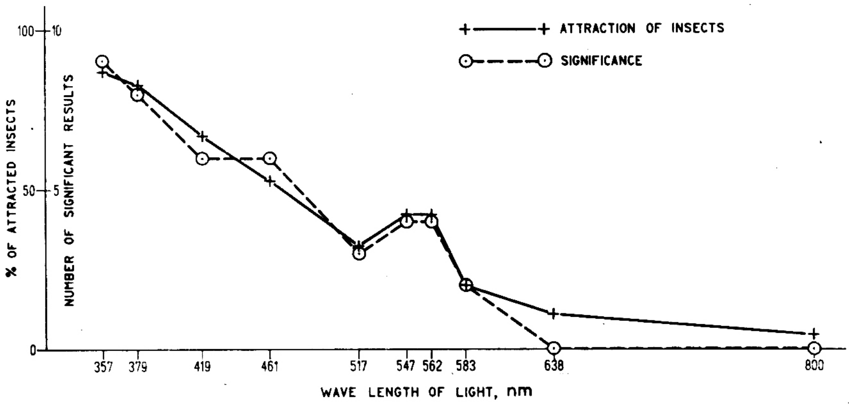

Fig. 3: Orientation of *Lixophaga diatraeae*

Similarly, adults of *L. diatraeae* (Tab. 2) are significantly attracted by light with wave lengths shorter than 550 nm. They distinctly prefer wave lengths shorter than 500 nm to all other lengths, i.e., they prefer blue, violet and ultraviolet light. As seen in Fig. 3 and Table 2, light with wave length around 550 nm showed some increased attraction, whereas that with wave length greater than 580 nm failed to attract the flies completely. Thus, light with short wave lengths is of the greatest importance for the orientation of tachinid flies, as is the case with flies in general.

The beetle *M. jamaicensis* (Tab. 2) also shows a significant photopositive response to violet and ultraviolet light (wave lengths 419 to 357 nm), mostly preferring light of shorter wave lengths to all others, markedly distinguishing them from one another. Again, it showed a certain capability of orientation in the range of green and blue light, i.e., wave lengths 461 to 547 nm. It significantly preferred this light to yellow, orange, red and infrared light, i.e., to wave lengths over 562 nm. The beetles of this species could hardly distinguish light colours in the range of blue to green. Similarly, they showed poor orientation within the range of yellow, orange, red and infrared light; their increased activity under these light colours indicates that the latter stimulated them as feeble light and hence they turned towards both sources with much the same frequency. Otherwise the activity of the beetles in our experiments varied around 60%.

The diagram in Fig. 4 shows two peaks of attraction of the beetle *M. jamaicensis* towards light: the light begins to be attractive to it in the transitory range between yellow and green and its attractiveness rises abruptly in the range of violet to ultraviolet. As the experiments lasted a longer period of time, they were mostly repeated. However, no difference has been found in the response of beetles of different age, nor has there been any difference in the behaviour of males and females; for this reason the results are not given separately.

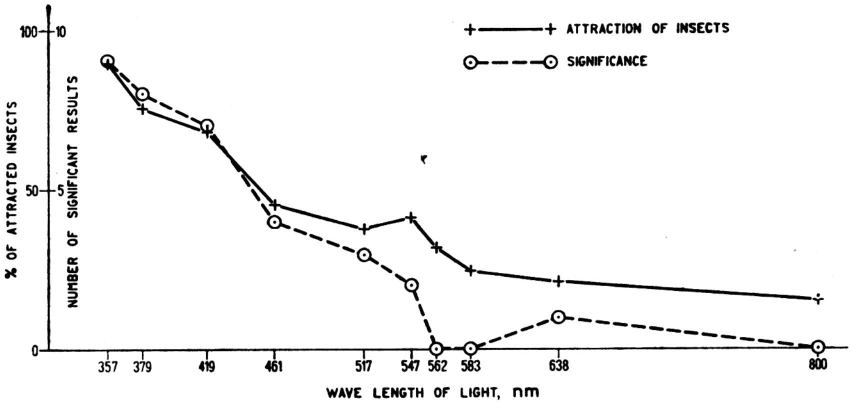

Fig. 4: Orientation of *Macroaltica jamaicensis*

2. Orientation to colour of substrate

It appears from Table 3 that there is no significant result indicating that alate aphids of *A. gossypii*, approaching colour discs placed on a brown background, would prefer to alight on yellow colour. The differences are so

TABLE 3

Alighting of alate forms of *Aphis gossypii* on coloured substrates

Colour of disc	No. of alighted aphids	alighted aphids %	Significance level
yellow	26	41	—
green	38	59	
yellow	17	65	—
blue-green	9	35	
yellow	34	48	—
blue	36	52	
yellow	18	58	—
red	13	42	

slight that it is impossible to estimate which colour would be preferred; hence, no other colour combinations were tested. This experiment involved aphids on the second day after having become winged, still volant in their cage but ceasing to do so in apparent search for their food plants. Thus, the colour of the substrate is not an essential factor for the orientation of these aphids.

DISCUSSION

The results of our observations on the orientation of the four above-mentioned insect species correspond roughly with existing knowledge of photopositive responses in insects. In some respects, however, they confirm the assupmtion of differences in the orientation of insects in the tropics. There are distinct differences from the results of previous detailed investigations on visual orientation in insects. Thus, for instance, adults of *Meligethes aeneus* were observed to be mostly attracted to violet and, to some extent, also green-yellow light. In our earlier studies, we found this to be true of all *Coleoptera* and *Hymenoptera* investigated (ŽĎÁREK & POSPÍŠIL, 1966; HARAGSIM & POSPÍŠIL, 1969). The application of physical and electro-physiological methods resulted in the discovery of the sensitivity of the eyes of some insect species to the violet and green-yellow ranges of the light spectrum (MAZOCHIN-PORSCHNJAKOV, 1959). While *M. jamaicensis* and *L. diatraeae* showed some increased response to green light, this was only just significant. Very likely, the differential responses of insects so far examined in the temperate zone and the tropics are due to the higher content of violet and ultraviolet light in the sunlight spectrum in latitudes between the tropics against that in the temperate zone. This is quite markedly expressed in the leafhopper *P. maidis*, which shows no increased photopositive response to green-yellow light although this insect species is bound to its host plant throughout its life. Quite different results were obtained with aphids. After the evaluation of the results obtained from *A. gossypii*, a representative of the aphids of the tropics, and *A. craccivora* of the temperate zone (the latter results being incomplete but quite significant as for, e.g., the response to ultraviolet light), it is possible to compare the orientation of the aphids in these two zones. It appears that there are fundamental differences in their visual orientation. While the range of the light spectrum lying around 550 nm, i.e., yellow to green-yellow light, is essential for the visual orientation of aphids of the temperate zone, that of the shorter wave lengths than 400 nm, i.e., ultraviolet light, is of much greater importance for the visual orientation of aphids of the tropics, the range around 550 nm, i.e., yellow to green light, being of less importance.

CONCLUSIONS

Alate aphids of *Aphis gossypii* GLOWER show visual orientation first of all to ultraviolet light, i.e., light with wave length shorter than 400 nm. From among the remaining parts of the light spectrum, they can perceive the whole part up to yellow light, i.e., to wave lengths up to 600 nm; they show no response to light with wave lengths longer than 600 nm. From the part of the spectrum perceptible for these aphids, they are slightly more sensitive to green-yellow light, i.e., the range around 550 nm, although not as markedly as to ultraviolet light. In alighting, alate individuals of *A. gossypii* do not prefer substrates yellow in colour.

The leafhopper *Peregrinus maidis* ASHMEAD shows visual orientation to light with wave lengths shorter than 550 nm, i.e., green-yellow, green, blue, violet and ultraviolet light, preferring it to light with greater wave length.

Adults of *Lixophaga diatraeae* TOWNSEND show visual orientation to light with wave length shorter than 580 nm, i.e., to yellow, green, blue, violet and ultraviolet light, preferring wave lengths shorter than 500 nm, i.e., violet and ultraviolet light. Light with wave length around 550 nm, i.e., green-yellow and yellow light, also appears to be of some importance for the orientation of this species.

Adults of *Macroaltica jamaicensis* FABR. show visual orientation to light with wave length shorter than 550 nm, i.e., to yellow, green, blue, violet and ultraviolet light.

The attractiveness of light for *M. jamaicensis* and *P. maidis* increases gradually with decreasing wave length of the light, ultraviolet light being the most attractive for these insect species.

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