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NOTES ON THE REACTIONS OF CERTAIN INSECTS TO DIFFERENT WAVE-LENGTHS OF LIGHT

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INTRODUCTION

In presenting these notes, on the responses of certain species of insects to light of different wave-lengths, it is our idea that they should be interpreted as indicating the general behavior of a majority of the organisms at a particular time. It is not our thought that the degree of exactness represented by the numbers responding to certain wave-lengths should be read into the results. Experimental work by various investigators supports the idea that color perception exists in insects and that they are especially responsive to the so-called shorter wave-lengths of the spectrum. There is also evidence indicating that light intensity is a factor that should by no means be neglected, as varying responses may be obtained by different intensities. We are aware of the possibility of error in attempting to ascribe insect behavior solely in terms of light responses when it is obvious that other important and seemingly immeasurable factors are operating simultaneously.

It will not do to think of the behavior of the insects under consideration as simple reflexes. Although their behavior on the whole is automatic and conforms to Loeb's physical interpretation of phototropism, their responses to certain wave-lengths do not appear to be such inflexible or precise acts as the theory of

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tropisms would imply. Such responses probably depend upon and are modified by a coordinated series of reflexes controlled or initiated by the nervous system. We do not view responses to light as completely tropic or as representing a complex of responses to such additional outer physical stimuli, as, for example, moisture and temperature. In addition there are metabolic conditions, reproductive and oviposition factors, etc., any one of which might take precedence over, or modify the response to light.

It is difficult to draw conclusions about the color responses of insects from experimental work in which lights of varying intensities are used, side by side, and when such intensities are measured by incorrect methods. Light intensity is difficult to measure, and unless some attempt is made to equalize the intensities, when the insects are exposed to different wave-lengths of light, it is impossible to determine whether the wave-length or the intensity is responsible for the behavior. At the outset it was thought that intensities might be measured by photographic means or by photoelectric cells, but we soon discovered that such devices were not equally sensitive to all wave-lengths, however suited they might be to the type of work for which they were designed.

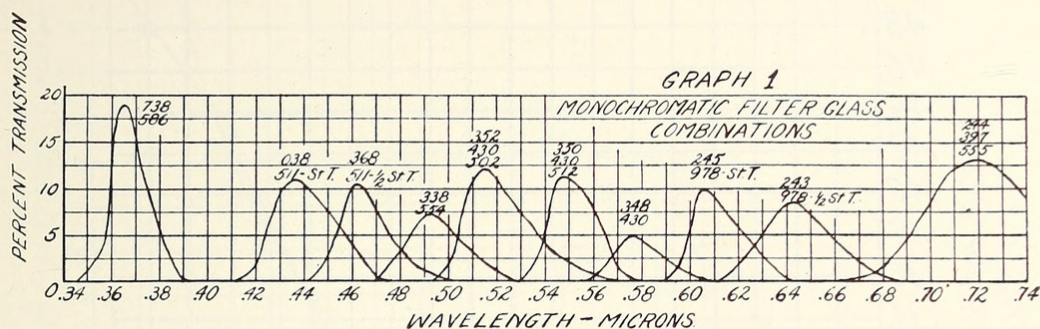
The purpose of these investigations was to determine the response of the insects to color alone, uncomplicated by varying intensities, and therefore it was decided to equalize the intensities of the various colors to which the insects were exposed. We felt that it was necessary to attempt such equalizations before the comparative effects of different wave-lengths could be evaluated.

COLOR AND INTENSITY OF LIGHT USED IN THE EXPERIMENTS

The color, or wave-length, of the light entering the test apparatus was determined by passage of the light given by the source lamps through the appropriate Corning monochromatic filter glass combinations. The physical intensity (as distinct from the human visual intensity) was regulated by the distance between the lamp source and the filter combinations.

The monochromatic filter glass combinations used limited the light transmitted to relatively narrow bands of the spectrum. The data on the transmission characteristics of the respective filter combinations appear in Table 1, and are also represented

graphically in Graph 1. Each filter combination is seen to transmit light over a certain wave-length band, with the maximum transmission of each combination occurring about midway of the transmission range. Thus, light characterized by a definite color is obtained.

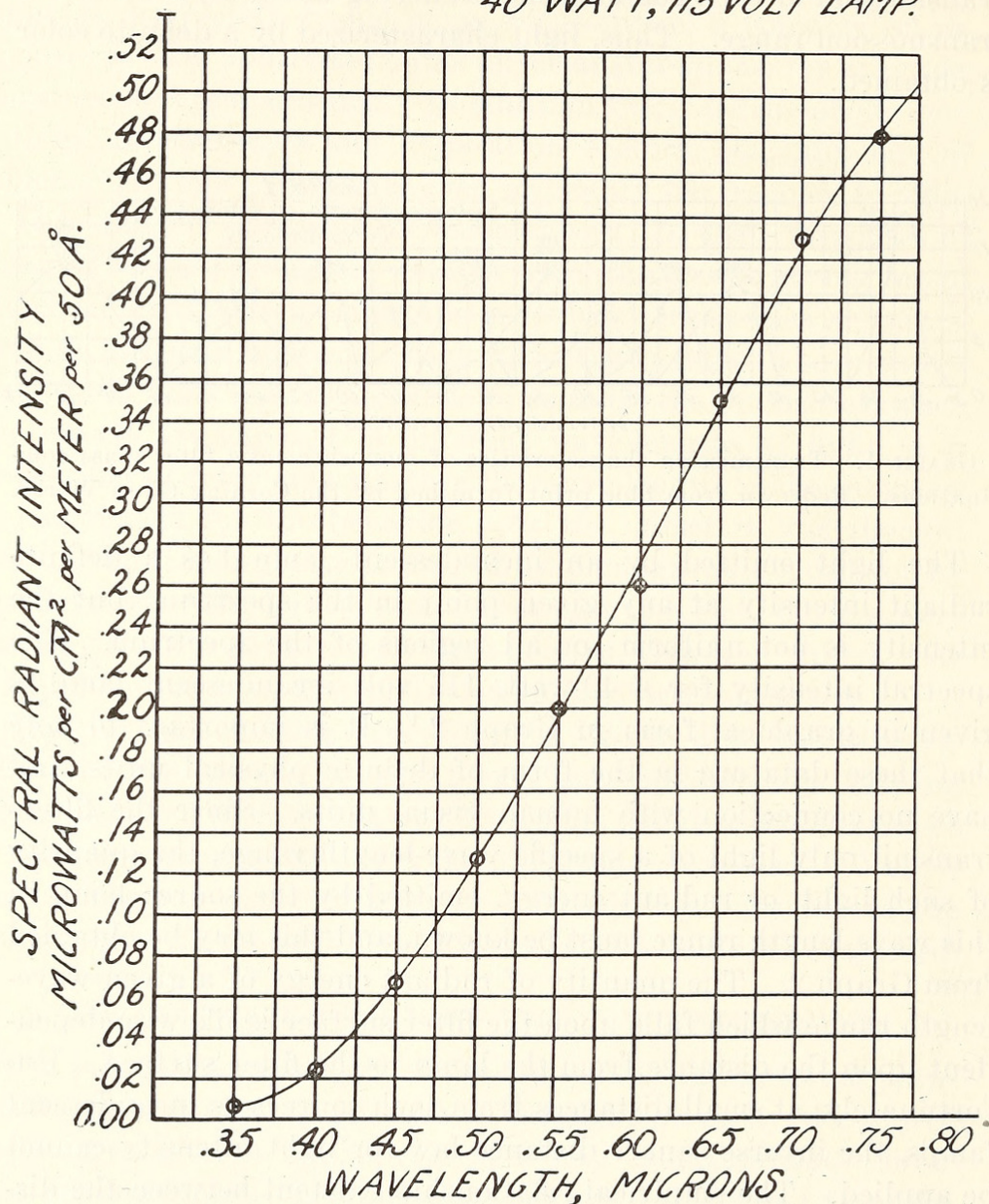


GRAPH 1. Transmission characteristics of monochromatic filter glass combinations. Redrawn from blue print furnished by the Corning Glass Works.

The light emitted by an incandescent lamp has a definite radiant intensity at any given point in the spectrum, but the intensity is not uniform for all regions of the spectrum. The spectral intensity for a 40-watt, 115 volt incandescent lamp is given in graphical form in Graph 2.¹ It is important to note that these data are in the form of definite physical units, and have no connection with human visual units. Since the filters transmit only light of a specific wave-length range, the quantity of such light, or radiant energy, emitted by the source lamp in this wave-length range must be known, and this may be obtained from Graph 2. The quantity of radiant energy of a given wave-length range which falls upon the filter surface is likewise dependent upon the distance from the lamp to the filter surface. Unfortunately, at small distances from such sources as incandescent lamps, the inverse square distance law for light intensity cannot be applied. The empirical relationship existent between the distance from the source for the 40-watt lamp used was obtained by taking readings with these lamps on an optical bench, and using a Weston photoelectric cell in making the measurements. The distance measurements were taken between the axial tip of the bulb, which was the proximal surface, and the Weston cell filter.

¹ Based on data of B. T. Barnes, Lamp Development Laboratory, General Electric Company, Cleveland, Ohio.

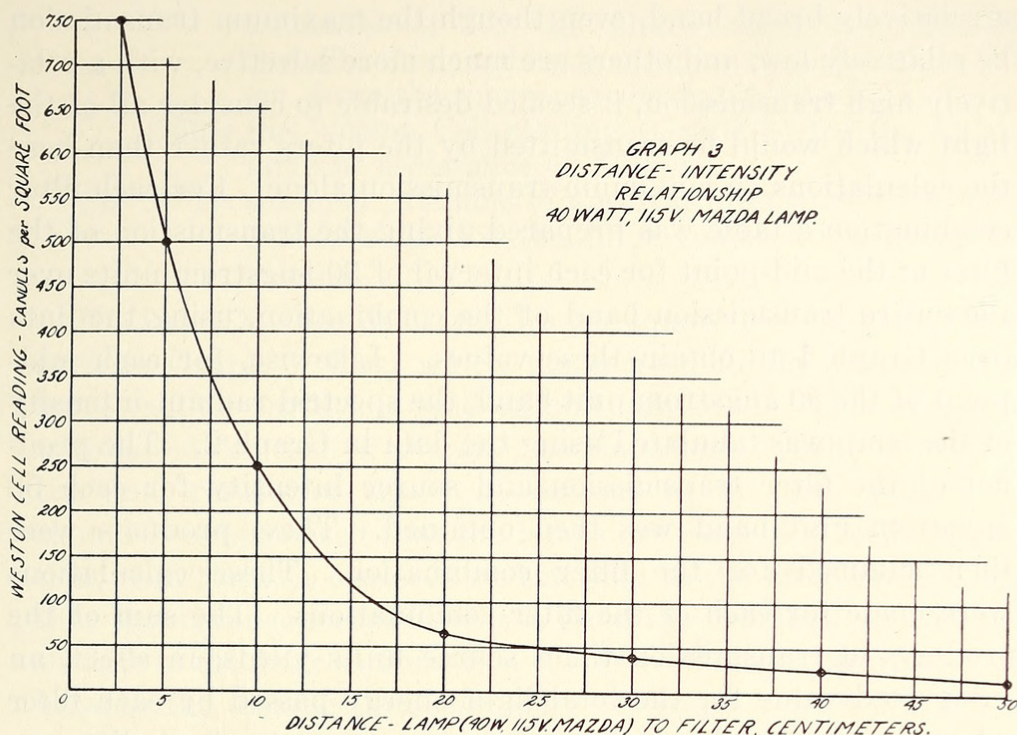
GRAPH 2
SPECTRAL RADIANT INTENSITY
40-WATT, 115 VOLT LAMP.



GRAPH 2. Spectral radiant intensity for a 40 watt, 115 volt incandescent lamp.

This same procedure was later followed in arranging the lamps and measuring to the filter surface. The data obtained in these measurements are presented in graphical form in Graph 3.

The quantity of light emitted at any wave-length by the 40-watt Mazda lamp is now determinable from Graph 2. The manner in



GRAPH 3. Distance-intensity relationship, 40 watt, 115 volt lamp.

which this quantity will change with various distances is determinable from Graph 3. The quantity of incident light which will be transmitted by the various filter combinations is determinable from Graph 1.

It is now possible to calculate the setting of the lamps with respect to the filters so that the light transmitted by the various combinations should be of an equal physical intensity, although it will be impossible to assign any physical unit of measurement to the quantity of transmitted light. Since the problem of this investigation is solely to determine the relationship of phototropic response to various portions of the spectrum, it is only necessary to equalize the intensities, or know definitely their numerical relationships one to another, and actual measurement in terms of physical units is not required.

In calculating the setting of the lamps, it is evident that light is transmitted over the entire wave-length band covered by the filter, although the greater portion will be transmitted close to the wave-length for which the filter combination has its maximum transmission. Since some of the filter combinations transmit over

a relatively broad band, even though the maximum transmission be relatively low, and others are much more selective, with a relatively high transmission, it seemed desirable to consider all of the light which would be transmitted by the filters rather than base the calculations on maximum transmission alone. For each filter combination a table was prepared giving the transmission of the filter at the mid-point for each interval of 50 ångstrom units over the entire transmission band of the combination, using the data from Graph 1 to obtain these values. Likewise, for each mid-point of the 50 ångstrom unit band, the spectral radiant intensity of the lamp was tabulated using the data in Graph 2. The product of the filter transmission and source intensity for each 50 ångstrom unit band was then obtained. These products were then summed for the filter combination. These calculations were made for each of the filter combinations. The sum of the products of transmission times source units yields, in effect, an integrated value for the total light energy passed by each filter when illuminated by each source lamp at a standard distance. Thus, filters with a high transmission over a narrow band are put on a comparative basis with filters having a low transmission over a wider band, and at the same time the relative energy distribution of the lamps at various wave-lengths is taken into consideration. The procedure also acknowledges the fact that the light transmitted is not strictly "monochromatic," and makes due allowance for that fact.

For the purpose of determining the relative positions of the lamps and various filter combination, that combination for which the sum of the products of emissivity times transmission was a minimum (038-511 Std. T.) was taken as a point of departure, and the distance from the nearest portion, or axial tip, of the bulb surface to the filter surface was arbitrarily assumed at 2.50 centimeters. The distance from bulb surface to filter surface was then determined for the other combinations, to yield an equal physical intensity, by the following equation and procedure:

$$X = \frac{(E' F') 750}{(E'' F'')}$$

Where X = a reading in candles per square foot on Graph 3.

(E' F') = summed products of spectral intensities times filter

transmission for the filter combination 038-511 Std. T., this combination being set arbitrarily 2.50 cm. from the source, as above explained.

750 = the Weston Cell reading (Graph 3) for the 40-watt lamp at a distance of 2.50 cm.

(E" F") = summed products of spectral intensities times filter transmission for the filter combination being calculated.

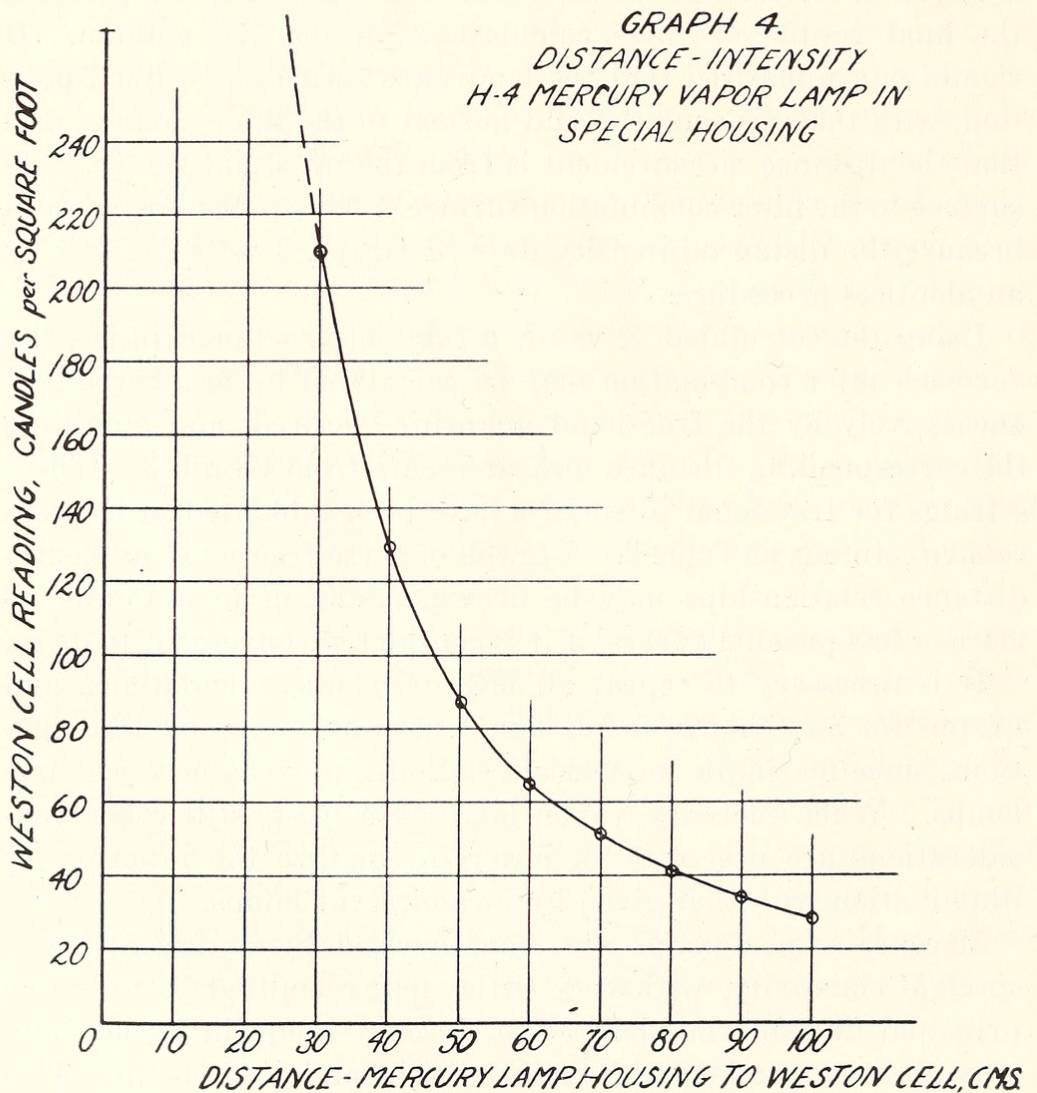
The value X, then, is in candles per square foot and is referred back to Graph 3, from which the corresponding distance from lamp to filter surface is read off and tabulated. This procedure is followed for each of the filter combinations. Table 2 presents the final results of these calculations in the 3rd column. It should be emphasized that the lamps are used in a reclined position, with the axis centered and normal to the filter surface, and that the distance measurement is from the proximal, or tip, bulb surface to the filter combination surface. This procedure is valid because the distance-intensity data of Graph 3 were derived by an identical procedure.

Using the calculated X value, a table of fractional intensities for each filter combination may be calculated by multiplying X successively by the fractional quantities desired, and obtaining the corresponding distance measurements from Graph 3. These settings for fractional intensities have been tabulated in the successive columns of Table 2. A graph of these fractional intensity-distance relationships may be drawn, resulting in a family of more or less parallel curves, if it is considered convenient to do so.

It is necessary to repeat all measurements, calculations, and graphs for any change in the lamps used as sources of illuminations, since no simple numerical relationship exists between such lamps. When mercury vapor lamps are used, still other considerations are necessary in order to equalize the intensity of illumination with that given by incandescent lamps.

Mercury vapor lamps are characterized by a discontinuous spectral emissivity, with very little energy emitted between the principal lines of emission. The mercury lamp, in its housing, must first be standardized against the incandescent lamp. This may be done by using the mercury line at 5461 ångstrom units, which is within the transmission range of the filter combination 350-430-512 and within the range of emission of the incandescent

lamp as well as the sensitivity of the Weston cell. The filter combination mentioned above must be used in order to limit the Weston cell readings with the incandescent lamp to the same range as is emitted in this portion of the spectrum by the mercury lamp. With this filter combination in place before the Weston cell, readings were taken with both the incandescent and mercury vapor lamp. Identical readings of 3.75 candles per square foot were obtained with the 40-watt lamp at 4.0 cm., and the mercury lamp at 37.8 cm. The manufacturer's data on the emission of the mercury lamp shows the ratio of emission at 5461 ångstrom



GRAPH 4. Distance-intensity relationship, H-4 Mercury vapor lamp in special housing.

TABLE 1
LIGHT TRANSMISSION CHARACTERISTICS OF CORNING MONOCHROMATIC FILTER COMBINATIONS

Filter glass combinations, Corning designation numbers	Color of light transmitted	Transmission range, Å	Wave-length of maximum transmission, Å	Maximum transmission, percent of incident light
244-397-555	Infra-red	6620-7400*	7200	13.0
243-978 ($\frac{1}{2}$ Std. T.)	Orange-red	6120-6860	6420	8.5
245-978 (Std. T.)	Yellow-orange	5900-6420	6060	9.8
348-430	Yellow-yellow-green	5550-6070	5750	4.9
350-430-512	Yellow-green	5300-5760	5460	11.2
352-430-502	Blue-green	4940-5660	5150	12.2
338-554	Blue-blue-green	4700-5280	4920	7.2
368-511 ($\frac{1}{2}$ Std. T.)	Blue	4420-5000	4640	10.5
038-511	Violet-blue	4120-4760	4360	11.0
738-586	Ultra-violet	3460-3900	3650	18.5

* The filter combination, 244-397-555, transmits light into the infra-red spectrum beyond 7400 Å. The data on transmission (Graph 1) beyond 7400 Å were not available.

TABLE 2
DISTANCE SETTINGS FROM 40-WATT LAMPS TO FILTER COMBINATIONS TO SECURE EQUAL LIGHT INTENSITY

Filter combination	Calculated "X" value.	Distance, cm. lamp to filter for equal light intensity	Fractional illumination distance settings, assuming column 3 = 100%								
			90%	80%	70%	60%	50%	40%	30%	20%	10%
	<i>Candles per sq. ft.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>
244-397-555	61	21.0	23.3	25.5	28.3	31.7	35.4	41.0	46.6
243-978 ($\frac{1}{2}$ Std. T.)	148	13.5	14.3	15.1	16.1	17.3	18.9	22.0	27.8	36.1	50.0
245-978 (Std. T.)	216	11.0	11.7	12.5	13.4	14.4	15.8	17.6	20.1	28.3	42.7
348-430	544	4.5	5.2	6.0	7.0	8.3	9.4	11.0	12.9	15.7	23.7
350-430-512	284	9.1	9.8	10.7	11.6	12.6	13.8	15.4	17.7	21.7	37.5
352-430-502	252	9.9	10.7	11.4	12.4	13.4	14.6	16.3	18.6	25.1	40.0
338-554	620	3.7	4.3	5.1	6.0	7.2	8.5	10.0	12.0	14.8	20.7
368-511 ($\frac{1}{2}$ Std. T.)	694	3.0	3.6	4.3	5.2	6.3	7.7	9.2	11.2	14.0	19.5
038-511	750	2.5	3.1	3.8	4.7	5.8	7.1	8.7	10.7	13.5	18.8
738-586											
Mercury lamp	Special	66.0	71.0	76.0	83.0	92.0	100.0

units to that at 3650-63 ångstrom units as 1.37, which, multiplied by 3.75 candles per sq. ft. equals 5.14 candles per sq. ft., and was found to be equivalent to a distance of 31.5 cm. for the mercury lamp, equivalent to 194 candles per square foot for the mercury lamp without filter. See Graph 4 for distance-intensity relationships of the mercury lamp without filter. The ratio of filter transmissions for the filter combinations 350-430-512 and 738-586 is as 1/1.65, which, multiplied by 194 equals 118 candles per square foot, or equivalent to 42.5 cm. distance from mercury lamp to 738-586 filter, to give equal intensity with the 40-watt lamp and 350-430-512 filter combination at 4.0 cm. However, the latter combination will be used at 9.25 cm., which gives only 0.475 times the light at 4.0 cm. Therefore, the mercury lamp must be placed to give a similarly reduced light, or 0.475×118 candles per square foot = 56 candles per square foot, which, from the mercury lamp distance graph is found to be equivalent to 66 cm. This, then, is the unit distance for the mercury lamp when used with filters 738-586, which gives an illumination at 3650-63 ångstrom units in the ultra-violet. The other intensity settings for the ultra-violet are found in a manner identical with that employed for the incandescent lamps.

APPARATUS

The testing equipment consisted of a low, cylindrical box made of galvanized iron (24 gage), the inside measurements being diameter 22 inches, height $4\frac{1}{2}$ inches (Fig. 1). The inside was divided into eight wedge-shaped compartments and a central octagonal compartment 11 inches in diameter. Each of the eight compartments was separated from the adjoining ones by solid walls, and from the central compartment by a gate hinged at the top. The gates were raised in such order that the first rested upon the second, the second upon the third, etc., and the eighth was held up by a rod. At the end of a test, the rod was pulled out and all the gates fell, closing each compartment. Each of the eight compartments was covered with a wire screen, and each contained a single side-window $1\frac{3}{4} \times 1\frac{3}{4}$ inches opening to the outside and cushioned with rubber. Glass filters were placed against the rubber cushion and fastened by a metal frame held

in place by thumbscrews (Fig. 2). A lid lined with felt strips to prevent light leakage, with a circular opening in the centre (for the introduction of the insects) was held in place by four

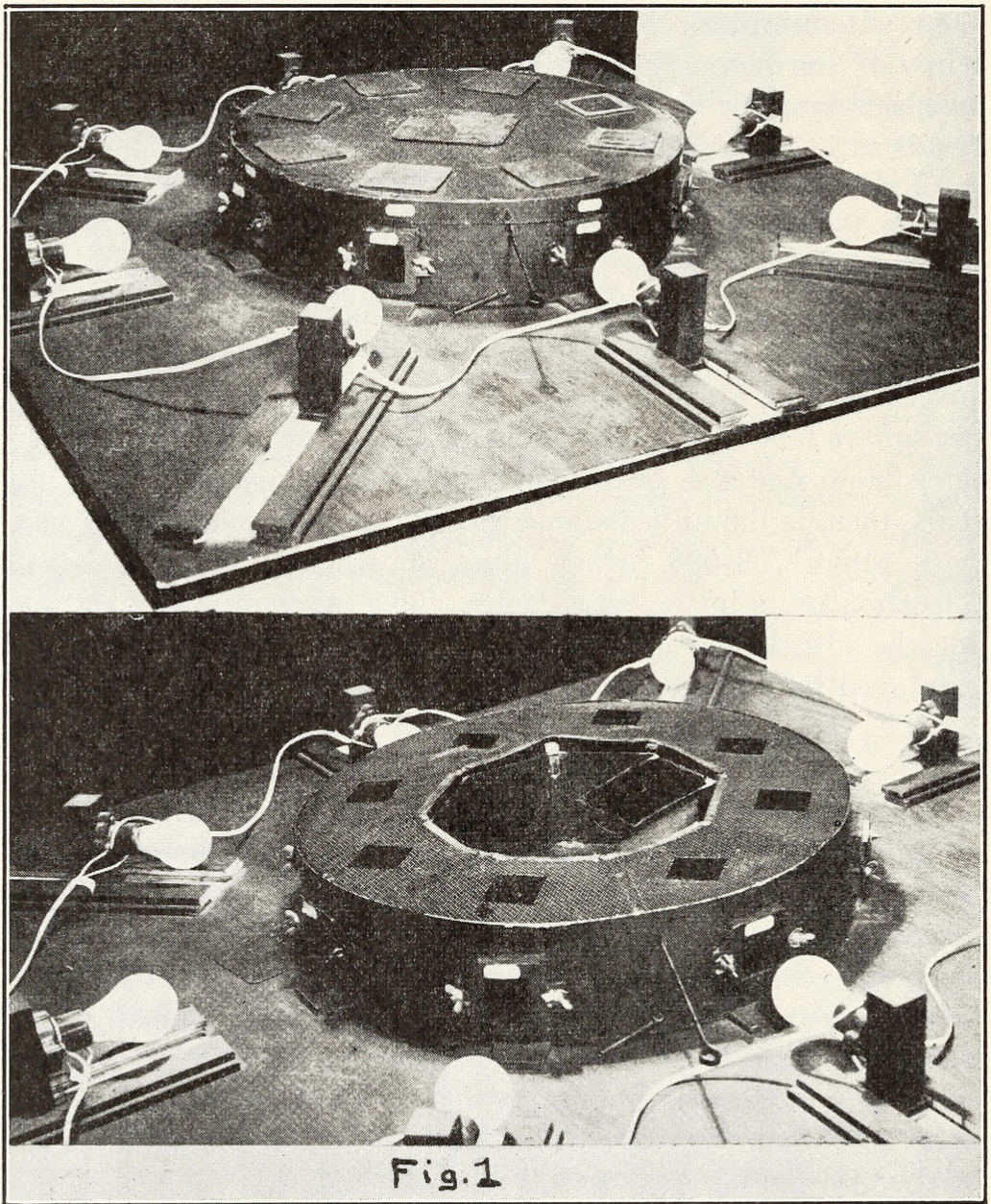


FIG. 1. Upper: Photograph of apparatus with lid on. Lower: With lid off and showing one hinged gate raised.

springs. During the tests, the circular opening in the lid was tightly covered. The entire box was painted dull black inside and out.

The testing box was placed in the centre of a flat board which carried eight grooved wooden tracks on which the mountings holding the lamps could be moved, thus bringing the lamps to the required distances from the windows holding the filters (Fig. 1).

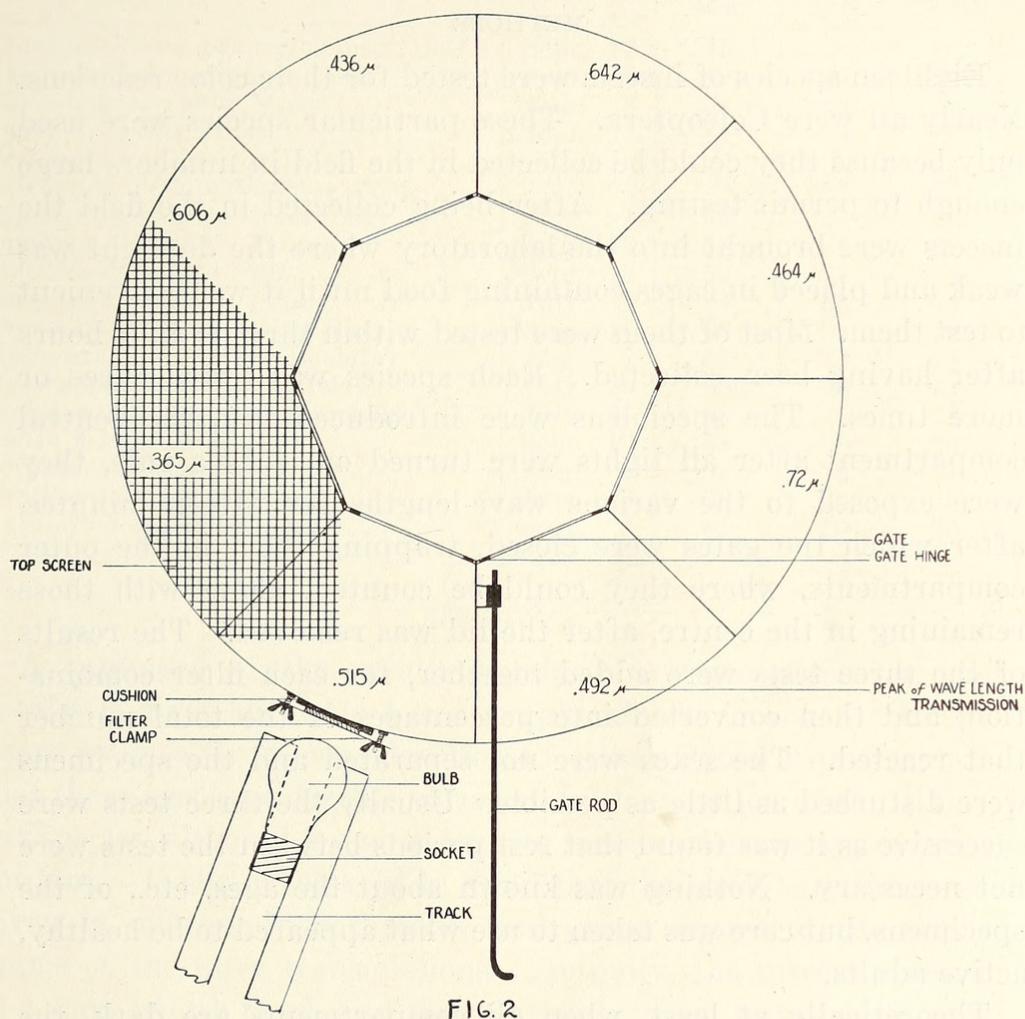


FIG. 2. Diagrammatic top view of apparatus with lid off showing details and also the peak of wave-length transmission for each chamber.

Forty-watt, frosted Westinghouse Mazda lamps were used and the ultra-violet light was supplied by a General Electric Mazda mercury lamp, type A-H4 (100 watts), in which the arc discharge takes place within a small, capsule-like tube of quartz.

Corning filter glasses were used in order to isolate specific portions of the spectrum. Each was $2'' \times 2''$, and every filter or

combination of filters, when in place, was equally distant from the central compartment into which the insects were introduced.

The distance settings, from the 40-watt lamps to the filter combinations, were, in all experiments, the same as those shown in column 3, Table 2.

METHODS

Eighteen species of insects were tested for their color reactions. Nearly all were Coleoptera. These particular species were used only because they could be collected in the field in numbers large enough to permit testing. After being collected in the field the insects were brought into the laboratory where the daylight was weak and placed in cages containing food until it was convenient to test them. Most of them were tested within three or four hours after having been collected. Each species was tested three or more times. The specimens were introduced into the central compartment after all lights were turned on. As a rule, they were exposed to the various wave-lengths for fifteen minutes, after which the gates were closed, trapping them in the outer compartments, where they could be counted, along with those remaining in the centre, after the lid was removed. The results of the three tests were added together, for each filter combination, and then converted into percentages of the total number that reacted. The sexes were not separated and the specimens were disturbed as little as possible. Usually the three tests were successive as it was found that rest periods between the tests were not necessary. Nothing was known about the ages, etc., of the specimens, but care was taken to use what appeared to be healthy, active adults.

Theoretically at least, when all compartments are dark, the insects, after being introduced through the central opening, should distribute themselves more or less equally in the compartments. This was tried with the squash bug *Anasa tristis* and with one or two other species and it was found that a fair degree of distribution, approaching equal numbers, was obtained by averaging three or four tests. The dates on which each species was tested and the relative humidity and temperatures during the tests are given in the following Table 3.

TABLE 3

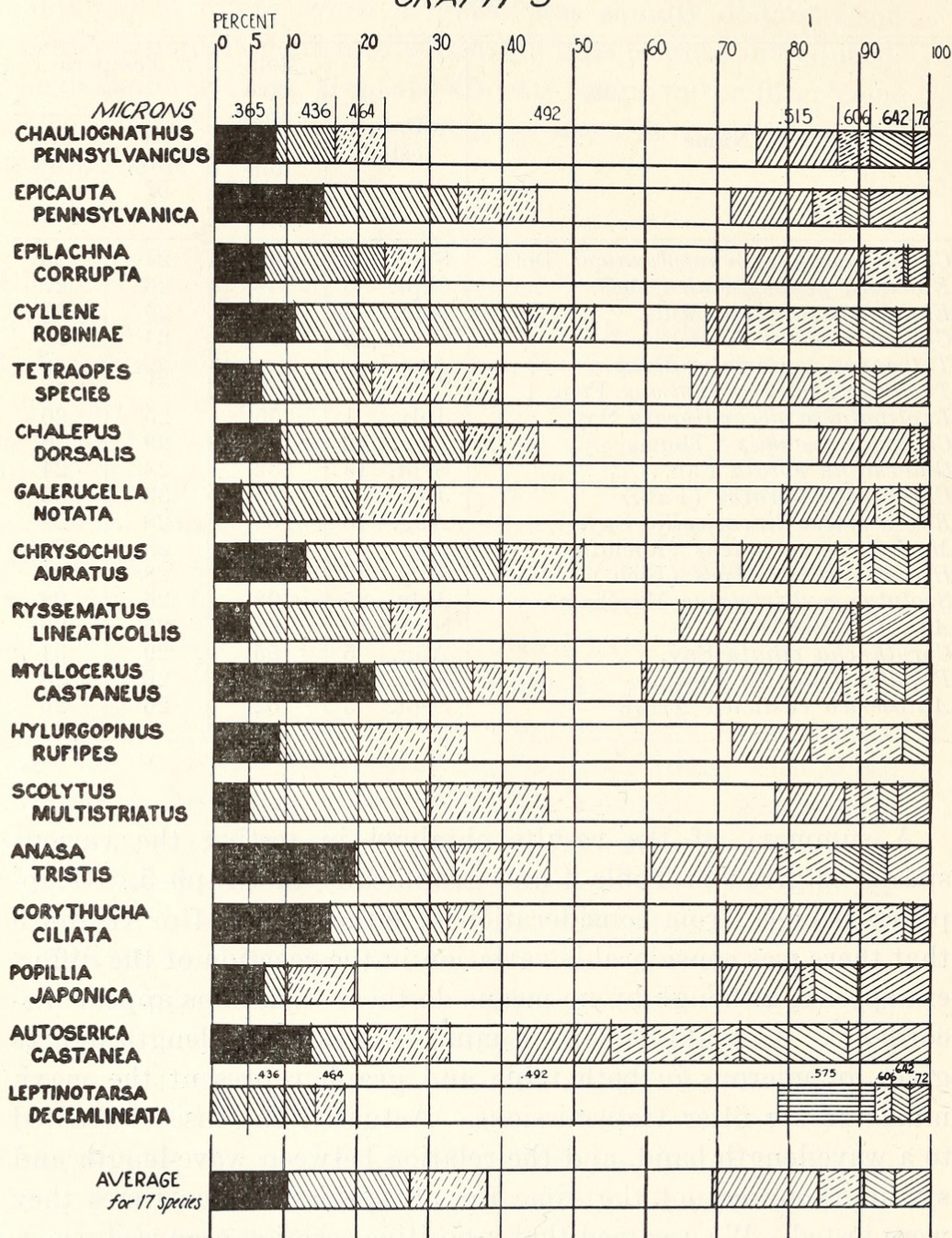
Name	Date tested	Relative humidity during test	Temperatures °C.	
			At start of test	At end of test
<i>Chauliognathus pennsylvanicus</i> DeG.	Sept. 12	46	24	26
<i>Epicauta pennsylvanica</i> DeG.	Sept. 6	48	26	27
<i>Epilachna corrupta</i> Muls.	Aug. 8	52	29	30
<i>Cyllene robiniae</i> Forst.	Sept. 12	46	24	25
<i>Tetraopes canteriator</i> Drap.	July 17	70	27	28
<i>Tetraopes tetraophthalmus</i> Foer.				
<i>Leptinotarsa decemlineata</i> Say.	July 1	50	25	26
<i>Chalepus dorsalis</i> (Thun.)	Aug. 12	58	29	30
<i>Galerucella notata</i> Fab.	Sept. 13	52	23	24
<i>Chrysochus auratus</i> (Fab.)	July 30	55	33	36
<i>Rhyssomatus lineaticollis</i> Say.	Aug. 15	60	28	29
<i>Myllocerus castaneus</i> (Roelofs)	Aug. 7	67	28	28
<i>Hylurgopinus rufipes</i> (Eich.)	July 25	68	28	31
<i>Scolytus multistriatus</i> Marsham	July 25	98	26	28
<i>Anasa tristis</i> DeG.	Sept. 10	68	25	26
<i>Corythucha ciliata</i> Say.	Aug. 5	55	29	31
<i>Popillia japonica</i> Newm.	July 15	68	26	28
<i>Autoserica castanea</i> Arrow	Sept. 3	62	26	26

RESULTS

A summary of the results obtained in testing the various species is given in Table 4 and graphically in Graph 5. It appears at once, from consideration of either Table 4 or Graph 5 that there was considerable variation in the reaction of the different species, although by no means do these variations appear discordant. It should be kept in mind that the wave-length figures given in microns in both table and graph represent the maximums of the filter transmissions. Actually, the insects reacted to a wave-length band, and the relation between wave-length and stimulation was not the same for all species, at the times they were tested. We assumed that a positive reaction occurred whenever an insect went into one of the compartments containing a light filter.

Of all specimens tested, a little over 72 per cent reacted positively to one wave-length band or another, while a little under 28 per cent remained in the central compartment. These percentages varied with individual species. Of those that reacted

GRAPH 5



GRAPH 5. Graphic presentation of the behavior of certain species of insects to various wave-lengths when the physical intensities are constant. Peak of wave-length transmission indicated by the figures at top of graph, and also by the types of shading below the figures. For example, 51.9 per cent of the individuals of *C. pennsylvanicus*, reacted positively to a combination of filters that transmitted a band from .470 to .528 microns but which had its transmission peak at .492 microns. For *Leptinotarsa decemlineata*, the peaks of wave-length transmission are shown above the bar for this species. The mercury vapor lamp was not available when this species was tested. The vertical guide lines in the graph enable one to roughly calculate the percentages reacting positively to the bands.

positively approximately 33 per cent went to the wave-length band 4700-5280² (blue-blue-green), 14 per cent to 4940-5660 (yellow-green), 14 per cent to 4120-4760 (violet-blue), 11 per cent to 4420-5000 (blue), and 11 per cent to a wave-length of 3650-3663 (ultra-violet). On the whole much smaller percentages went to the longer wave-lengths 5900-7400 (yellow-orange, orange-red, infra-red). It therefore may be concluded that under the conditions described and at the time the particular species were tested, the stimulating efficiency of wave-lengths from 3650 to 5280 was much greater than that of wave-lengths from 5900 to 7400+. If wave-lengths from 4120 to 5280 (violet-blue, blue, blue-blue-green) are considered as one unit, it may be noted that approximately 60 per cent of the total number reacted positively to that band, which apparently is a region of maximum stimulation. It should be kept in mind that this is simply a generalization, for convenience, of the behavior of the species tested. The data for the potato beetle are not included in these generalizations.

The behavior of the particular species took place when the filter combinations were arranged in the order shown in Fig. 2. Changing the order in which the filters were arranged with respect to one another did not appear to influence the results.

At this time we have done little more than report the behavior of the eighteen species as it took place under the conditions outlined. Some of the insects went to every choice that was open to them, from infra-red to ultra-violet, however, certain wave-lengths were more stimulating to them than others. All were Coleopterous species, with the exception of two Hemipterous ones and much work remains to be done with representatives of additional orders.

It has been asserted by Mast that the reaction of animals with image forming eyes to light is a very much complicated one; that there is little evidence that any one color is much more attractive than another, and that they may be positive to one, at one time, and negative at another time. There is no doubt about

² Wave-length bands are given in Ångstrom units. One Å = $\frac{1}{10,000}$ micron.

the behavior of insects to light being complicated. The types of compound eyes and ocelli perhaps need to be considered. If insect behavior, including the reaction to light, depends upon the physiological state of the specimen and if all movements are secondary to this state and the factors producing it, the problem of explaining is indeed complicated. As the movements of our experimental specimens took place in a closed box, we do not know if their orientation was immediately direct or direct after a series of preliminary movements. Neither do we have any idea of the importance of photochemical reactions which may have taken place in retinal cells or in photosensitive areas. Neither do we know if the behavior can be explained entirely on the basis of chemistry and physics. There may be a psychic factor which regulates behavior with respect to time and direction.

Mast in his work with unicellular and colonial forms, concluded that his animals were devoid of true color vision. He found that in the species studied, stimulation depended upon the wave-length, but that the wave-length was not independent of luminous intensity. His work demonstrated that although there was a clear wave-length region of maximum stimulating efficiency, it was possible to increase the stimulating effects of wave-lengths on either side of the maximum, by increasing their intensities.

Peterson and Haeussler in their work with the Oriental peach moth, and the codling moth found that intensity is a factor that should be considered as influencing the reactions of insects to different wave-lengths. In our work as outlined in this paper, we attempted to equalize the physical intensities within each chamber, in order that the wave-length could be evaluated by itself. We have no reason for believing that the behavior could not be changed by varying the intensities.

Of our eighteen species of insects all except one are active in daylight. The exception is *Autoserica castanea* which feeds at night. For this species the least stimulating wave-length band was the one most stimulating for the daylight species. On the other hand this species is photonegative to daylight and its behavior as recorded may have been a dispersal in search of dark-

ness which it could not find in the apparatus. It is doubtful if the experimental set-up was suitable for testing photonegative insects. In considering the reactions of the other species there is a faint idea that with the testing of many more additional species, it might be possible to correlate their behavior to various wave-lengths with some of their general habits in the field, at particular times.

ACKNOWLEDGMENTS

We are greatly indebted to Mr. Robert J. Sim for collecting in the field, many of the species mentioned herein, and also to Mr. Lewis P. Hoagland, and Mr. C. W. Collins for supplying certain species in numbers sufficient for testing. And we are especially grateful to Mr. S. G. Hibben, Director of Applied Lighting, Lamp Division, Westinghouse Electric & Manufacturing Company, for his advice and helpful criticisms.

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³ In view of the availability of numerous references to the subject, this list includes only such papers as were of immediate interest to us.



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