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PHOTOTROPIC SENSITIVITY IN RELATION TO WAVE LENGTH

(WITH TWO PLATES)

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## INTRODUCTION

Asymmetric growth resulting from unilateral stimulus has been designated tropism. Growth curvatures following unilateral illumination are usually classified under the term phototropism. Different plants respond in different degrees to light, but perhaps those most frequently used in phototropic experiments are the sporangiophores of *Phycomyces* and the coleoptiles of *Avena*. In such studies the intensity, the wave length, and the duration of exposure to light each acts as a contributing factor toward the final result. Just as there appears to be a threshold of intensity for a given duration of light exposure, so there are wave lengths which seem to exert no influence on these growth responses, but with exposures to other wave lengths the plants show distinct degrees of sensitivity. Not only do different plants vary in their sensitivity, but separate portions of the same plant respond differently. Recent work on growth substances indicates the presence of factors other than light in this complex plant-response.

In the present paper the subject is limited, in the main, to the influence of radiation of different wave lengths on phototropism as shown by the response of the coleoptiles of *Avena sativa*. The variety used is Culberson, C.I. no. 273, for which the author wishes to thank Mr. T. Ray Stanton, of the United States Department of Agriculture. All the light intensity measurements were made by Dr. E. D. McAlister, to whom credit for that part of this work is given.

## HISTORICAL SURVEY

Many of the early experiments on phototropism have been reviewed by Parr (1918) and the data classified under four general theories: 1. The "intensity" theory originating with De Candolle in 1832 and adhered to in a more or less modified form by Wiesner, Darwin, Engleman, Oltmanns, Yerkes, Loeb, and Davenport. 2. The ray-

direction theory advanced by Sachs in 1876 and supported by the experiments of Strasburger, Davenport, and Canon. 3. The wavelength theory first investigated by Payer in 1842. 4. The energy theory first mentioned by Müller in 1872 in which the maximum response of cress seedlings shifted in the spectrum for different energy values of the wave lengths studied.

The basis for much of the recent quantitative work on phototropism was laid by Blaauw (1909, 1914, 1915, 1919). His studies were perhaps the first serious attempt made to interpret this growth response in terms of modern physics. Plant responses were studied in different spectral regions of sunlight and of the carbon arc and compared with the energy values calculated from Langley's (1884) tables. Blaauw found the most effective region of the carbon spectrum for phototropic response of *Avena* seedlings to lie between 4660 and 4780 Å, while the red and yellow regions were ineffective. According to Blaauw (1914), the curvature of a plant resulting from unilateral illumination is caused by the light-growth responses on the opposite sides which are illuminated differently. The minimum amount of radiation required to produce phototropic response was found to be 20 meter-candle-seconds. It also appears from his work that for equal effects the product of light intensity and time of exposure is a constant.

It is impossible to evaluate the effect of wave length in many of the early phototropic experiments because of the lack of accurate physical data. Some 10 years after the early quantitative studies of Blaauw, Parr (1918) made a study of the responses of *Pilobolus* to different wave lengths and intensities of carefully measured artificial light. The results of these quantitative studies are best summarized in her own words:

- (1) *Pilobolus* responds to the light of all the regions of the visible spectrum.
- (2) The presentation time decreases gradually from red to violet. There is no indication of intermediate maxima or minima.
- (3) The presentation time does not vary in direct ratio with the measured value of the energy of the light in the different regions of the spectrum.
- (4) The presentation time varies in inverse ratio to the square roots of the wave frequency.
- (5) The product of the square root of the frequency times the presentation time, decreases with the decrease in the energy value of the spectral regions, and is an approximate constant for a given light-source.
- (6) The spectral energy in its relation to the presentation time may be expressed approximately in the Weber-Fechner formula, if the wave-frequencies be made a function of the constant.
- (7) The relation of the spectral energy to the presentation time may also be approximately expressed in the Tröndle formula, the wave-frequencies being made a function of the constant.

About the same time Hurd (1919) showed wave-length effect on young rhizoids by equalizing the intensity of the light coming through a series of Wratten filters. Only the blue (4700 to 5200 Å) and violet (4000 to 4700 Å) lights produced phototropism, negative in direction. The other lights at the intensity of 1800 meter-candles had no effect. However, with a greater intensity the green light (5200 to 5600 Å) exerted a negative phototropic effect as well as the blue and violet.

For the purpose of investigating the wave-length effects of radiation on phototropic bending of young plants, Johnston (1926) constructed and described a simple plant photometer. The apparatus consisted of a long box divided into three compartments. Each end compartment contained an electric lamp which could be moved toward or away from the light-filter window in the partition separating it from the central or plant compartment. Plants which easily respond in their directional growth to differences in light intensities were employed in place of the adjustable indicator or photometer screen in the ordinary Bunsen photometer.

Sonne (1928-1929) determined the necessary amount of energy of different wave lengths to produce a minimum phototropic response in oats. The young plants were so placed that about 1 cm of their tips were exposed at different distances from the light of a monochromator for different exposure periods. The visible part of the spectrum of a Hefner lamp was used as a standard of comparison. Minimum response was obtained at  $0.86 \times 10^{-5}$  g. cal. per  $\text{cm}^2$  in 1 second. The energy was measured by a thermo-element. The results are summarized in table 1.

TABLE 1.—*Sonne's Data showing Phototropic Sensitivity Determined from the Amount of Energy Required to Produce a Minimum Response in Oats*

Wave length (Å)	Absolute energy	Phototropic effect
5700	588	0.17
5460	371	0.27
4360	0.028	3572
4050	0.06	1667
3660	0.10	1000
3130	0.66	152
3020	0.96	104
2800	2.3	44
2650	32 and 15?	7
2530	19	5
2400	77	1

It will be seen from this table that the amount of energy which barely causes phototropic curvature varies with the wave length. The yellow (5700 Å) is about 600 times as intense as is the white light necessary to bring about the same response, while the green (5460 Å) is approximately 400 times as intense, and the blue (4360 Å) only .03 as strong as the energy of his standard white light. The blue is thus approximately 10,000 times as effective phototropically as the green and 20,000 times that of the yellow. The violet (4050 Å) is also very effective but only about half that of the blue.

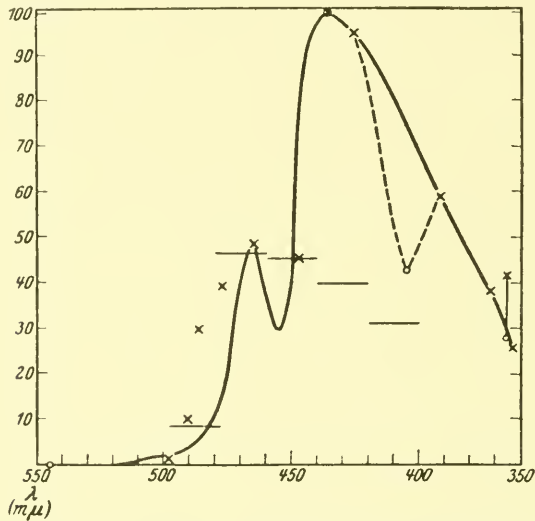


FIG. 1.—Graphs from Bachmann and Bergann showing the sensitivity of *Avena sativa* to wave lengths of light (continuous line) compared with their corrected values of Blaauw (crosses), of Sonne (circles), and of Koningsberger (horizontal lines).

Bergann (1930) made a very careful study of the effects of monochromatic light on the growth and bending of *Avena sativa* as well as the effects produced by a change of intensity and length of exposure. Employing the method of placing the young plant between two opposing lights, he concludes that the regions other than the red and infra-red produce corresponding growth reactions for suitable intensities. In unilateral light equal bending is shown for corresponding intensities, first positive, then negative, and finally positive. Light curvatures and light-growth reactions are parallel processes. The stronger the light-growth reaction in a given wave-length region, the greater will be the phototropic response. The seedlings "choice" in the compensation experiments between two wave-length ranges is always that which corresponds to the stronger growth reaction.

Bachmann and Bergann (1930) review the early work of Blaauw and correct the energy values of his data for light absorbed by  $\text{CuSO}_4$  and water filter, surface reflections, and color filter in order to compare his results with those obtained by Bergann. The results of Sonne and Koningsberger are also corrected and compared. These data are represented graphically in figure 1, in which the continuous line is the sensitivity curve. The data from Blaauw's work are indicated as

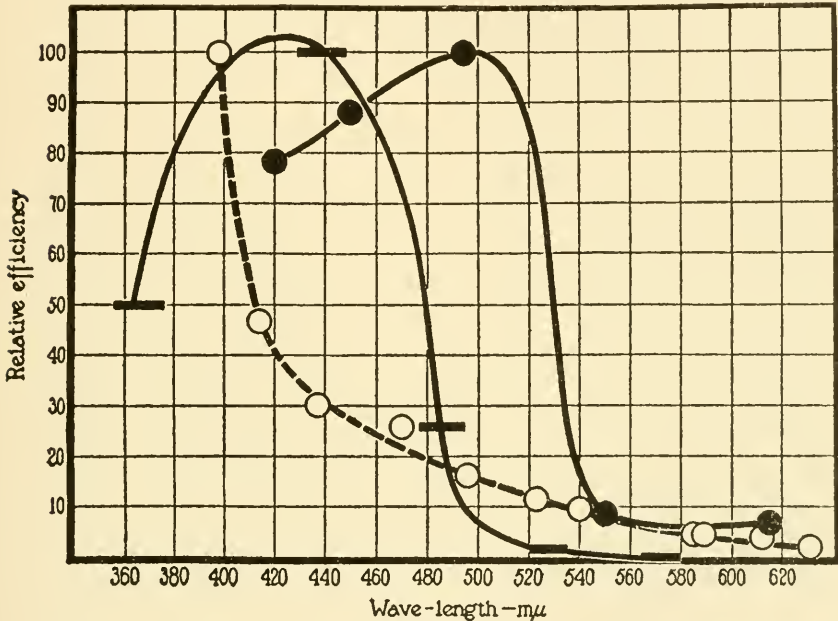


FIG. 2.—Graphs from Castle showing the relative efficiencies of different wave lengths in their stimulation on *Phycomyces blakesleanus* (horizontal lines), on *Phycomyces nitens* from data of Blaauw (solid circles), and on *Pilobolus* calculated from data of Parr (open circles).

small crosses, those of Sonne as circles, and those of Koningsberger as horizontal lines. The multiplier for Blaauw's data in the short-wave-length region is 2.5.

From this work it is concluded that there are two maxima in the phototropic curve and that these correspond in general to the maximum light absorption regions of chromolipoids. It appears that the phototropic curvatures in the different wave-length regions follow the absorption of light by specific substances or their compounds in these same regions.

The sensitivity of the sporangiophores of *Phycomyces* to light of different wave lengths was investigated by Castle (1931). The



sporangiophores were placed between two light sources. The intensities were adjusted until the phototropic effects of the different spectral regions were equal. At this point the efficiency of each region was taken as proportional to its relative energy content. Wratten filters were used in conjunction with a copper chloride filter. The most sensitive region proved to be in the violet (4000-4300 Å). In figure 2 Castle compares his results with those obtained by Blaauw and Parr. It is pointed out that because of the presence of "accessory" pigments in these sporangiophores care must be taken in correlating these results with those obtained from the absorption spectrum of the photosensitive substance.

#### PRELIMINARY EXPERIMENTS

The general method of studying the wave-length effects on phototropism as described by Johnston (1926) was used by Johnston, Brackett, and Hoover (1931) with an improved plant photometer for evaluating four spectral regions in terms of plant response. The general procedure was to place an oat seedling between two different and oppositely placed lights, and after an interval observe the growth curvature. If, for example, when the seedling was exposed to blue and to green lights, a distinct bending was noted toward the blue side, the lights were so adjusted as to increase the green or decrease the blue intensity. Another seedling was then used and the process repeated until a balance point was reached where the effect of one light neutralized the effect of the other. When this balance point was determined, a specially constructed thermocouple replaced the plant and the relative light intensities were measured. From these experiments it was found that no measurable phototropic response was found for wave lengths longer than 6000 Å (Wratten no. 24—red filter), while a noticeable bending was found with the yellow filter (Corning's heat-resisting yellow—yellow shade), whose cut-off on the short-wave-length side was 5200 Å. The threshold for wave-length influence was found to lie somewhere between 5200 and 6000 Å. The effects of green and blue light (Wratten filters nos. 61 and 47 respectively) were progressively greater, being in round numbers 1,000 for the green and 30,000 for the blue times that of the yellow.

These results justified a more elaborate and better controlled experiment wherein narrower spectral regions could be investigated. For this purpose Johnston (1931) used the specially constructed monochromator illustrated in plate 1. Care was taken to eliminate scattered light and to keep the conditions surrounding the coleoptile



symmetrical, with the exception of the wave-length region being investigated. A double-walled glass cylinder with water between the walls slowly rotated about the axis of the coleoptile. Two strips of paper blackened on the inside and separated 1 cm from each other were wrapped about the cylinder in order to shield all but a restricted region at the tip of the coleoptile from the light. The cylinder was encased in a light-proof box which contained two oppositely placed side windows. Through one window, light was passed from the monochromator, and through the other, light from the standard lamp. The standard used was a 200-watt, 50-volt projection Mazda lamp with the filaments in a plane. The standard lamp was enclosed in an air-cooled brass housing with one small glass window opening toward the plant. The light from the standard was passed through a number 6.0 Corning line filter, a heat-absorbing glass, and a water cell before entering the rotating cylinder surrounding the plant. The number 6.0 Corning line filter transmitted wave lengths from about 4400 Å to 5800 Å and from 7000 Å to 12800 Å of the light transmitted by the water filter. The radiation intensity of the standard was 0.37 micro-watts/cm<sup>2</sup> at a distance of 25 cm. This value, of course, varied with different lamps and also with the same lamp as it aged. A photographic red lamp was used behind the small rear window of the plant box for properly placing a coleoptile at the beginning of each exposure. Previous experiments showed the coleoptile to be insensitive for all practical purposes to this particular light. The monochromator lamp was located outside the phototropic room, which was a small room with no outside walls located in the west basement of the Smithsonian building. Very little daily temperature fluctuation occurred in this room because of its ideal location.

Coleoptiles of oats, *Avena sativa* Culberson, were used in all these experiments. The seeds were germinated at approximately 25° C. between glass plates covered with moist filter paper. The plates were so placed in moisture chambers that the seedlings grew vertically. A careful selection of the seedlings was made for straightness when they had attained a length of 2 to 4 cm. One was then transferred to a small Erlenmeyer flask fitted with a cork stopper. It was supported by means of a little cotton in a small hole of the stopper. The flask was filled with distilled water so that the roots were entirely immersed. With the cross hairs in a small telescope as a guide, the seedling was adjusted to a vertical position within the glass cylinder located between the two lights.

The general experimental procedure was to illuminate the coleoptile on its two opposite sides, preferably the narrow edges, and after a

time interval to note the resulting growth curvature. If the light adjustment was very much out of balance as indicated by the plant, a bending similar to that shown in plate 2 occurred in 20 to 30 minutes. An adjustment was then made in the proper direction and the used seedling discarded for a new one. As the balance point was approached the exposure time necessarily increased. Finally on moving the standard light back and forth through a distance of 1 cm, the plants could be made to curve repeatedly toward one light then toward the other. The balance point was taken to be the midpoint between these two positions. Care was always used not to expose the fresh seedlings to any light but red in the preliminary handling. Priestley (1926) has shown that light affects normal and etiolated shoots very differently. The amount of light required to induce phototropic curvature in normal light-grown shoots is greater, and must be continued longer, than that required to bring a similar curvature in etiolated shoots.

After a balance point had been determined and tested by using several seedlings, a specially constructed thermocouple was inserted into the glass cylinder occupied by the seedlings and the light intensities measured at the balance position. The junction of the thermocouple was made of a short length of fine bismuth wire and one of bismuth-tin alloy, each about 25 microns in diameter. The alloy was made up of 95 percent bismuth and 5 percent tin. Utmost care was needed in measuring the light intensities since the plants were found to be much more sensitive to the light than the best physical instruments available. It should be remembered, however, that the seedling integrates the effect of radiation over a relatively long period, while the thermocouple responds in a few seconds.

The results of this experiment are presented in table 2. The ratio of the intensity of the monochromator light to that of the standard light is given in the third column for corresponding wave-length ranges shown in the first column. Where filters were used in combination with the monochromator they are indicated in the second column. No phototropic responses were obtained in any of the first six wave-length ranges. The first quantitative measurements that could be made were for the range 5040 to 5160 Å. In the last column of the table the relative phototropic effectiveness of the different wave-length ranges is given. The ratio 29.10 was arbitrarily taken as unity.

With unilateral illumination through the monochromator and a number 77 Wratten filter in the region 5430 to 5670 Å, bending oc-

curred in four hours. This indicated the approximate threshold region of phototropism. In order to determine this point more accurately a mercury arc in pyrex glass was substituted for the Mazda lamp of the monochromator, and by passing this light through a number 77 Wratten filter, a seedling was unilaterally illuminated by the 5461 mercury line. In five such tests, each lasting from two to several hours, two gave positive bending and three no bending. With reason-

TABLE 2.—*Data from the Preliminary Experiment Showing Phototropic Effectiveness of Restricted Regions of the Spectrum. That for Wave-length Region 5040-5160 Å is Taken as Unity*

Wave-length range (Å)	Filter <sup>a</sup> used with monochromator	Light intensity ratio (Monochromator/standard)	Relative phototropic effectiveness
7250-7700	W 88		
6900-7300	W 88		
6550-6950	CLF 2		
6250-6600	CLF 2		
5940-6270	CLF 3		
5670-5950	TR		
5430-5670	W 22; CLF 5.1		
5200-5430	W 77		
5040-5160	CLF 6.1	29.10	1.0
4940-5070	CLF 6.1	2.49	11.7
4810-4930	CLF 6.1	0.68	42.8
4670-4800	CLF 6.1	0.54	53.9
4550-4670	CLF 7	0.29	100.3
4450-4550		0.27 <sup>b</sup>	107.8
4410-4500		0.34 <sup>b</sup>	85.6
4360-4450		0.36 <sup>b</sup>	80.8
4280-4360		0.41 <sup>b</sup>	71.0
4210-4280		0.47	67.0
4130-4220		0.84	34.6
4070-4135		1.49	19.5

<sup>a</sup> W, Wratten; CLF, Corning line filter; TR, thermometer red.

<sup>b</sup> With the standard lamp at a fixed position from the plant, the intensity of monochromator light was varied by changing the resistance in its lamp circuit until a balance point was obtained.

able certainty it can be concluded that under these particular experimental conditions the threshold wave-length effect is at or very near 5461 Å.

When the phototropic effectiveness is plotted against wave length, a curve is obtained as shown in figure 3, with its maximum at about wave length 4550 Å. The horizontal lines represent the wave-length ranges for which balance points were determined. Points where filters were used in addition to the monochromator are represented as circles.

There is a slight suggestion of two other maxima, one on each side of the peak. It could not be determined from these data whether or not these secondary maxima were real. Furthermore, certain conditions existed during this preliminary experiment which make it impossible to consider this sensitivity curve more than approximately correct. Although an attempt was made to burn the lamps at a constant voltage, there was some fluctuation during the exposure of the seed-

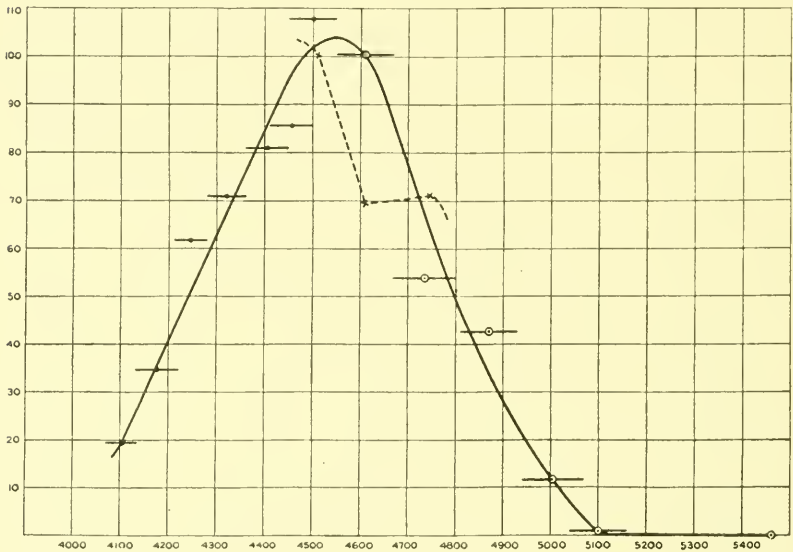


FIG. 3.—Phototropic sensitivity curve of preliminary experiment (continuous line). The ordinates are relative sensitivity values, the abscissae, wave lengths in angstroms, and the horizontal bars indicate the wave-length ranges of the balance points. Circles indicate points obtained with filters combined with the monochromator. Points more accurately determined are indicated by crosses and connected by dash lines.

lings and during the intensity measurements. Also, in some of the work the standard lamp as well as its filter cell was cooled by tap water. This resulted in an accumulation of iron on the glass surfaces during the time required for determining the balance points. These uncontrolled factors undoubtedly modified to some extent the character of light transmitted.

Because of the suggested secondary maximum on the longer-wave-length side, three points on this side were again determined. This time the lamps were connected to a battery of storage cells and the current held more nearly constant. These three wave-length regions with the

corresponding phototropic effectiveness are given in table 3 and the midpoint of each band plotted in figure 3. Here a distinct break in ascent of the curve is shown.

TABLE 3.—Data from the Second Experiment Showing Phototropic Effectiveness in the Spectral Region Indicating the Presence of a Double Maximum

Wave-length range (Å)	Light intensity ratio (monochromator/standard)	Relative phototropic effectiveness
4460-4560	.29	100.3
4558-4662	.42	69.3
4685-4805	.41	71.0

#### IMPROVED EXPERIMENTATION AND RESULTS

Another experiment was planned and carried out in which the technic was further improved. A motor generator was installed wherein the current used for the light sources was automatically controlled. Both the monochromator lamp and the standard lamp were connected in series and replaced at the same time when one burned out. These lamps were the Mazda projection type rated at 200 watts, 50 volts, with an average life of 50 hours. They were burned at four amperes. The water jacket around the standard lamp was removed and the filter cooled by a thermosiphon method in which distilled water was used. In the longer-wave-length regions the light from the monochromator was passed through suitable glass filters to reduce the effect of scattered light of shorter wave lengths affecting the seedlings. Unfortunately no filters which transmitted an adequate percentage of light were available for wave lengths of 4500 Å or shorter when used in connection with these projection lamps.

The data from this more accurately controlled experiment are presented in table 4 and shown graphically in figure 4. The maximum phototropic effect occurs at 4400 Å, a region about 150 Å shorter than the maximum found in the earlier experiment. A secondary maximum occurs at approximately wave length 4750 Å with the intervening minimum at about 4575 Å. From this double maximum the sensitivity of *Avena* falls off rapidly to 5000 Å on the long-wave-length side, and to 4100 Å on the short-wave-length side. It would be interesting to determine if the limit of sensitivity in the case of *Avena* continues to fall off on the short-wave-length end of the spectrum, as some previous work would indicate. At some future date it may be possible to extend this curve into the violet and ultraviolet regions.



Considerable difficulty was experienced in obtaining a satisfactory balance point in the region of 4800 Å. It was necessary to repeat this part of the experiment several times. All other points gave consistent data. It is possible that a slight shift of the seedling, one way or the other from the center of the light beam, in this particular portion of the spectrum was sufficient to account for the difficulty of obtaining entirely satisfactory data. If this were true, then it would indicate a considerable change in sensitivity over a range of only 100 angstroms at about wave length 4800 Å.

TABLE 4.—*Data showing the Phototropic Effectiveness of Restricted Regions of the Visible Spectrum. That for the Hg Line 4358 Å is taken as Unity*

Wave-length range (Å)	Filter <sup>a</sup> used with monochromator	Light intensity ratio (monochromator/standard)	Relative phototropic effectiveness
4945-5055	SG	9.37	.05
4873-4970	NC	1.78	.27
4760-4840	HRN	.54	.89
4650-4750	SG	.51	.94
4530-4620	SG	.58	.83
4470-4545		.49	.98
4360-4440		.42	1.14
4270-4335		.48	1.00
4170-4230		.65	.74
4072-4125		1.18	.41

<sup>a</sup> SG, Sextant green (1.94 mm); NC, Noviol "C" (4.15 mm); HRN, heat resistant Noviol (3.04 mm).

As mentioned above, the light source for this experiment was the Mazda projection lamp. Most of the regions investigated were approximately 100 angstroms wide. For the five points on the short-wave-length side no filters were used. It is believed that the amount of scattered light coming through the optical system of the monochromator in this end of the spectrum did not greatly change the character of the sensitivity curve. It is much more important to eliminate the scattered light at the long-wave points. However, it seemed advisable to determine one or two points on the short-wave-length side by using the lines of the mercury arc that fall in this particular region. A mercury arc in pyrex glass was set up in front of the monochromator, and balance points were determined for lines 4047 Å and 4358 Å. These points gave ratio values of 1.08 and 0.48 respectively, and phototropic effectiveness values of 0.44 and 1.00. Both points are indicated by crosses on the graph in figure 4. Because of the purity of the 4358 Å mercury line its value was taken as unity for all the points given in table 4 and shown in figure 4.



The efficiency value for line 4358 Å falls below the curve. This is to be expected if the points on the curve adjacent to wave length 4358 Å contained scattered light of more phototropic effectiveness. The value for the 4047 Å line is above the curve. It may be noted that this radiation was not exactly monochromatic, since an examination with the spectroscope showed very faintly the presence of lines 4078 Å

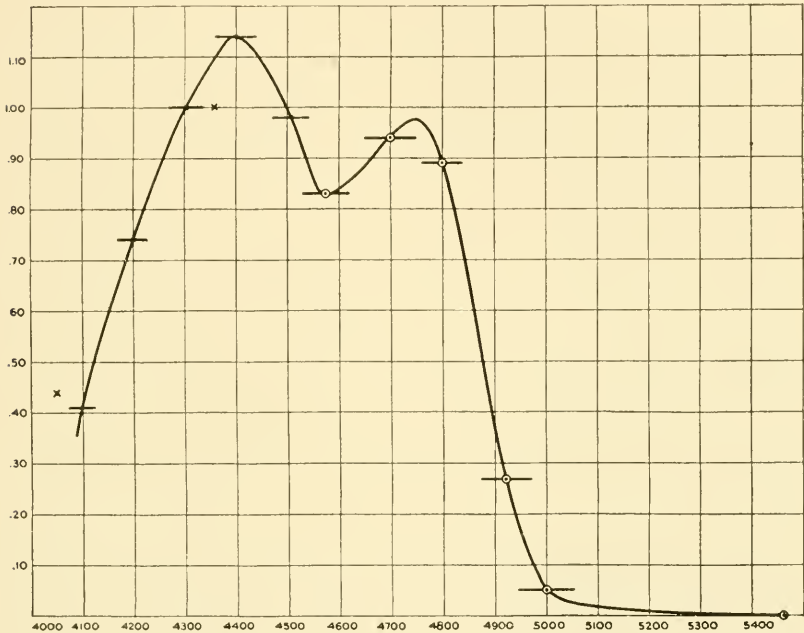


FIG. 4.—Phototropic sensitivity curve. The ordinates are relative sensitivity values, the abscissae, wave lengths in angstroms, and the horizontal bars indicate the wave-length ranges of the balance points. Circles indicate points obtained with filters combined with the monochromator. The crosses show where mercury lines were used.

and 4358 Å. This would make the apparent effectiveness of this line (4047 Å) greater than its actual effectiveness and hence raise it above the curve. On the other hand, the curve itself is doubtless a little higher than that which would have been obtained had it been possible to use filters in addition to the monochromator for this region. It may be possible that the phototropic sensitivity curve actually begins to rise at this point, although there is no indication of this from the other data obtained in this work. It is to be expected that in the ultraviolet region the curve would rise, owing to injury of cells on the proximal side of the seedling.

## DISCUSSION

The use of the plant photometer in determining the sensitivity of seedlings to light has in its favor the elimination of the operator's judgment at many points during the experiment. The plant itself is used as a null point instrument. After a time interval the plant has grown toward or away from the standard light. There is no need for the operator to estimate the angle of curvature or the exact time at which bending begins. Repeated experiments demonstrate that by moving the standard lamp 0.5 cm toward or away from the plant when located at a balance distance of approximately 25 cm, the curvature of seedlings can be changed from one direction to the opposite. It is interesting to note that repetition of balance points seldom differed from each other by more than 5 percent. Very rarely was an unorthodox seedling or an apparently nonsensitive seedling found.

One possible objection to this method might be raised. Each point on the phototropic curve is not strictly comparable to the others. This arises from the fact that the plant was at a fixed distance from the monochromator. The intensity of the various wave lengths used was different. The intensity of the standard light was changed to balance that of the monochromator light. A better method perhaps would be to maintain the standard light at a fixed intensity with respect to the plant and change the monochromator light to balance the standard light.

It is of interest to note that the maximum phototropic response occurs at wave length 4400 Å. This point lies midway between the greatest absorption maxima of chlorophyll *a* and chlorophyll *b* recently measured by Zscheile (1934) by an improved method. It is also the position of one of the maxima found by Hoover (1934, data unpublished) for carbon dioxide absorption by young wheat plants. Since phototropic response is an index of growth retardation it would at first appear that photosynthesis progresses best at a point in the spectrum where growth is least. Such is not the case, however, when the other and somewhat greater maximum of carbon dioxide absorption is considered. This occurs in the region of 6400 Å. Here there is no phototropic response and no retardation in growth.

The absence of any phototropic effect in the red and infrared, as shown in these experiments as well as by those of other investigators, and the sharp rise in the curve from about 5000 Å into the blue, is typical of an electronic photochemical reaction. The photochemical nature of at least some of the underlying processes involved in phototropism is also suggested by the part played by auxins.

Went and his school have shown that small pieces of agar and gelatine impregnated with this growth-promoting substance when placed asymmetrically on decapitated coleoptiles bring about a growth curvature with the small agar or gelatine block above the convex portion of the coleoptile. The amount of bending can be influenced by exposing the tips to light before impregnating the agar or gelatine blocks. It would appear that light either prevents the formation of the auxins or destroys their activity. Furthermore, Kögl (1933) and Kögl, Haagen-Smit, and Erxleben (1933) show this growth-promoting substance to be an unsaturated acid of the formula  $C_{18}H_{32}O_5$ , which loses its growth-promoting activity on oxidation.

Recently Flint (1934) has called attention to a very interesting relationship between light and the germination of lettuce seed. Certain varieties fail to germinate unless exposed while in a moist condition to a small amount of light. In his preliminary work it is shown that light of wave lengths shorter than about 5200 Å inhibits germination, while that longer than about 5200 Å brings about changes resulting in germination. Furthermore, he has shown that normal or non-light-sensitive seeds could be made light-sensitive by subjecting them in a moist condition to strong blue light. These seeds would not germinate until exposed to light of wave lengths longer than 5200 Å.

All of this work is very suggestive of a common photochemically responsive growth-promoting substance in these lettuce seeds and in the coleoptiles of oats. Light in the visible spectrum of wave length shorter than 5200 Å exerts an inhibiting influence on the oat seedling. Likewise this same wave-length region exerts a decided inhibiting action on the germination of these lettuce seeds. However, an exposure to light of longer wave length is necessary for the germination of the light-sensitive seeds, even though the exposure is of as short a duration as one minute. This stimulating effect of the red was not noted in the phototropic experiments. All that can be said is that red light did not exert an inhibiting action. The seedlings were handled in red light, so that if a stimulating action were present, it could not be detected, since no corresponding experiments were tried in total darkness.

#### SUMMARY

The influence of radiation of different wave lengths on phototropism is briefly reviewed and discussed.

Experiments are described in which the plant photometer was used to determine the sensitivity of the coleoptile of *Avena sativa* to the different wave-length regions of the visible spectrum.

The phototropic sensitivity curve rises sharply from 4100 Å to a maximum at 4400 Å. It then drops off to a minimum at about 4575 Å and again rises to a secondary maximum in the region 4700 to 4800 Å. The fall is very rapid from this point to 5000 Å, from where it tapers off very gradually to the threshold on the long-wave-length side at about 5461 Å.

Phototropism, because of its photochemical nature, its relation to auxins and the fact that it is a specific light-growth reaction, places in the hands of the experimenter an important tool for investigating the fundamental relationship of plant growth processes to light.

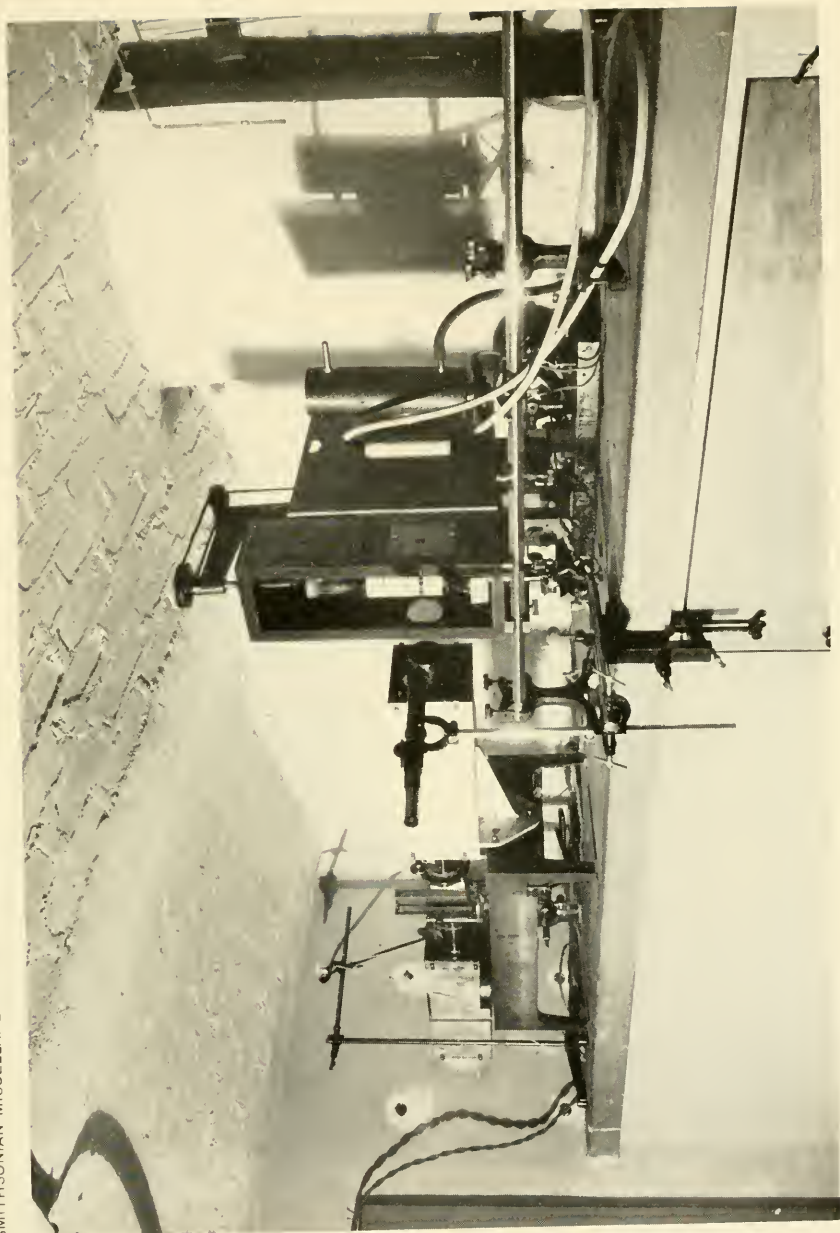
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GENERAL VIEW OF IMPROVED PLANT PHOTOMETER WITH MONOCHROMATOR ON LEFT, THE PLANT CHAMBER WITH FRONT REMOVED AND SHOWING DOUBLE-WALLED GLASS CYLINDER IN CENTER, AND THE SLIDING STANDARD LIGHT HOUSING TO RIGHT



PHOTOTROPIC CURVATURE OF AN OAT SEEDLING RESULTING FROM A DIFFERENCE IN WAVE LENGTHS OF LIGHT ILLUMINATING IT FROM OPPOSITE SIDES