THE PHOTOTROPIC EFFECT OF POLARIZED LIGHT

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PLATE 1

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I

An explanation has been given of the greater absorption of light in the farther half of a single, cylindrical cell illuminated in air with parallel light from one side (Castle, 1933 b). Measurements of light paths within two halves of a cylindrical lens in air show that a greater total distance is traversed by the refracted rays in the far half than in the near half. The explanation is based largely on the idea that the primary action of light is on the cell protoplasm rather than on the wall. This interpretation has been tested in the experiments described in this paper, by making use of differences in the phototropic effectiveness of different planes of polarized light.

II

The upright sporangiophore of Phycomyces placed between two sources of light opposed at 180° is remarkably sensitive to differences in intensity between the two beams. Massart (1888) found that the cells responded to an intensity difference between the two sides of 18 per cent; Castle (1931) found a differential sensitivity of about twice Massart’s value, in the vicinity of 8 per cent. Response is manifested by an inclination to and growth toward the more intense light. The cell does not reach a true position of equilibrium with reference to the two beams, and it is therefore best used as a “null” indicator, to show equal effects on opposite sides.

In the present experiments, two opposed beams of light plane polarized at right angles to each other were used. With reference to the vertically growing sporangiophores, one beam of light was polarized horizontally, the other vertically.
PHOTOTROPIC EFFECT OF POLARIZED LIGHT

As shown in Text-fig. 1, two 3 candle power 6 volt automobile lamps were set up 2 meters apart and run in series on a 12 volt direct current line from the central storage battery of the Biological Laboratories. Voltage fluctuations thus tended to affect both lamps equally. A large Nicol prism was interposed in each beam, and adjusted so that the transmitted beams were plane polarized at right angles to each other, one vertically, the other horizontally.

Text-fig. 1. Side view of the apparatus used to obtain opposed beams of polarized light. a, 3 candle power 6 volt automobile lamps run in series on a 12 volt line. b, movable lamp used to obtain vertical growth of cells before an experiment. c, culture of Phycomyces in a glass cell. The axes of the two Nicols are at right angles, so that the left beam is polarized horizontally, the right vertically.

A culture of Phycomyces was placed in a rectangular glass cell on a movable block at a particular place on the optical bench, and by means of a small electric lamp directly above the culture, sporangiophores were caused to grow up through a slit in the metal cover of the culture vessel. When the cells were at the proper stage of development, the overhead light was put out, and the lamps illuminating the cells from opposite sides with polarized light were turned on. Undisturbed growth was allowed to continue for 3 hours, then a photograph was taken of the cells from the side. Deviations from the vertical became more marked if the experiment continued for longer times. By using different cultures and varying the position on the optical bench, a region of phototropic balance was found where cells were either "indifferent," bending toward neither one side nor the other, or where approximately equal numbers bent in each direction. The conditions for equal phototropic effect of light polarized in each plane were determined by measuring the relative intensity of each beam at this region, using a Weston photronic cell and a Leeds and Northrup type "R" galvanometer with a 50 ohm shunt. Since the intensities of light were low, the photocell method proved the only satisfactory means of measurement. To avoid errors due to changes in the sensitivity of the photocell, the ratio of galvanometer deflections obtained from each beam at a given point on the optical bench was obtained. The measurements are expressed in terms of this intensity ratio, which proved reproducible to within
2 per cent. The sensitivity of the photocell to different planes of polarization was
tested by rotating it in a beam of polarized light. No significant difference in the
galvanometer deflection was observed. Any polarization effect in the photocell
must amount to less than 1 per cent.

The end-point for equal and opposite phototropic effect is not as sharp as might
be desired, for several reasons: (1) a positively phototropic organism is not in a
condition of stable equilibrium under the circumstances of the experiment, since
a random movement may place it under the sole orienting influence of either light
source to the exclusion of the other. Furthermore, with equal phototropic stimu-
lation on opposite sides, there is nothing but a weak negative geotropism to keep
the cells upright in a plane perpendicular to the axis of the optical bench. Angular
deviations of the sporangiophores from the vertical in this plane will alter, cancel,
or reverse any differences between the effects of the two oppositely polarized
beams. An experiment must therefore not be continued for such a long time that
deviations from the vertical become prominent. (2) Until a certain intensity
difference is reached between the two sides, no differential growth is perceptible.
Massart found the critical difference to be 18 per cent, but this estimate is cer-
tainly too high. For the present experiment, this means that a definite zone will
be found within which approximate phototropic balance prevails. (3) Phototropie
balance is achieved by equating two different kinds of light, having different
distributions of intensity within the cell. It is assumed that each half of the
cell in effect summates the light absorbed within it, irrespective of the particular
place of absorption. If this assumption is not completely justified, there will be
room for more specific phototropic effects in the action of light polarized in differ-
ent planes. Such effects, if existent, would complicate the conditions for photo-
tropic balance.

III

The critical experiment consists in placing a culture at a position
where the intensities of the two opposed beams are equal, differing only
in plane of polarization. Plate 1, Fig. 1 b, shows a typical photograph
taken at the end of such a test. The mature, actively growing cells
have almost all bent to the left, showing that light which is polarized
horizontally is phototropically more effective than light of equal energy
polarized vertically. Examination of the other photographs of Plate 1,
Fig. 1, confirms this finding, and shows that for equal phototropic effect
the beam polarized vertically has to be 10 to 15 per cent more intense
than the beam polarized horizontally. It is clear from these typical
records that a more precise statement of the results is not justified,
yet that a real difference exists in the effectiveness of the two beams.

Light polarized horizontally will undergo a smaller reflection loss at
PHOTOTROPIC EFFECT OF POLARIZED LIGHT

most angles of incidence on the cell surface than light polarized vertically. The loss in each case may be computed from Fresnel's formulae. For light polarized horizontally,

\[ I_{\text{reflected}} = \frac{\tan^2 (i - r)}{\tan^2 (i + r)} I. \]

For light polarized vertically,

\[ I_{\text{reflected}} = \frac{\sin^2 (i - r)}{\sin^2 (i + r)} I, \]

where

\[ I = \text{incident intensity} \]
\[ i = \text{angle of incidence} \]
\[ r = \text{"refraction} \]

For both planes of polarization, when \( i = 0 \)

\[ I_{\text{reflected}} = \left(\frac{n - 1}{n + 1}\right)^2 I \]

where

\[ n = \text{refractive index of the cell surface} \]

The percentage reflection losses of representative rays incident on the cylindrical surface of the cell at angles ranging from 0° to 90° were computed for both planes of polarization, and are given in Table I. In Text-fig. 2 the corresponding intensities transmitted into the cell are plotted against the angles of incidence. It is evident that in the case of light polarized horizontally, a large proportion of the rays incident on the cell at angles around 50° are refracted into the cell with little loss of intensity. As previously shown (Castle, 1933 b), it is especially these more tangential rays which have a long path in the back half of the cell relative to the front half. Consequently, greater relative absorption of light will take place there than in the case of light of equal intensity polarized vertically.

The magnitude of the difference which might be expected may be estimated by formulating the conditions necessary for phototropic balance. The basic assumptions and the general procedure of the
method have already been described (Castle, 1933b), and will not be
detailed here. Use of polarized light is assumed only to alter the

### TABLE I

Reflection loss and relative absorption in each half of a cylindrical cell of light plane polarized as described. $I_1$ and $I_2$ are taken from Castle (1933b).

<table>
<thead>
<tr>
<th>Angle of incidence ($i$ degrees)</th>
<th>$\sin i$</th>
<th>Intensity loss by reflection</th>
<th>Intensity of refracted beam</th>
<th>Relative length of light pathway</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Horizontally polarized</td>
<td>Vertically polarized</td>
<td>$I \times h$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$I$</td>
<td>$I'$</td>
<td>$I \times h'$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>per cent</td>
<td>per cent</td>
<td>per cent</td>
</tr>
<tr>
<td>0.0</td>
<td>0</td>
<td>4.0</td>
<td>4.0</td>
<td>96.0</td>
</tr>
<tr>
<td>11.7</td>
<td>0.203</td>
<td>4.2</td>
<td>95.8</td>
<td>0.981</td>
</tr>
<tr>
<td>23.8</td>
<td>0.404</td>
<td>5.0</td>
<td>95.0</td>
<td>0.925</td>
</tr>
<tr>
<td>37.0</td>
<td>0.602</td>
<td>7.0</td>
<td>93.0</td>
<td>0.816</td>
</tr>
<tr>
<td>44.5</td>
<td>0.701</td>
<td>9.0</td>
<td>91.0</td>
<td>0.739</td>
</tr>
<tr>
<td>53.4</td>
<td>0.803</td>
<td>13.1</td>
<td>86.9</td>
<td>0.629</td>
</tr>
<tr>
<td>64.3</td>
<td>0.901</td>
<td>21.3</td>
<td>76.9</td>
<td>0.478</td>
</tr>
<tr>
<td>72.3</td>
<td>0.953</td>
<td>34.0</td>
<td>66.0</td>
<td>0.352</td>
</tr>
<tr>
<td>90.0</td>
<td>1.0</td>
<td>100.0</td>
<td>0</td>
<td>1.380</td>
</tr>
</tbody>
</table>

$\times$ 100

### TEXT-FIG. 2
Intensity of refracted rays for different angles of incidence, computed from Fresnel's formulae. $a$, incident beam polarized horizontally; $b$, incident beam polarized vertically. The index of refraction of the cell surface is taken as 1.5, that of air as unity.

amount of surface reflection and thus the relative intensities of particular rays within the cell. The further assumption is implicit that
the effect of continuous light of low intensity in producing phototropism is directly proportional to the intensity.

Though it has been shown that light is refracted through these cells as if they had a mean refractive index of 1.38, in treating surface reflection the refractive index of the reflecting surface should be used. For the chitinous cell wall a value of \( n = 1.50 \) was used in the present calculations, although the light paths inside the cell were considered as within a cylindrical lens of refractive index 1.38. Reflection losses at the internal interface wall/protoplasm were neglected for the sake of simplicity.

\[
I = \text{intensity of transmitted ray polarized horizontally}
I' = \text{" " " " vertically}
I_o = \text{intensity of incident ray polarized horizontally}
\]

**Text-Fig. 3.** Diagrammatic cross-section of a cell illuminated from opposite sides with polarized light. Only one ray in each beam is shown. Detailed description in the text.

Let Text-fig. 3 represent a cross-section of a cell illuminated with parallel light from two sides, the beam on the left being polarized horizontally, that on the right polarized vertically. For simplicity only one ray in each beam is represented. Let the cell be considered in terms of the two halves, (1) and (2). Furthermore, let

\[
I_o = \text{intensity of incident ray polarized horizontally}
I'_o = \text{" " " " vertically}
I = \text{transmitted intensity of ray polarized horizontally}
\]
$I'$ = transmitted intensity of ray polarized vertically
$a = \text{absorption of horizontally polarized ray in (1)}$
$b = \text{" \ " \ " \ " \ " \ " \ " \ "} \ (2)$
$c = \text{" \ " vertically \ " \ " \ " \ "} \ (2)$
$d = \text{" \ " \ " \ " \ " \ " \ " \ "} \ (1)$

Also, for any ray let

\[ l_1 = \text{length of light pathway in front half of cell}^1 \]
\[ l_2 = \text{" \ " \ " \ " \ " \ " \ " \ " \ back \ " \ " \ "} \]

The condition for phototropic balance is simply that the total absorption in the two halves must be the same, or that for all rays

\[ \Sigma(a + d) = \Sigma(b + c) \]

The evaluation of $a$, $b$, $c$, and $d$ is greatly simplified if the absorption coefficient, $\alpha$, is regarded as infinitely small. If this assumption is made, the usual exponential form of the absorption law can be dispensed with, and relative absorption written equal to the product of intensity and length of absorbing path. Thus on this basis

\[ a = I \times l_1 \quad c = I' \times l_1 \]
\[ b = I \times l_2 \quad d = I' \times l_2 \]

The validity of this simplification depends on the exponent in the absorption law being small, implying either a thin absorbing layer or a small absorption coefficient, or both. Probably both of these conditions hold in the cell of *Phycomyces*. In any case, the following solution is for the limiting case of zero absorption. See Table I.

To obtain the summated values of $a$, $b$, $c$, and $d$ for all rays, graphic integration is carried out as previously described (Castle, 1933b).

\[ \Sigma(a) = 2 \int_0^1 l_1 d \sin i \quad \Sigma(d) = 2 \int_0^1 l'_1 d \sin i \]
\[ \Sigma(b) = 2 \int_0^1 l_2 d \sin i \quad \Sigma(c) = 2 \int_0^1 l'_2 d \sin i \]

The areas under the curves in Text-figs. 4 and 5 represent the relative amounts of absorption from two polarized beams of unit intensity.

\(^1\)"Front" half of the cell is here used to denote that half of the cell through which any incident ray first passes.
PHOTOTROPIC EFFECT OF POLARIZED LIGHT

incident as described. Table I gives the data from which the curves were made. It will be noted that the ratio of absorption in the two halves of the cell is different in the cases of the two oppositely polarized beams.

Considering $I_0$ as constant and equal to 1, what is wanted is the value of $I'_0$ which will fulfill the condition

$$\Sigma(a + d) = \Sigma(b + c)$$

$I'_0$ is therefore allowed to increase, which means that the areas under the curves in Text-fig. 5 will simply be multiplied by whatever value of $I'_0$ is used. Table II shows that $I'_0$ must increase to between 1.20 and 1.30 before the desired conditions are fulfilled.
This means that for phototropic balance the intensity of the vertically polarized light must be more than 20 per cent greater than that of the horizontally polarized light. The experimentally found figure was between 10 and 15 per cent. Considering the end-point of the experiment, it is clear that the difference between these values is not significant. The agreement could be made better if a small, finite value of absorption coefficient were used in the computations.

The magnitude of the difference found between the effects of vertically and horizontally polarized light can therefore be completely accounted for in terms of the suggested mechanism of absorption. This does not prove that the assumptions underlying the explanation are correct. Verification of the expected polarized light effect is, however, circumstantial evidence in favor of the suggested explanation.

### TABLE II

Ratio of light absorbed in two halves of a cell illuminated from opposite sides with polarized light as described in the text. The incident intensity of the horizontally polarized beam is unity; that of the vertically polarized beam ($I_v'$) is allowed to increase until the conditions for phototropic balance are met.

<table>
<thead>
<tr>
<th>$I_v'$, incident intensity of vertically polarized light</th>
<th>$\frac{2(a + c)}{2(a + d)}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.00</td>
<td>1.021</td>
</tr>
<tr>
<td>1.10</td>
<td>1.010</td>
</tr>
<tr>
<td>1.15</td>
<td>1.006</td>
</tr>
<tr>
<td>1.20</td>
<td>1.001</td>
</tr>
<tr>
<td>1.30</td>
<td>0.993</td>
</tr>
</tbody>
</table>

A few tests have been made of the possible specific action of plane polarized light on living organisms, largely with negative results. Most conspicuously, the use of polarizing optical instruments implies that the human eye registers the intensity of light irrespective of its plane of polarization. Crozier and Mangelsdorf (1923) tested the phototropic efficiency of plane polarized light on several arthropods, and found no difference between it and non-polarized light of equal intensity. Macht (1927) reported that seedlings of several different kinds of plants grew faster in polarized light than in non-polarized
light of the same intensity. His published data do not warrant this conclusion. He measured and summated the growth of the roots of different seedlings, usually twenty in number, half of which grew in ordinary and half in plane polarized light. In every case the total growth was numerically greater in the polarized light. Due to the extreme variability in the growth rate, the whole question is whether the numerical differences found are statistically significant. Computation of the probable errors of the differences in the case of Macht's squash seedlings shows that the differences are less than twice the probable errors of the differences. Similar computations for his *Lupinus* seedlings show differences ranging from less than one to four times the probable errors of the differences. Moreover, since the experimental conditions for securing light of identical spectral composition in the two experimental chambers were not rigorous, the possibility of a small consistent difference in spectral quality of illumination is not excluded.

The present experiments demonstrate a difference in the effect of light depending on its plane of polarization with reference to the axis of the cell. The difference which is found can be wholly accounted for by differences in the reflection losses at the cell surface and consequently in the relative intensities of certain rays of light within the cell. There is no need to postulate a more specific effect of plane polarized light on the growth processes of the cell. The difference which might be expected between the effects of polarized and unpolarized light has not been determined. It should be smaller than the effect measured above, and its detection more difficult.

I am indebted to Mr. William Arnold for suggesting the use of polarized light in these experiments and for many helpful discussions.

**SUMMARY**

For the growing cell of *Phycomyces*, a difference in the phototropic effect of light is described depending on its plane of polarization with reference to the axis of the cell. The difference which is found is primarily due to differences in the reflection losses at the cell surface. The magnitude of the effect approximates that deduced from the theory of phototropism suggested for this system. No specific effect
of plane polarized light on the growth processes of the cell need be postulated.

REFERENCES

Castle, E. S., 1933 a, *J. Gen. Physiol.*, 17, 41.
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PHOTOTROPIC EFFECT OF POLARIZED LIGHT

EXPLANATION OF PLATE 1

Fig. 1. a, b, c, d, e, and f are photographs, taken at the end of 3 hours, of separate experiments in which cultures of originally straight cells were placed singly between two sources of light, the left polarized horizontally, the right vertically. The relative intensities of the lights on the two sides are expressed by the ratio given at the bottom of each plate. The top half of each photograph corresponds to the region where the intensities were measured, and where the mature, growing sporangiophores were. The degree of crowding in a culture is exaggerated, since the cells grew through a slit 2 cm. long perpendicular to the plane of the paper, and are here seen superimposed in silhouette. Real crowding and shading may be seen in the lower half of a. Note (1) that in b where the intensity ratio is nearly 1:1 the cells bend definitely to the left, and (2) that d and e represent approximate phototropic balance.