Differential Growth and Phototropic Bending in *Phycomyces*

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ABSTRACT Using present knowledge of the cell's optical and growth mechanisms, a theoretical bending speed of about 5° min.$^{-1}$ is calculated for unilateral irradiation by a single beam of normally incident visible light; this figure is of the magnitude found experimentally. Between beams of light opposed at 180°, the resultant bending speed is given by the difference-to-sum ratio of the light intensities of the two beams. Valid comparisons between cells differing in size, growth speed, or optical properties are made by expressing bending speed as a fraction of each cell's bending response to unilateral irradiation. With multiple beams differing in intensity and azimuth, the resultant bending speed follows from vector addition of phototropic components proportional to the flux fraction of each beam. The bending speed in Oehlkers' experiment where a luminous area is the light source also appears compatible with this rule. In such experiments, the bending speed quantitatively matches the scaled asymmetry of the pattern of flux incident upon the cell. Resolution experiments support the assumption that light intensity enters into steady state phototropic formulations as the first power of I.

Phototropic bending of the *Phycomyces* sporangiophore is a motion sensitively manifesting asymmetric growth and having direction, sign, and magnitude. The magnitude of the response is appropriately measured by the angular bending speed, which is affected by the cell's absolute speed of elongation, by its diameter, and most relevantly by the asymmetry of illumination across it. This paper seeks a quantitative interpretation of steady state bending in terms of the cell's optical and growth mechanisms, attention being restricted to the action of unfiltered visible light incident normal to the cell's long axis. Dennison (1965) has recently studied a set of related problems. The light responses of *Phycomyces* have been reviewed by Banbury (1959), Thimann and Curry (1960), Reichardt (1961), Delbrück (1962), and Shropshire (1963).

The phototropic response initiated without complicating transients shows striking regularities: (*a*) the cell after a delay bends toward the light source at a nearly constant angular speed; (*b*) the speed of bending is over a wide range

independent of the incident light intensity; (*c*) the growth speed of the half of the cell distant from the light source is increased while the growth of the near half is proportionately slowed. Suitable experiments further show that bending can continue indefinitely; hence it is basically a steady state process in which the cell continuously "sees" the light and does not adapt to it. The fundamental reason for these regularities lies in the interplay between a constant *ratio* in the action of light across the cell and the cell's *fixed growth output* under steady state conditions.

Faster growth of the far half has long been considered somehow due to the concentration of light there by the cell's own lens action. Delbrück and Shropshire (1960) have discussed in detail how two opposed optical mechanisms determine the net difference in the action of light across the cell: (*a*) the decrease in intensity (attenuation) by absorption and by scattering along the light path through the cell: this factor favors greater action in the near half; (*b*) the refraction of light within the cell (the lens effect): this factor conversely favors greater action in the far half. For visible light, attenuation is small relative to the lens effect and the cell curves concavely toward the light source. For wavelengths below 300 mμ, strong attenuation outweighs the lens effect and the cell curves convexly away from the light source (Curry and Gruen, 1957). Shropshire (1962) has unmistakably validated the role played by refraction in these responses.

But there are difficulties in applying these ideas quantitatively. Slowed growth of the near half cannot be a direct response to light. Light does not inhibit growth in *Phycomyces* but only promotes it, provided that other conditions within the cell permit this positive action to be expressed. Hence regionally slowed growth caused by light must be a secondary consequence of the whole cell's finite growth capacity, which is set by a supply system basically independent of light (Castle, 1961). Moreover, the bending cell is geometrically constrained to distribute its limited growth around the periphery of its cross-section according to a cosine function, and this distribution does not match the peripheral light intensity distribution at the cell wall as computed by Reichardt and Varjú (1958). For example, the lens action strongly illuminates a median strip of the far wall while areas adjacent to this strip remain essentially in the dark (Fig. 1). Nevertheless, points in these "dark" areas have consistently faster elongation rates during bending than do symmetrically located and directly illuminated points in the near half. Thus there is no simple relation between the illumination of a local area of the wall and its rate of elongation. For this reason it seems improbable that light acts directly on the wall itself, and Delbrück and Shropshire (1960) so conclude from other evidence.

It is a useful analytical artifice to consider the action of light as essentially "lumped" in the near and in the far halves of the cell's cross-section; optically,

these constitute two compartments through which an incident light beam passes in series. Paradoxically, the effect of light is greater in the second compartment, although the flux through this cannot exceed, and indeed due to attenuation must be less than, the flux through the first compartment. Two principal theories of the lens mechanism have been proposed: (*a*) the path length theory, according to which more quanta are absorbed per unit time in the far half because the total absorptive pathway is longer there (Castle,

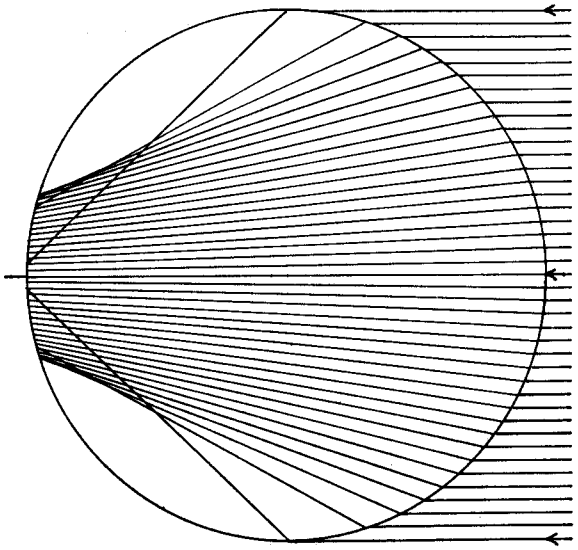

FIGURE 1. Diagram of calculated light paths within the cell's cross-section when irradiated in air by a unilateral beam of normally incident parallel light. The internal anatomy of the cell is neglected, and its refractive index is taken to be 1.38; scattering and internal reflection are ignored. Only the axial ray is shown emergent. Note the paired areas in the far half that are not directly illuminated.

1933); (*b*) the mechanical advantage theory of Buder and Jaffe, according to which quanta absorbed in the far half are situated on the average nearer the light beam's central axis through the cell and hence have a greater phototropic vector along that axis than corresponding quanta absorbed in the near half (Jaffe, 1960).

The mechanisms of these two theories are not mutually exclusive, and difficulties beset the use of each. The path length theory necessarily assumes that the photoreceptors are in essence uniformly distributed throughout the cell's cross-section, and this is questionable if the central core of the cell is an axial vacuole (Cohen and Delbrück, 1959) and if the photoreceptors are spatially oriented (Jaffe, 1960). On the other hand, the mechanical advantage theory must almost necessarily assume the photoreceptors to be in, or close to, the

wall. Indirect evidence against absorption of light by the wall has been cited above. Fortunately, as noted by Jaffe, these two theories though distinct in mechanism are linked by the geometry of refraction so as to give the same quantitative result. The mechanical advantage theory is used below to obtain a plausible estimate of the magnitude of the lens effect despite underlying theoretical uncertainties.

Calculation of Absolute Bending Speed

Consider a cell in air struck from one side by a horizontal beam of parallel visible light. Constant flux conditions are assumed, and if the light intensity is within the broad range termed "normal" by Reichardt and Varjú (1958), the absolute value of intensity is irrelevant. Bending speed depends on elongation speed and on cell diameter; characteristic values for these are inserted later. There are five main steps in the computation.

1. The relative action of light in each half of the cell due to refraction alone is calculated, and the far half/near half *action ratio* is denoted R'. Thus, using the mechanical advantage theory[1] and the symbols of Fig. 2:

$$R' = \frac{\int_0^1 t \cos(2r - i)\, d(\sin i)}{\int_0^1 t \cos i\, d(\sin i)} \qquad (1)$$

where t is a transmission factor calculated from Fresnel's formula for reflection loss at the air/cell interface, assigning to the cell a refractive index of 1.38 (*cf.* Castle, 1933). Reflections of rays at the back surface of the cell are neglected. Series of values of the integrands are calculated, plotted against sin i, and the areas under the two curves measured by planimetry. R' thus calculated is approximately 1.22. This value may be considered to express the advantage of the far half relative to the near half in terms of phototropic effect per quantum absorbed.

2. The calculated advantage due to refraction is next diminished by a correction for attenuation. Shropshire (1962) showed that cells immersed in a fluid medium of refractive index 1.295 exhibit null phototropism when irirradiated unilaterally by visible light. In this condition of phototropic balance, the advantage given the cell's far half by refraction is numerically equal to the advantage given the near half by attenuation. The refraction advantage for this immersion experiment, R'_{im}, when evaluated by the method used in the paragraph above, is found to be 1.09. Thus the attenuation advan-

[1] Dr. Jaffe has most kindly shown me his unpublished quantitation of this theory. If I have perverted his ideas in making modified use of them, I am to blame.

tage of the near half may be considered 9 per cent.[2] Assuming this factor to be independent of the medium surrounding the cell, the *net action ratio*, R, for the case of unilateral irradiation by visible light in air may be written

$$R = R'/R'_{\text{im}} = 1.22/1.09 = 1.12$$

This step contains the assumption that the action of light in the two halves of the cell is a linear function of its intensity. The validity of this assumption is discussed below.

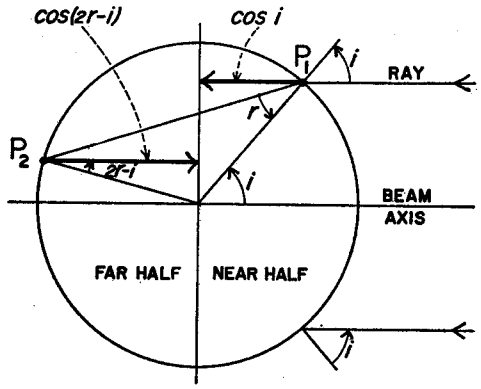

FIGURE 2. Diagram illustrating the basis of the mechanical advantage calculation. One light ray is shown incident on the cell's circular cross-section at P_1, at angle of incidence i; this ray is there refracted at the angle r and crosses the cell to point P_2. At P_1 and at P_2, phototropic unit vectors are established directed toward the cell's center; the components of these along the beam's axis are measured by cos i and by cos $(2r - i)$ respectively (heavy arrows). The components perpendicular to this axis are neglected because cancelled by equal and opposite components (not shown) generated by the symmetrical ray in the two lower quadrants. Equation (1) of the text integrates these axial vector components for all rays incident on the first quadrant, after correction for reflection loss at incidence.

3. The *average speed* of membrane elongation in each of the two semicircles of wall, $\bar{v}_2$ for the far half and $\bar{v}_1$ for the near half, is now assumed proportional to the light action in the related half of the cell. This step equates the ratio of the average growth speeds to the light action ratio, that is

$$\bar{v}_2/\bar{v}_1 = R = 1.12 \qquad (2)$$

4. The condition that the cell's total rate of growth is constant is applied, specifically the fact that speeded growth of one half is coupled with equally

[2] Shropshire (1962) by the use of simplifying assumptions estimated this advantage to be about 14 per cent.

slowed growth of the other half. In particular, the growth speed of the cell's central axis is taken to be unaltered and equal to unity. Thus

$$(\bar{v}_2 + \bar{v}_1)/2 = 1 \tag{3}$$

Solving equations (2) and (3),

$$\bar{v}_2 = 1.06, \qquad \bar{v}_1 = 0.94, \qquad \bar{v}_2 - \bar{v}_1 = 0.12$$

This step yields a 12 per cent difference between the average growth speeds that is symmetrically divided between the two halves.

5. Both the action of light and the distribution of growth speed have been considered up to this point as lumped, that is, as average values pertaining to the cell's two halves. We must now distribute growth speed around the periphery according to the cosine function required by the geometry of bending. The speed at any point on the periphery is given by the relation

$$v = 1 - \frac{v_2 - v_1}{2} \cos \theta \tag{4}$$

where v_2 and v_1 are the maximum and minimum elongation speeds at the poles of the convex and concave flanks respectively, and θ is the angular position measured from the light beam's central ray (Fig. 3). We know from solution of equations (2) and (3) the normalized *average* values of v for the two semicircles of wall, and we want from equation (4) the particular values v_2 and v_1.

By definition, the average values $\bar{v}_1$ and $\bar{v}_2$ relate to v thus:

$$\bar{v}_1 = \frac{2}{\pi} \int_0^{\pi/2} v d\theta; \qquad \bar{v}_2 = \frac{2}{\pi} \int_{\pi/2}^{\pi} v d\theta \tag{5}$$

Substituting for v in equations (5) its value given by the right hand side of equation (4), integrating, and solving for v_2 and v_1:

$$v_2 = 1.094; v_1 = 0.906$$

Thus the growth speed difference between the two points across the cell in the plane of bending, $v_2 - v_1$, is about 19 per cent. The cell's real bending speed is directly proportional to this difference. If the cell diameter, D, is taken as 0.1 mm and the growth speed of the cell's central axis, v_0, as 0.05 mm min.$^{-1}$,

$$\begin{aligned} \text{Bending speed} &= \frac{v_0}{D} (v_2 - v_1) \\ &= 0.094 \text{ radians min.}^{-1} \\ &= 5.4^\circ \text{ min.}^{-1} \end{aligned} \tag{6}$$

This calculated figure agrees well for order of magnitude with measured bending speeds, which are commonly found to range from about 3° min.$^{-1}$ to 7° min.$^{-1}$.

A closer comparison was made with a sample of 18 cells having a mean diameter of 0.145 mm, a mean growth speed of 0.052 mm min.$^{-1}$, and a mean bending speed of 4.56° min.$^{-1}$. The dispersion of the measured bending speed was high, the standard deviation of its mean being ± 1.30° min.$^{-1}$. The theo-

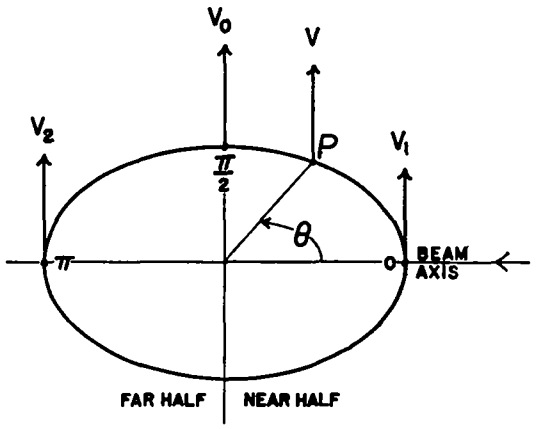

FIGURE 3. Perspective view of the cell's cross-section, illustrating symbols of equations (4) and (5) in the text. P, a point in the peripheral cell wall having growth speed v. v_2 and v_1 are the maximum and minimum speeds at the poles, v_0 the speed of the central axis. In bending, $v_2 > v_0 > v_1$, and $(v_2 + v_1)/2 = v_0 = 1$. Growth speeds shown here diagramatically in one horizontal section result in fact from integration of differential elements over the growth zone's length; this longitudinal distribution is not relevant for the purposes of this paper.

retical bending speed calculated by equation (6) for the average cell of this sample was 3.9° min.$^{-1}$. By the t test, the difference between 4.56° min.$^{-1}$ and 3.9° min.$^{-1}$ is barely significant.

The cells of this sample were large; cells of small diameter may show distinctly higher bending speeds. One small cell studied had a diameter of 0.065 mm and an axial growth speed of 0.065 mm min.$^{-1}$. Its measured bending speed was 15° min.$^{-1}$, but its calculated bending speed from equation (6) was only 11° min.$^{-1}$. This difference might be due to overestimation of attenuation. Although the advantage of the far half due to refraction should be independent of the cell's size, the converse advantage of the near half due to attenuation might be expected to vary directly with the diameter. Assuming such a linear relation, the attenuation correction for this cell would be 6 per cent rather than 9 per cent, and the calculated bending speed would be 14° min.$^{-1}$. The theory is therefore not inconsistent with the occurrence of high bending speeds in small cells.

Bending Speed with Two Beams of Light Opposed at an Angle of 180° and Varied in Intensity

Bending toward a single source of light under steady state conditions gives no sign that the cell is capable of intensity discrimination, since the speed of bending is constant and independent of the incident light intensity. These facts follow directly from the cell's optics and from its fixed growth capacity. The two determining conditions may be formally summarized thus:

$$\frac{v_2}{v_1} = \frac{Ia}{I} = a; \qquad v_2 + v_1 = c \tag{7a, 7b}$$

where v_2 and v_1 are maximum and minimum growth speeds across the bending cell, and I is the intensity of the light beam; a is a constant greater than 1 representing the advantage given by the optical mechanism, and c is a constant expressing twice the average value of the growth speed. Intensity vanishes from the formulation. Since both the ratio and the sum of the growth speeds are constant, their difference, $v_2 - v_1$, to which bending speed is proportional, is also constant.

But when a cell is struck simultaneously by two beams of light differing in intensity, its bending speed readily discriminates the intensity difference. This is because the light action ratio across the cell is no longer invariant as in the one beam case. Analysis of the two beam situation proceeds from the following assumptions:

(*a*) For each beam considered separately, the advantage given growth of the far half is constant and independent of the light intensity.

(*b*) The relative effect of each beam of light is proportional to its intensity.

(*c*) Each of the two beams contributes a component to the net action of light in each half of the cell, the two components being additive.

(*d*) Speeded growth in one half of the cell is accompanied by correspondingly slowed growth in the other half.

Fig. 4 diagrams the case of opposed phototropism. I_1 and I_2 are the intensities of two representative rays; v_2 and v_1 are the elongation speeds, determined by the action of light in the left and right halves of the cell respectively, each action being the sum of two components shown inscribed therein.

The assumptions above are embodied in the following two equations:

$$\frac{v_2}{v_1} = \frac{aI_1 + I_2}{I_1 + aI_2}; \qquad v_2 + v_1 = c \tag{8a, 8b}$$

Solving these equations for v_2 and v_1,

$$v_2 - v_1 = c\,\frac{(aI_1 + I_2) - (aI_2 + I_1)}{(aI_1 + I_2) + (aI_2 + I_1)} \tag{9}$$

This states that bending speed should be proportional to the difference-to-sum ratio of light action in the two halves of the cell.

Since absolute bending speeds vary from cell to cell, equation (9) is best tested in practice by expressing measured bending speed as a fraction of the cell's normal speed of bending toward a single light source. This fraction may be termed the *relative bending speed.* Applying equation (9) to the single beam case with I_2 as zero, I_1 cancels out and the equation reduces to the statement that bending speed is constant:

$$v_2 - v_1 = c\frac{a-1}{a+1} \tag{10}$$

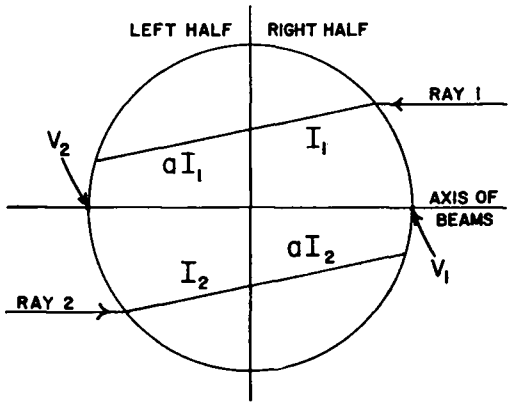

FIGURE 4. Diagram of the cell's circular cross-section irradiated by two beams of light opposed at an angle of 180°. One ray of each beam is represented. The resultant elongation speeds (normal to the plane of the paper) at the opposite poles are v_2 and v_1. Inscribed within the circle are the components which add to determine the respective growth speeds of the left and right halves of the cell. See equation (8 *a*) of the text.

The predicted relative bending speed for the two beam case is then obtained by dividing equation (9) by equation (10). This step gives

$$\text{Relative bending speed} = \frac{I_1 - I_2}{I_1 + I_2} \tag{11}$$

Thus relative bending speed should simply be proportional to the difference-to-sum ratio of the incident light intensities. Significantly, this result is independent of the numerical magnitude of the advantage given by the optical system. Both constants are absent from equation (11), and comparisons between cells that differ in basic growth speed, c, or which might differ in optics, a, are thereby explicitly validated.

Fig. 5 shows four average values of measured relative bending speed

plotted against the difference-to-sum light intensity ratio. The line drawn must pass through the origin and also through the point with coordinates 1, 1. The experimental values follow satisfactorily the linear relation predicted by equation (11).

Bending Speed with Two or More Beams of Light Varying in Azimuth

A simple vectorial formulation is possible here. Any incident beam may be considered to evoke bending directed along the beam's axis with a magnitude equal to the fraction of the total incident flux that is contained in that beam. For a single beam, the response is a unit vector independent of the incident flux. With two beams opposed at an angle of 180°, the two vectors are parallel, opposite in sign, and have magnitudes equal to the respective flux fractions;

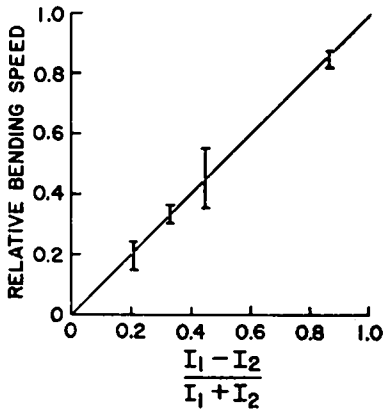

FIGURE 5. Relative bending speed (ordinate) plotted against the difference-to-sum ratio of the light intensities (abscissa) for the case of two beams of light opposed at an angle of 180°. A total of 19 cells, at four intensity ratios. The height of each vertical bar represents twice the standard deviation of the mean measured relative bending speed.

this case reduces to equation (11) above. In general, where the beams differ in intensity and in azimuth, the resultant direction and the relative bending speed follow directly from vector addition. Thus if angles of azimuth, θ, are measured from the resultant direction of bending as projected on the horizontal plane, with the cell as origin, the phototropic contribution of any beam is $f \cos \theta$, where f is the flux fraction. Summing the components,

$$\text{Relative bending speed} = f_1 \cos \theta_1 + f_2 \cos \theta_2 + \cdots f_n \cos \theta_n \qquad (12)$$

This formulation has been tested with two and three beams of light at selected angles of azimuth.

It was convenient, but not necessary, to use beams of equal intensity. A principal requirement was to initiate bending without appreciable change in the total flux incident upon the cell; this was done by the use of neutral filters and by light sources constituted of two small incandescent bulbs separately switched on or off. Intensities of the beams were matched at the position of the

cell by photometry, the illumination given there by one beam being about 1 ft-c. Bending was photographically recorded, usually at 1 minute intervals, by methods previously described (Castle, 1961, 1962). The time course of bending was plotted from angular measurements on the projected negatives. After bending is established, the slope of the plot is essentially linear for bend angles from 0° to at least 40° (Reichardt and Varjú, 1958); the plot was fitted by eye to the best straight line. Bending speed was normalized in terms of each cell's phototropic response to a single light source; hence every determination required comparison with one or more separate ones with a single beam. Measurements were made an hour apart to allow the cell to straighten. If the basic growth speed was found to have changed significantly over this interval, or if the bending plot was not linear, the experiment was useless.

There is delayed and reduced control of bending when the cell is irradiated from a wide angle: the transition from straight growth to steady bending is slower, and the direction of bending may deviate perceptibly from the theoretical resultant. Deviation is not random, and is considered to be due to the cell's consistent axial twist during growth; it reduces the apparent angle of bend. Dennison (1965) has analyzed this effect in detail in long term experiments. Aiming errors of the magnitude found by him were seldom apparent here.

CASE 1 Two horizontal beams of equal intensity separated by an angle of 60°. Since the bending cell bisects this angle, the beams strike the cell at angles of azimuth of $+30°$ and $-30°$. By equation (12), the expected relative bending speed is $\frac{1}{2} \cos 30° + \frac{1}{2} \cos 30° = 0.87$. Five cells gave a mean measured relative bending speed of 0.78 with a standard deviation of $\pm$ 0.13. The difference between predicted and mean measured speeds is not statistically significant.

CASE 2 Two horizontal beams of equal intensity separated by an angle of 90°, making the angles of azimuth of the beams $+45°$ and $-45°$. By equation (12), the theoretical bending speed is $\cos 45° = 0.71$. A sample of 9 cells gave a mean measured relative bending speed of 0.72 with a standard deviation of $\pm$ 0.06. Theory and experiment agree closely.

CASE 3 Three horizontal beams of equal intensity at azimuth angles of 0°, 80°, and 260°. The last two beams are separated by an angle of 180°; their phototropic effects, being equal and opposite, should cancel—irrespective of the pair's position in azimuth. By equation (12), the expected resultant bending speed should be $\frac{1}{3} \cos 0° = 0.33$, directed at the angle $\theta = 0°$ toward the third, unpaired light source. A sample of 6 cells gave a mean measured relative bending speed of 0.33 with a standard deviation of $\pm$ 0.02. The agreement is by chance precise.

CASE 4 A luminous strip, which may be considered an assemblage of

many point sources. Oehlkers (1926) showed that a large illuminated ground glass plate placed vertically near a sporangiophore caused phototropic curvature toward the plate; he cited this against the idea of lens action. Such diffuse, wide angle irradiation gives an illumination pattern within the cell profoundly changed from that shown in Fig. 1.

Oehlkers' experiment was repeated using a rectangular plate of dimensions 30 × 10 cm placed vertically, with its long axis horizontal, as near the sporangiophore as possible (5 cm, due to the dimensions of the moist chamber). The plate was illuminated evenly by a distant bright source. This case is actually intermediate between the limiting cases of an infinite plane sheet and an infinite horizontal row of lights; for an approximate prediction of bending speed, it will be considered as a row. Formulation in terms of the vector mechanism is analogous to calculation of electric field strength using Coulomb's law with evenly distributed charges and the whole field normalized.

The flux, dF, coming to the cell from any small element of the row is proportional to the element's horizontal extent times $\cos\theta$, which is $\sec^2\theta\, d\theta \times \cos\theta$, and inversely proportional to the square of the distance from the cell, which is $\sec^2\theta$. Each phototropic vector component, dP, is then $(dF/\int dF) \times \cos\theta$. Summation of dP gives[3]

$$P = \text{relative phototropic bending speed} = \int \frac{\cos^2\theta}{\int \cos\theta\, d\theta}\, d\theta \qquad (13)$$

Integrating and evaluating between the limits 0 and $\pi/2$ give $P = \pi/4 \simeq 0.78$ for the theoretical infinite row case. In the experiment, half the length of the row subtended the angle $\theta = 72°$; integrating from 0 to this lesser limit gives $P = 0.82$ for the finite row.

Oehlkers did not make rate determinations but noted that, after some hours, bending was almost equal to that induced by a single beam of light. The present experiments were troubled by aiming errors, but speeds determined for two stably bending cells were 0.81 and 0.88, near the theoretical figure $P = 0.82$ for the finite strip.

Lower theoretical values are found for circular areas than for rows of the same dimension. Comparable formulation gives $P = 0.72$ for a circular area of radius 9.8 cm having the area of the rectangle used. It should be noted that light in the horizontal plane traverses the cell in that plane, whereas rays incident from above or below are more complexly refracted (*cf.* Dennison, 1965); it is uncertain whether such highly oblique rays add phototropically in

[3] I am greatly indebted to M. Delbrück for pointing out a basic mathematical mistake when this paper was in manuscript, and for helping me to correct it. He also pointed out that, by Lambert's law for radiation from a surface, a cosine term is required in the formulation of dF as it is not for the case of discrete point sources.

the manner of horizontal rays. This problem has generally been avoided here, and since the cell is a cylinder and not a sphere or a point, it does not necessarily follow that an equivalent *vertical* row of lights would have the same phototropic effect as a horizontal one.

DISCUSSION

This paper concerns two asymmetries around the cell's central axis and the connection between them: asymmetry of the distribution of growth speed, and asymmetry of the flux incident upon or acting within the cell. The expected net *difference* in the rate of action of light across the cell in the case of a unilateral beam is first calculated; translation of this into expected bending speed requires a series of assumptions, the most arbitrary of which equates the light action ratio to the ratio of the *average* growth speeds of the two semicircles of wall. The predicted absolute bending speed is of the order of magnitude found experimentally. Such agreement cannot resoundingly confirm the complex argument, which is flexible and might contain compensating errors, but it is encouraging.

In multiple beam experiments, the interpretation of which does not depend upon any theory of the internal optical mechanism, the cell integrates the several received fluxes so that its relative bending speed is directly related to the light input. This is best shown by scaling the two asymmetries numerically. The asymmetry of growth is already scaled from zero to one by the relative bending speed itself. Asymmetry of irradiation may be comparably scaled: a single beam is given the maximum asymmetry of one, irrespective of its intensity; with more than one beam, the vector component of each in the prime direction is taken, multiplied by the flux fraction of that beam, and the resulting numbers added. The symmetry axis of the irradiation pattern is chosen as the prime direction. Summing thus these cosine terms gives an *asymmetry index* between zero and one for the distribution of the radiation impinging on the cell.

This index is identical in form with equation (12) above, derived for the relative bending speed. The identity results from parallel formulation, and specifically from normalization of the total flux in both cases. But the argument is not circular because the reason for normalization is different in the two cases. On the one hand, absolute flux is irrelevant for the cell's *bending*; on the other hand, the absolute value of flux is irrelevant for the *definition* of asymmetry, which is characterized by shape (hence a ratio) and not by size.

Therefore the theoretical relative bending speed has the same value as the asymmetry index, and the cell's growth matches the scaled asymmetry of irradiation to the extent that predicted and measured bending speeds agree. This agreement was found satisfactory. The cell's differential growth is therefore quantitatively responsive to the distribution of light incident upon it. It

would be remarkable were this not so, since many studies have shown that the "resultant law" holds for the angle of phototropic orientation of plant organs between light sources (*e.g.*, Dennison, 1958).

The first power of I, the light intensity, has been used in all the formulations in this paper. The simplest photochemistry supports this assumption, as does Blaauw's (1909) classic proof that time and intensity are interchangeable for threshold phototropic responses. Recently Dennison (1965) has considered possible models of the lens mechanism with I assigned an exponent greater than one. But in the present multiple beam experiments, the cell's bending speed is found proportional to the resolved fluxes, where each flux is given by the first power of the incident light intensity. If light acted within the cell in proportion, say, to I^2, this would require the seeming contradiction that external beams are resolved according to I^1 through the operation of internal mechanisms dependent on I^2. That the *differential* action of light in steady state phototropism is properly formulated in terms of I therefore seems clearly supported by the present experiments.

The specifically optical mechanisms in phototropism of the oat coleoptile are obscure, and their quantitative relation to growth especially so. Zimmerman and Briggs (1963) conclude from dosage-response experiments that while the light gradient across the tip determines the direction of bending it has no bearing on the magnitude of the response. Regrettably, such experiments depart maximally from steady state conditions and permit the primary differential action of light to be masked by secondary complications. In the phototropic inversion of *Phycomyces* evoked by abrupt changes in light intensity (Reichardt and Varjú, 1958; Castle, 1962), the underlying simplicity of the optical situation is similarly overridden. If bending in *Avena* could be studied under steady state conditions and with knowledge of the growth speed distribution, a relation between the conditions of irradiation and the magnitude of the response must emerge.

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