Phototropic Curvature in *Phycomyces*

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ABSTRACT The distribution of curvature and of bending speed along the cell's growing region are studied during steady state phototropic bending. At the start, elemental bending speed parallels the known axial distribution of growth rate. Hence regional phototropic sensitivity is initially determined by the local growth rate, and unilateral visible light acts proportionally at all levels of the growth zone. In the later course of bending, the bending speed distribution shifts downward instead of progressing upward in step with the cell's elongation. Furthermore, during phototropic inversion *reversed* bending begins high in the growth zone and progresses downward while normal bending continues below. These spatial and temporal changes in the distribution of differential growth are considered to be due to a fixed rate of supply of material used in growth that is transported from lower regions of the cell and asymmetrically distributed within the growth zone.

This paper examines the development of phototropic bending in the sporangiophore of *Phycomyces* exposed to unilateral illumination. Curvature of the cell's central axis is determined from enlarged serial photomicrographs and is studied as a function of position in the growing zone and also as a function of time.

Phototropic bending results fundamentally from growth changed in distribution about the cell's axis but unchanged in total amount (Castle, 1961 *b*). Given this fact and also a persisting effect of unilateral light, the cell's total bending rate can be constant in time, as found so by Dennison (1958) and by Reichardt and Varjú (1958). Such pleasingly lawful behavior derives from steady state conditions, and implies that both straight growth and light-induced asymmetric growth are regulated by the same underlying light-independent cellular mechanisms. In particular it is implied that the growth rate of any part of the cell is affected by the growth rates elsewhere, their sum not to exceed the total steady state growth capacity.

This regularity applies to the cell's *total* output of growth or of bending, these being integrals of elemental growth and of elemental bending over the length of the growing zone. Under steady state conditions the values of these integrals are fixed, but the spatial patterns of elemental growth and bending

may change while keeping the same integral values. Such changes will affect *where* the cell is growing or bending but not the total rate, and should be most apparent in the development of curvature where elemental bending speed is visibly integrated over time.

The central thought of this paper is that complexities in the phototropic behavior of *Phycomyces*, such as the inversion effect of Reichardt and Varjú (1958) and the responses to zonal stimulation studied by Cohen and Delbrück (1959), involve spatial and temporal changes in the distribution of growth within the larger orderly limitations outlined above. We suggest below that these changes in growth pattern result from growth speeded by light and yet limited by a supply of material coming from the lower regions of the cell.

MATERIAL AND METHODS

Individual mature sporangiophores of *Phycomyces* were grown and photographed at 1 or 2 minute intervals during bending as recently described (Castle, 1959, 1961 *b*). Vertically growing cells were adapted for 30 min. to two opposed horizontal beams of unfiltered white light of equal intensity. At time zero the left beam was cut off and the right beam doubled in intensity. Bending was thus initiated under the simple conditions of constant radiant flux (Castle, 1961 *b*), except when a special study was made of the inversion phenomenon.

All measurements were made on enlarged prints with a total magnification of 46 times. The primary measurements were *distance* (arc length), s, along the bright line representing the cell's central axis, and *slope angle*, ϕ, of points along this axis (Fig. 1). s measured upward from a marker attached below the growth zone, and therefore fixed relative to the ground, is designated as s_y; s measured downward from the base of the sporangium is designated s_x, and thus uses a coordinate axis moving away from the ground at the growth speed. Arc lengths were approximated by "walking" dividers along the axis and totalling the secant distances.

ϕ was measured at 1 cm intervals along the curved axis on the enlargement. This first differentiation can be carried out on the sharp white central line of the black cell with remarkable precision. Following a suggestion in Lipka (1918), we used a small vertical front-surfaced mirror to establish a line normal to the curve by sighting along it and repeatedly setting the mirror for the position of no perceptible discontinuity in the curve and its reflected image. Our mirror was attached to a triangle, one side of which was at right angles to the mirror in the horizontal plane; its direction permitted the tangent of the slope angle to be read directly from a fixed coordinate grid. ϕ was then taken from tables to the nearest tenth of a degree.

Large scale plots of ϕ against s were graphically differentiated to give κ, curvature, which is $d\phi/ds$. Plots of κ against s show quantitatively the distribution of curvature along the cell's central axis, κ being taken as positive when the axis is concave toward the stimulating light. The time derivative of curvature, termed elemental bending speed, b, was obtained by subtraction of paired κ values (at fixed s) from enlargements following each other in time.

We deal with varying properties or activities of the cell's essentially cylindrical envelope that are spatially distributed in two ways: *along* the cell's axis, and *around* the cell's axis. There are three such relevant properties, each of which is a differential coefficient: *growth rate, curvature,* and *elemental bending speed.*

Growth rate, r, is the instantaneous rate of cell elongation at any point. r integrated over the growth zone is the cell's total elongation rate or *growth speed, v.* In straight growth the distribution of r around the axis is constant, in bending its distribution is a sine curve with a maximum (r_2) on the cell's convex flank and a minimum (r_1) on the concave flank; only these extreme values need be considered here. The distribution of r along the axis in straight growth has been determined by the use of markers (Cohen and Delbrück, 1958; Castle, 1937, 1959). During bending we know that $r_2 > r_1$, but the differing distributions along the two opposite flanks of the cell for technical reasons cannot be directly determined. Inferences about these flank distributions from the evidence of bending largely occupy us below.

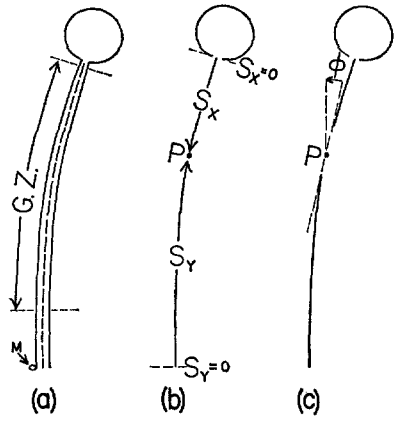

FIGURE 1. Diagram of a sporangiophore phototropically bent in the plane of the paper, in response to light coming horizontally from the right. (*a*) General view of the cell in profile. *G.Z.*, growth zone; *M*, marker. Continuous dashed line is central axis. (*b*) *P*, a point on the axis; s_y, s_x the point's axial distance from the marker and from the sporangium respectively. (*c*) ϕ, slope angle at point *P*.

Curvature, κ, serves to characterize locally the shape or profile of the cell as viewed perpendicular to the plane of bending; its relevant distribution is along the cell's central axis, and κ is in fact determined from measurements made on this axis.

Elemental bending speed, b, is the time derivative of curvature; it too is referred to the cell's central axis, and its relevant distribution is along that axis. b measures relative phototropic sensitivity, the distribution of which along the growth zone is therefore represented by the axial distribution of b.

The three quantities above are defined thus:

$$\text{growth rate, } r = dv/ds$$

$$\text{curvature, } \kappa = d\phi/ds$$

$$\text{elemental bending speed, } b = d\kappa/dt$$

where v is growth speed, s is distance along the axis, ϕ is the slope angle at points along the axis, and t is time. Curvature and bending speed are in practice derived from finite measurements, but for simplicity we use the differential rather than the delta notation.

RESULTS

Fig. 2 gives the record of phototropic bending for a cell whose behavior is analyzed below. Following bilateral adaptation, the horizontal beam of light on the left was cut off and that on the right doubled at time zero; bending begins after a delay of about 6 min. The primary measurements of position and slope angle are given in Fig. 3; Fig. 4 shows the distribution of curvature along the axis at successive 2 min. intervals, and Fig. 5 the distribution of bending speed during these intervals.

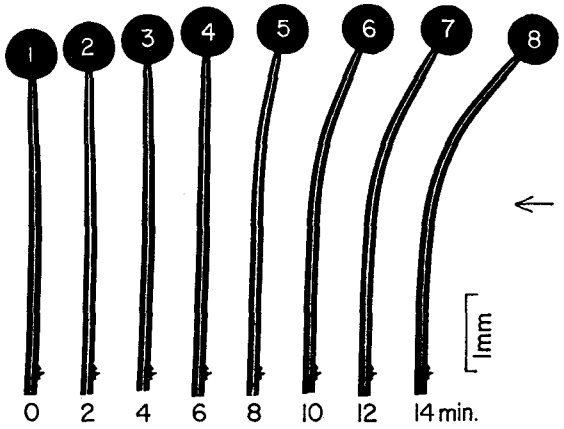

FIGURE 2. Photographic record of phototropic bending at 2 min. intervals. Unilateral illumination from the right begins at time zero. The growth speed of this same cell during bending has been previously reported (Castle, 1961 *b*). Fig. 2 is reprinted from *J. Gen. Physiol.*, 1961, **45**, 42.

Increasing curvature with time is seen in the family of curves in Fig. 4. Several facts are apparent from this figure: (*a*) curvature rapidly spreads over a distance of 2.5 mm or more along the cell, which is the usual extent of the growing zone;[1] (*b*) the distribution of initial curvature is skew, and falls slowly toward the bottom of the growth zone and more steeply toward the top of the cell; (*c*) as curvature develops with time, its maximum keeps about the same s_y value and hence the same position relative to the ground; this confirms the observations of Cohen and Delbrück (1959) on the location of the "bend center"[2].

The distribution of bending speed at the start of bending is of particular interest. This is shown in the bottom curve of Fig. 5, and also in curve *A* of Fig. 6 where the abscissa is s_x and position in the growth zone is better represented. Bending clearly begins all along the cell's normal growth zone and has

[1] At least in cells with a large sporangium, there is clear evidence of elastic bending below the growth zone as the cell inclines from the vertical. This effect is small, it is not a growth phenomenon, and we ignore it here.

[2] Their bend center is essentially that value of s where ϕ is half the cell's total bend angle. This is not precisely the maximum of curvature unless the cell is symmetrically curved above and below this point, which it is characteristically not.

its maximum at a distance between 0.5 and 1.0 mm below the sporangium. Initial bending speed in a different, faster growing cell is shown in curve *B* of Fig. 6. These distributions at the start of bending cannot be distinguished in (*a*) extent along the cell, (*b*) position of the maximum, and (*c*) skew shape

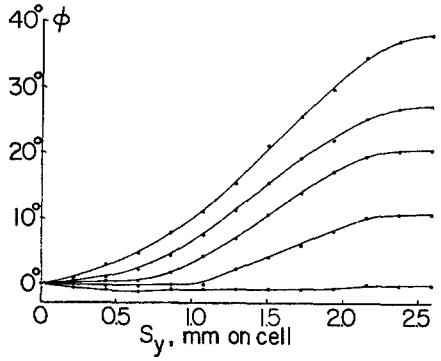

FIGURE 3. Slope angle, ϕ, as a function of position during bending of the cell in Fig. 2. Reading from the bottom, the five curves represent times 6, 8, 10, 12, and 14 min. in Fig. 2.

from the average growth rate distribution in straight growth (Castle, 1959). We conclude that phototropic bending begins at a speed determined by the cell's growth rate at each level in the growth zone.

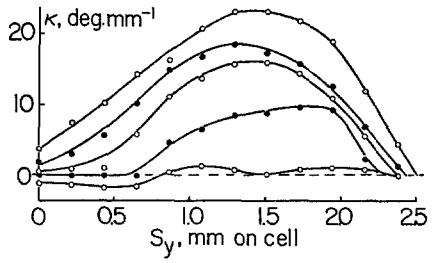

FIGURE 4. Curvature, κ, as a function of position during bending of the cell in Fig. 2. Horizontal dashed line is zero curvature; the bottom curve shows characteristic small fluctuations in curvature along the cell's axis. Reading from the bottom, the five curves represent times 6, 8, 10, 12, and 14 min. in Fig. 2.

The further course of bending is necessarily more complex, and is affected by the cell's own elongation. For example, during straight growth the growth zone propagates itself upward, relative to the ground, at the growth speed; its position and extent relative to the upward-moving sporangium are thereby kept constant. In particular the growth rate distribution shifts upward with time, relative to the ground, at the growth speed. If in phototropism the bending speed distribution did likewise, it also should shift upward and the de-

veloping curvature, which is bending speed integrated over time, should show an upward trend (diminishing with time) in the position of its maximum. Fig. 7 pictures these theoretical expectations on the basis outlined.

But in fact, as seen in Fig. 4 and for a different cell in Fig. 10, developing curvature keeps its maximum at a nearly fixed position relative to the ground.

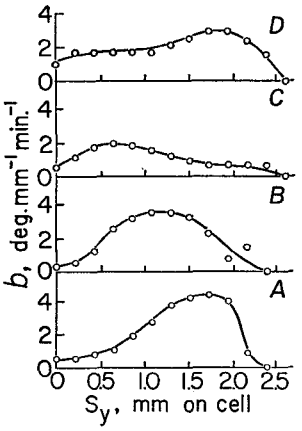

FIGURE 5. Elemental bending speed, b, as a function of position during bending of the cell in Fig. 2. *A*, bending speed distribution for the initial 2 min. interval in bending (6 to 8 min. in Fig. 2); *B*, *C*, *D*, distributions for successive 2 min. intervals between following curves in Fig. 2.

This means that the bending speed distribution must shift *downward*, relative to the ground, after the start of bending. Such a shift is indeed shown in the curves of Fig. 5. We think that this effect reflects changes in the *shapes* of the growth rate distributions along the near and far flanks of the cell, and hence

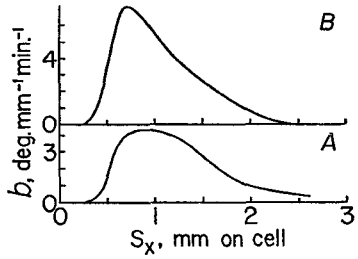

FIGURE 6. Initial bending speed distributions for two different cells, position being plotted relative to the sporangium. *A* is the transposed bottom curve from Fig. 5; *B* is the smoothed distribution for another, faster bending cell.

in the difference $r_2 - r_1$ that determines elemental bending speed. This interpretation cannot be validated directly, but it seems strongly supported by the fact that the *total* rate of bending, integrated over the growth zone, remains constant (Reichardt and Varjú, 1958) just as axial growth speed during bending does (Castle, 1961 *b*). These facts indicate a change in the *distribution* of growth since the *amount* of growth in unit time remains constant.

Striking evidence of regional change in growth rate is seen in phototropic inversion, where a temporary phase of *reversed* bending is caused by a step-up in intensity of the unilateral stimulating light after normal phototropic bend-

ing has begun. Essentially this illumination program superimposes the effects of a light-growth response on an existing background of asymmetric growth; it departs from steady state conditions, and the response is therefore inherently complex. One example will be given here.

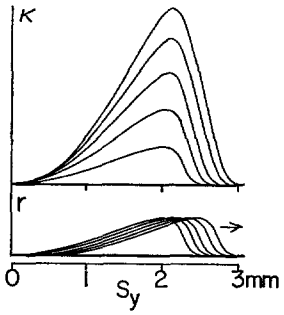

FIGURE 7. Theoretical development of curvature pictured at 2 min. intervals based on a constant, steadily upward moving growth rate distribution; ordinates arbitrary. *Below*, five positions of the assumed r function as it is propagated up the axis (arrow) at a speed of 0.065 mm $min.^{-1}$ *Above*, curvature obtained by progressive integration of the curve below over time and for the five positions shown. Bending speed is assumed proportional to r, as in equation (2) of the text. Thus the first (lowest) κ plot is simply the r distribution, the second κ plot is obtained by adding ordinates of the first *two* r functions, and so on. The point of maximum curvature shifts slowly to the right (up the cell's axis), but not in proportion to the assigned steady progress of the r distribution.

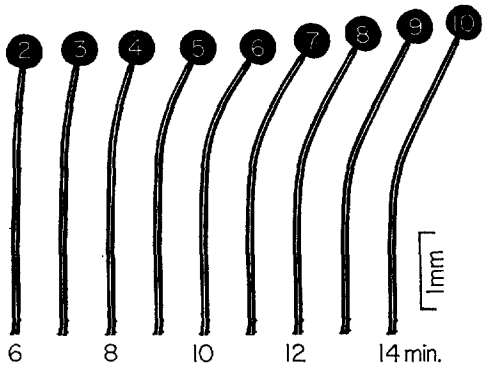

FIGURE 8. Photographic record of phototropic bending at 1 min. intervals, with inversion appearing toward the end of the series. At time zero (before record begins) unilateral illumination starts from the right; its relative intensity = 1. At time 6 min., intensity of light on right increased to 10 and maintained.

Fig. 8 is the record of a cell photographed at 1 min. intervals and showing inversion in the last few pictures at the right end of the series. Figs. 9 and 10 show slope angle and curvature during the initial period of normal phototropic bending, and are comparable to Figs. 3 and 4 above. This cell is of small diameter and bends much faster than the cell previously discussed but its curvature develops comparably; maximum curvature again first appears at a position between 0.5 and 1.0 mm below the sporangium.

The early part of the inversion phase proper is represented in Figs. 11 and 12. It will be seen that *reversed* bending first appears high in the growth zone, while simultaneously normal positive bending continues below: this subtracts curvature above and adds it below, so that the maximum of curvature shifts very rapidly toward the base of the growing zone (Fig. 12). For several minutes, therefore, negative bending in one part of the cell coexists with posi-

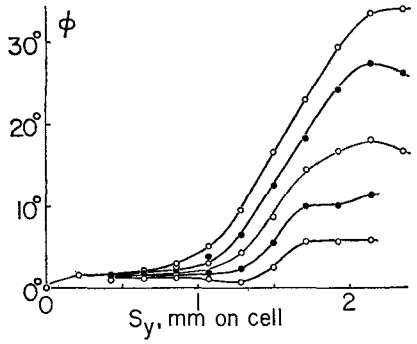

FIGURE 9. Slope angle as a function of position during the period of normal phototropic bending of the cell in Fig. 8. Reading from the bottom, the five curves represent times 6, 7, 8, 9, and 10 min. in Fig. 8.

tive bending in another part of the cell, although the optical conditions, except for the raised intensity of the stimulating light, are precisely the same as during normal phototropism. It is clear that "adaptation" as ordinarily understood cannot account for this fact.

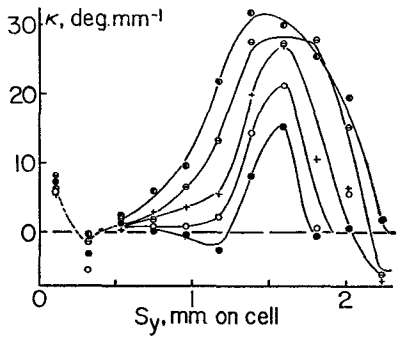

FIGURE 10. Curvature as a function of position during the period of normal phototropic bending of the cell in Fig. 8. The five curves are those of Fig. 9 differentiated. The maximum curvature reached here is about 30° per mm, a limit also found for several other cells and not connected with the subsequent inversion in this case. If continued in a phototropic helix in the manner of Dennison (1958), this curvature would give a coil diameter of just under 4 mm.

DISCUSSION

At any level in the growth zone elemental bending speed is for geometrical reasons proportional to the difference in growth rates across the cell:

$$b = c(r_2 - r_1) \tag{1}$$

where c is a constant. But the *magnitudes* of r_2 and r_1 cannot be found from the *difference* between them. Thus from the determined axial distribution of b we

regrettably cannot deduce the distributions of r_2 and r_1 along the cell's convex and concave flanks. However, we saw above that the axial distribution of b at the start of bending parallels, by available criteria, the axial growth rate distribution in straight growth (Delbrück's "stretch function"). It follows

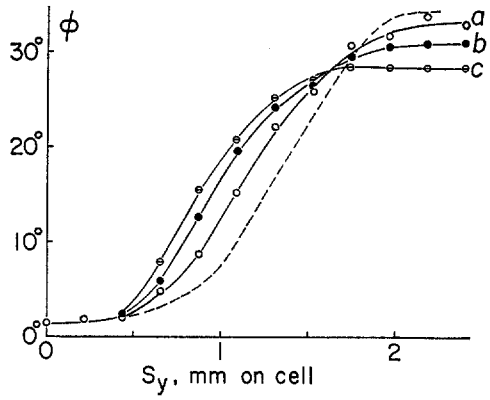

FIGURE 11. Slope angle during the early phase of reversed bending (inversion) of the cell in Fig. 8. Dashed line is top curve from Fig. 9, representing the maximum total bend angle just before reversed bending begins (at 10 min. in Fig. 8). Then follow in time curves *a*, *b*, and *c*, corresponding to times 11, 12, and 13 min. in Fig. 8. Data on the cell at 14 min. are not plotted.

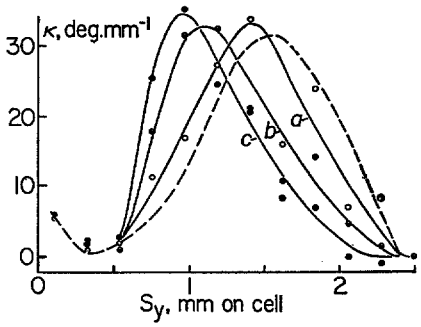

FIGURE 12. Distribution of curvature during reversed bending (inversion) of the cell in Fig. 8. Dashed line is curvature just before reversed bending begins (at 10 min. in Fig. 8). Then follow in time curves *a*, *b*, and *c*, corresponding to times 11, 12, and 13 min. in Fig. 8.

that the initial effect of unilateral light must be proportional, at different levels in the growth zone, to the rate there affected; that is

$$(r_2 - r_1) \propto (r_2 + r_1)/2 \propto r$$

Substituting r for $r_2 - r_1$, equation (1) becomes

$$b = c' r \tag{2}$$

where c' is a constant containing a factor for the effect of unilateral light, and r is approximately known from separate measurements on straight growth.

Equation (2) formally states our inference that, at the start of bending, elemental bending speed parallels, and is founded upon, the axial growth rate distribution. b in effect also represents relative phototropic sensitivity, which therefore at the start of bending is similarly based on the axial growth rate distribution. The proportional action of light everywhere in the growing zone further shows that optical conditions (for visible light) cannot vary significantly along it.

In a series of papers Delbrück and collaborators (Delbrück and Reichardt, 1956; Cohen and Delbrück, 1958, 1959) have concluded that the upper part of the growth zone though growing maximally participates neither in the light-growth response nor in phototropic bending. In a previous study of the light-growth response we could not confirm this view, finding, on the contrary, proportional participation of the whole growing zone in the maximum of the response (Castle, 1959); in the present study of phototropism we similarly find no evidence for permanently separate cellular zones of growth and of sensitivity to light, though we do find, as discussed below, a state of reduced bending at the top of the growth zone as bending progresses. Delbrück investigated the light-growth response by a method using frequent, repetitive stimulation; a detailed reinterpretation of these relatively complex measurements is not possible, but we doubt that they necessitate the conclusions drawn from them.

The later course of bending is potentially affected by many things: (*a*) the cell's own elongation, (*b*) consistently faster growth on one flank of the cell than on the other, (*c*) the spiral component of growth, (*d*) changed incidence of light on the cell and changed internal light pathways, (*e*) action of a gravitational bending moment as the cell inclines from the vertical, (*f*) geotropic response. Yet in spite of these possible complications, constancy of integrated phototropic bending speed with time and constancy of integrated axial growth rate during bending show the basic regularity of phototropic behavior.

We believe that points (*a*) and (*b*) above are clearly important for the course of bending, and that points (*d*), (*e*), and (*f*) may be neglected until their relevance is shown. Point (*c*), the role of spiral growth, remains uncertain. Delbrück and Reichardt (1956) have argued that bending must be confined to the bottom of the growth zone, else the spiral component of growth would swing the bending cell out of the normal plane of bending. But bending is not so confined, hence we conclude that the cell has dynamic, not yet adequately studied ways to reconcile axial twist with approximate bending in a plane.

Fig. 7 shows how in theory the cell's elongation would affect developing curvature if the distribution of bending speed, b, stayed constant and if this distribution moved upward in step with elongation. The curves in Fig. 5 show that in fact the distribution of b changes in shape, shifting downward after bending has started. Thus, for values of s_y high in the growth zone b diminishes

with time, indicating a local decrease in $r_2 - r_1$; this may happen either because r_2 decreases or because r_1 increases or both. In any case, after the start of bending the upper regions of the growth zone come to bend more slowly or not at all, and thus approach the condition of growth without phototropic response inferred by Cohen and Delbrück (1959). The difference is that we show this region *has earlier been* bending, and *can again be made to bend*, as in the inversion response. Thus the state when b is locally zero and r_2 equals r_1 is a temporary balance between unilateral light acting to increase r_2 relative to r_1 and some other process opposing it; the latter we take to be the supply of material used in growth and in part rate-determining for it, as described below.

Light affects the rate and disposition of growth in *Phycomyces* but clearly only within limits otherwise determined. We suggest (*a*) that the cell's total steady state growth rate is set by a fixed rate of transport into the growth zone from below of material, M, used in growth; this limitation can be briefly relieved by an increase in light intensity, giving a light-growth response, but then becomes reestablished; (*b*) that the concentration of M decreases from the bottom of the growth zone upward because of use, and enters into the determination of local growth rate, becoming decisive for it at high levels in the growth zone; (*c*) that the axial growth rate distribution is itself a steady state as the cell literally grows away from its supply of M; the shape of this distribution may be expected to alter and its extent to shorten following adjustment to a step-up in light intensity; (*d*) that the reciprocal speeding and slowing of growth across the cell induced by unilateral light reflect unequal use of M available at that level, and imply a net lateral transport of it during phototropism.

Some aspects of this interpretation have been discussed earlier (Castle, 1961 *a*, 1961 *b*). We do not know what M is, but assume it to be a metabolite entering stoichiometrically into growth. We do not know the mechanism of transport of M from lower parts of the cell into the growth zone, though it might well be by the cell's conspicuous cytoplasmic streaming. The linear speed of any longitudinal transport mechanism must surpass or at least equal the cell's linear growth speed in order to sustain steady state growth; it is therefore interesting that Cohen and Delbrück (1959) report upward streaming at a speed more than twice the growth speed. Similarly we infer the existence but do not know the mechanism of the *lateral* transport of M in the growth zone that must supply faster than average growth on the cell's convex side during bending. With symmetrical illumination we assume longitudinal transport to be essentially symmetrical around the axis; it is possible that streaming rendered asymmetric by unilateral light is an intermediate mechanism in phototropism, but we have no evidence on this matter.

Full understanding of the light responses of *Phycomyces*, all of which are, significantly, growth *rate* changes, depends on detailed knowledge of how r is

determined. Delbrück and Reichardt have been specially concerned with the role of light intensity and accompanying adaptation phenomena; we for our part emphasize the homeostatic control exercised by supply and distribution mechanisms. All these factors operate by converging on r where their joint actions are not yet understood.

We seek here limited understanding of changes in the spatial distribution of growth. The distribution of M in the growth zone is easily deduced from our assumptions. Suppose that m units of M constantly enter the growth zone from below in unit time; simultaneously m units are expended throughout this zone in steady state growth. Then at some level s_y in the growth zone the steady state amount of M present but not yet used will be

$$[M]_{s_y} = m - a \int_{s_y=0}^{s_y} r \, ds_y \tag{3}$$

where a is a constant. Thus $[M]$ decreases upward over the growth zone along a sigmoid curve that is the integral of growth rate, becoming zero at the top; this may be called the *distribution of available M*. It is $[M]$ that we consider to enter into the determination of r.

But light also undeniably acts to increase r, hence in accordance with equation (3) increase in light intensity will reduce $[M]$. Thus the shape of the growth rate distribution will change (specifically, the growth zone will shorten), even though the steady state growth output does not change. Regionally this effect will be most pronounced where available M is least, at the top of the growth zone; at the bottom, available M is present in greatest excess. Thus through its primary action on growth rate, light can in an integrated system affect *where* growth occurs, that is, its distribution.

Phototropic bending begins with a differential effect on the growth rates across the cell that is proportional to the average steady state rate at that level. We assume that faster growth on the convex side initially draws on the reserve of available M there, evidence for this being the essentially simultaneous start of bending all along the growth zone. But now faster than average growth of the convex flank must be sustained by extra M from across the cell. Somewhere along the growth zone lateral transport of M must take place, though we see no way of anticipating its axial distribution.

We cannot quantitatively account for the observed downward shift of the bending speed distribution after the start of bending. As noted above, this effect is marked at high levels in the growth zone where its basis is a reduction in the difference $r_2 - r_1$ across the cell. This is the part of the growth zone where M is in shortest supply and below which lateral transport of M has certainly been occurring. A complex steady state of growth and of bending exists in which both light intensity and M are asymmetrically distributed

around the cell's axis. Across the cell *more* light and *less M* can balance *less* light and *more M* if, as we think, both act to determine r.

We remark again that since the integrals of r_2 and of r_1, that is the growth speeds of the cell's far and near flanks, remain constant (Castle, 1961 *b*), the basic problem must be one of *changed axial distributions* of r_2 and of r_1. Possibly the lateral transport of M leaves the axial distribution of $r_2 - r_1$ for a time unstably determined; thus the top curve in Fig. 5 shows a reversal of the erstwhile downward shift of bending speed, and small transient *negative* curva-

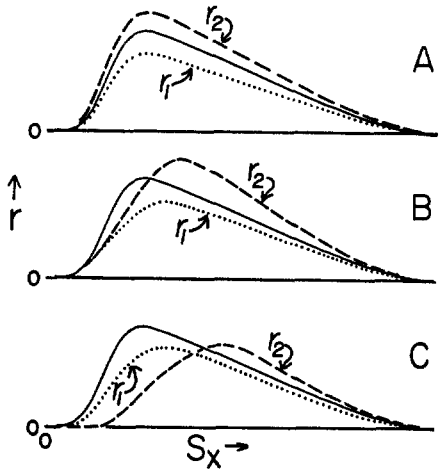

FIGURE 13. Growth rate distributions presumed to underlie: *A*, initial bending; *B*, later bending; and *C*, inversion. The *solid* curve in each figure represents the assumed steady state growth rate distribution in straight growth, r. The *dashed* curve in each represents the growth rate distribution along the flank of the cell away from the light source, that is, r_2. The *dotted* curve in each represents the growth rate distribution along the flank of the cell toward the light source, that is, r_1. In *A*, elemental bending speed (determined by $r_2 - r_1$) parallels the straight growth distribution. In *B*, the form of the bending speed distribution is shifted to the right (down the cell). Both *A* and *B* are steady state conditions and the curves should be drawn so that in each $\int r_1\,ds + \int r_2\,ds = 2\int r\,ds$. In *C*, reversed bending (inversion) occurs when $r_1 > r_2$ (at the top of the growth zone), normal positive bending when $r_2 > r_1$ (toward the bottom of the growth zone).

tures are seen high in the growth zone in some of the intermediate curves in Fig. 10. Steady state phototropic bending *par excellence* occurs in the continuous helix formed in the rotation experiments of Cohen and Delbrück and of Dennison; knowledge of the bending speed distribution in this situation would be of great interest.

Our interpretation is supported most strongly by the inversion phenomenon. Here a sudden rise in light intensity given an already bending cell first of all produces faster axial growth without detectable change in total bending speed, then reversed bending sets in high in the growth zone and passes down-

ward; meanwhile normal positive bending continues below. This means that at the top of the cell r_1 exceeds r_2, while at the same time r_2 exceeds r_1 toward the bottom of the growth zone. The abrupt fall of r_2 near the top occurs where two conditions uniquely apply: (*a*) fastest growth has definitely taken place there during antecedent bending; (*b*) inferentially the reserve of available M is lowest there. Thus speeded growth following the rise in light intensity first exhausts M on the cell's convex side high in the growth zone, r_2 falls locally there as a consequence, r_1 comes to exceed r_2 because M has been spared on the slower growing concave flank, and the observed reversed bending follows.

More time is taken for exhaustion of M at lower levels because, as seen above, progressively more M is present toward the bottom of the growth zone. Hence the wave of reversed bending passes downward tracing by its course the increasing availability of M. Only some rate-determining property of the cell with such a polar distribution can account for these simultaneous regional differences in response. That the plane in which reversed bending takes place bears no relation to the drection from which the high intensity stimulating light comes (Castle, 1961 *a*), certainly shows that previous growth has left a spatially oriented record in the cell. We think, therefore, that the idea of axial motion of the phototropic response which Cohen and Delbrück (1959) found it necessary to introduce can be understood in terms of shifting distributions of M and without recourse to the "inner wall" hypothesis of these authors.

Fig. 13 diagrammatically summarizes the growth rate distributions we imagine to underlie (*a*) initial bending, (*b*) later bending, and (*c*) inversion.

Received for publication, September 13, 1961.

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