

## THE TOPOGRAPHY OF TIP GROWTH IN A PLANT CELL

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### ABSTRACT

Tips of young *Phycomyces* sporangiophores were dusted with starch grains, and growth photographically recorded. Rates of longitudinal displacement from the cell tip of individual markers were determined, also corresponding rates of change of cell diameter. From these the magnitude and spatial distribution of "relative elemental growth rates" along both longitudinal and circumferential axes of the cell were obtained.

Growth rates in these two directions are functions of distance from the cell apex, and have different spatial distributions. In particular, rates of growth in cell circumference are complexly patterned. Relative elemental growth rates in length and in girth are approximately equal and maximal at the cell's apex, with a value of 2.4 mm. mm.<sup>-1</sup> hr.<sup>-1</sup>. The characteristic shape of the tip is maintained constant in the face of its changing substance and position. This shape reflects a steady state of the cell's constituent growth patterns.

At every point the growing membrane simultaneously expands in the two dimensions of its surface. The degree of polarization or directional preference of growth is measured by the ratio of longitudinal to circumferential relative elemental growth rate at any point. The ratio is not constant, but changes with position along the tip. This fact does not support the idea that membrane growth is based upon a quantal "growth event." Possible causal factors in oriented membrane growth are discussed.

Many plant cells such as pollen tubes, root hairs, and fungus hyphae grow in area only at their distal tips, the rest of the cell envelope being fixed in area and configuration. The tip advances by the addition of new material, and at an equal rate older wall material is displaced from the tip and subtracted from the growing region. A single cell may thus maintain and actively propagate a terminal area of continuously growing membrane much as do multicellular organs like roots. The term "tip growth" is used here to describe this one mode of plant cell enlargement and implies nothing about the submicroscopic mechanisms of membrane growth. What establishes within a single cell this steady state of growth and maintains its characteristic spatial distribution is unknown.

The conspicuous aspect of tip growth is cell elongation. But since the tip of cells growing in this manner is always rounded or pointed, lengthening of the

cell is in all cases accompanied by increase in girth. In other words, the membrane in the growing zone enlarges in circumference as well as in the direction of the cell's long axis. Moreover while a growing tip moves continuously forward (relative to the substrate) as a result of its own growth processes, its characteristic shape or profile remains very much the same. This means that both longitudinal and circumferential aspects of membrane growth are patterned in some stable, continuing, and essentially balanced fashion within the area of the growing tip.

The present studies were primarily made to learn in detail the distribution of areal growth processes taking place in a growing tip, using the immature sporangiophores of *Phycomyces*. The large size of this multinucleate cell, its aerial habit, and the fact that the tapered growing tip may be as much as 2 mm. long are favorable conditions. The findings bear on the presently obscure mechanics of membrane growth, and on the unsolved problem why so many plant cells assume and perpetuate a generally cylindrical form.

#### Methods

The growing tip of a sturdy young *Phycomyces* sporangiophore in the first stage of its development is commonly 1 to 2 mm. long, tapering from a smoothly rounded apex to reach a maximum diameter of 0.1 to 0.2 mm. at the base of the growing zone. Below this point there is no growth in area, the cell keeps an approximately cylindrical form with the diameter already attained, and the wall becomes visibly dotted with droplets of exudate.

The method in these studies was simply to put numerous small markers on the growing region and to follow the positions of the markers as time passed, recording their positions by serial low power photomicrographs. On the photographic negatives, the distances of identified markers from the cell tip could be measured and displacements per unit time determined; likewise, changes in cell diameter at the locus of a particular marker were measurable.

Cultures of *Phycomyces blakesleeanus* (+ strain) in small glass vessels on 1½ per cent potato agar were placed in a closed glass chamber saturated with water vapor and kept close to 26°C. in temperature. Vertically oriented growth of the juvenile sporangiophores was secured by dim white overhead light diffused into the chamber by its ground glass cover. The terminal few millimeters of a selected cell were photographed from the side, in profile, with a Leitz makam photomicrographic camera in a horizontal microscope. The objective was a microtessar lens of 32 mm. focal length, giving an enlargement of 27.3 times on the film. During the exposure the cell was briefly illuminated from behind by strong red light from a projection lamp, a Corning signal red filter, and a water filter. Eastman process panchromatic film was used for maximum contrast and sharpness of the cell's profile. Consecutive pictures were easily obtained of a particular cell at regular intervals of 10 minutes or longer (Fig. 1).

Starch grains (Baker's soluble powdered starch) dusted or gently blown onto the

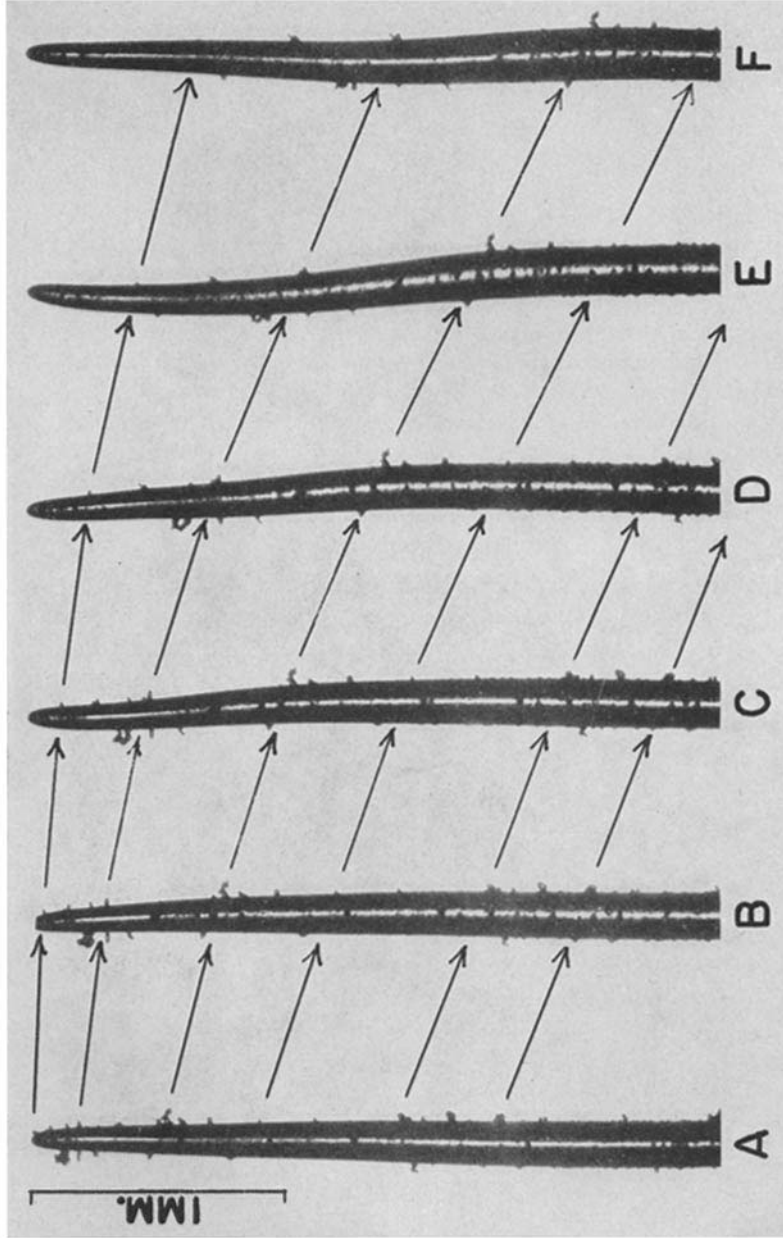


FIG. 1. *A* to *F* are six successive pictures of a growing tip, photographed at 15 minute intervals. The figure is composite, the tips having been adjusted to touch a single horizontal line. Growth in length (upward) is thus eliminated, and the starch grain markers appear to move downward away from the tip's apex. In *A*, six individual markers on the *right* edge of the cell are in line with the tails of the arrows. The heads of the arrows point to the positions of these same markers on the *right* edge of the tip in succeeding pictures. Slight curving motions of the tip are discernible ("nutations").

cell adhered and photographed well, and unless present in great excess did not interfere with growth. A cell ready for use was removed from its moist chamber, quickly dusted under red light, replaced in the chamber, and the first photograph taken. The starch grains that chanced to fall on the growing tip and were visible as protuberances on the otherwise smooth cell profile were the markers used in this work. Individual particles, or small individual groups of adhering grains, were usually clearly traceable from picture to picture. Since the marginal markers do not pass into eclipse it is clearly shown that this stage of the sporangiophore does not have spiral growth (*cf.* Castle, 1953).

Relevant strips of the photographic negatives were mounted between glass slides. Distances of particles from the tip apex were measured on the film with a vernier-equipped mechanical stage on a low powered compound microscope. Measurements of cell diameter on the film were made with an ocular micrometer scale. Since cell diameter, length of growth zone, and rate of growth vary notably from cell to cell, no statistical treatment has been made. The analysis given below is based on information obtained principally from the individual cell shown in Fig. 1; other cells studied confirm the growth pattern found for this one.

#### RESULTS

In the case of tip growth it seems probable from the outset that regions near the extreme tip make a larger contribution to the cell's total rate of elongation than do regions more remote from the tip; indeed at and below the end of the growing zone the contribution is zero. To find the magnitude and distribution of such local growth rates within the cell's growing area is our present concern.

The most appropriate frame of spatial reference for tip growth takes the tip apex as the origin of coordinates. By this means the growing tip is thought of as standing still in space, and all marked points on the tip appear to recede from this origin as time passes. In Fig. 1 are six consecutive pictures of a cell marked with starch grains. The photographs were taken at 15 minute intervals, and during each interval the cell actually elongated (upward) about 0.35 mm. But in this composite figure the cell tips have all been adjusted to touch a single horizontal line, and it will be seen that the *apparent* movement during growth is a downward displacement of all the markers. It will further be noted that markers near the apex move away from the apex slowly, while those farther from the apex move away more rapidly. The increased rate of displacement at greater distances shows that progressively more and more of the cell's total elongation is occurring in the lengthening region between the apex and the marker. When any marker reaches the end of the growth zone, it has attained a constant limiting rate that is numerically equal to the whole cell's rate of elongation.

The chief information derived from the serial photographic records consists of (1) the rate of displacement of markers from the cell apex as a function of their distance from the apex, and (2) the rate of increase in cell diameter as a

function of distance from the apex. From these the spatial distribution and magnitude of local growth rates, both longitudinal and circumferential, may be obtained.

*Longitudinal Growth.*—The cell shown in Fig. 1 had fifteen individually identified markers on its distal 2 mm. Let  $x$  be the distance of any marker, measured along the cell's long axis, from the cell apex, and  $t$  the time between successive photographs. Then  $\Delta x/\Delta t$ , the displacement occurring in 15 minutes, is obtained by subtraction of measurements on two successive pictures. In Fig. 2 rates of displacement obtained from the first pair of photographs are plotted against positions on the tip; each point relates to a separate marker. The curve, fitted by eye, rises from a presumptive displacement rate of zero at

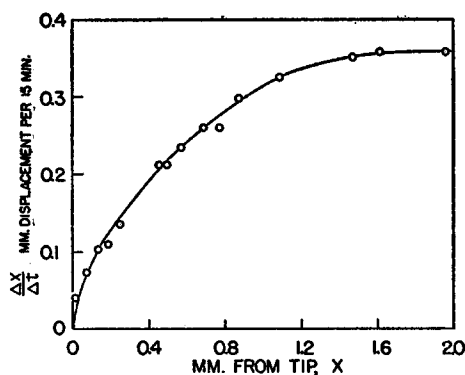


FIG. 2. Rate of displacement of markers plotted against distance from the cell tip.

the extremity of the cell and reaches a limiting value at the end of the growth zone. As mentioned above, this limiting rate is equal to the whole cell's rate of elongation. The total length of the zone contributing to the cell's growth is the value of  $x$  when the constant limiting value of  $\Delta x/\Delta t$  is reached, about 1.8 mm. in this case. That the total growth of the cell is by no means equally contributed to by equal lengths of the growing zone is shown by the fact that half the maximum rate of displacement of a marker is attained when it is only about 0.4 mm. from the apex, or roughly one-fifth the length of the growth zone; this distal one-fifth of the tip region contributes as much to the elongation of the cell as the whole proximal four-fifths.

The cell in Fig. 1 was elongating at a nearly steady rate of 1.4 mm. per hour, but an hour's total growth consisted of the sum of local increments added along the whole length of the growing zone; moreover the local increment clearly varies with the position in the growth zone, being large near the tip and smaller near the base of the cell's growing region. How shall we best express and com-

pare quantitatively the differing rates of membrane growth at different points on the cell?

Several pertinent analyses of the distribution of growth rates in root tips have recently been made. Although a root tip is a complex of many cells variously engaged in division and in extension, the methods and problems of these studies are similar to ours. Erickson and Sax (1956) have fully discussed the choice of terms and expressions for the comparison of growth rates, and have introduced the term "relative elemental growth rate." Erickson's fundamental analyses have been indispensable in the derivations to follow; the full mathematical details available in his papers will not be repeated here (*cf.* Erickson and Goddard, 1951; Erickson and Sax, 1956).

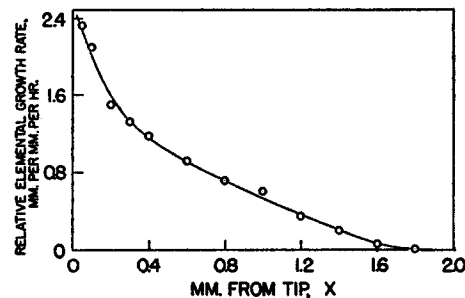


FIG. 3. Relative elemental longitudinal growth rate as a function of distance from the cell tip.

Briefly, a relative elemental growth rate is the second derivative, with respect to position, of the time-displacement curve of a marker moving away from the root tip's apex:  $d(dx/dt)/dx$ , in which  $x$  is distance and  $t$  time as above. It has the dimensions unit length per unit length per unit time; multiplied by 100 it represents the percentage increase per unit time of an infinitely small length or section of the growing object.

Goodwin and Avers (1956) have determined relative elemental growth rates for *Phleum* roots, and have clearly discussed methods for their experimental approximation. Measurements of growth are commonly made at finite intervals and the growth increments are, as in the present studies on *Phycomyces*, themselves finite. As a measure of relative elemental growth rate the expression  $d(\Delta x/\Delta t)/dx$  will therefore be used here to approximate the one given above in differential notation. For longitudinal growth its values are obtained by graphical differentiation of a rate of displacement curve ( $\Delta x/\Delta t$  plotted against  $x$ ). Relative elemental growth rates may thus be determined by comparatively simple means for elongating systems known to maintain a substantially constant pattern of growth.

Fig. 2 is a rate of displacement curve for markers plotted as a function of

distance from the cell tip. The slope of a tangent to this curve at any point yields a value for  $d(\Delta x/\Delta t)/dx$ , the relative elemental growth rate at that distance from the tip. Figures so obtained are plotted in Fig. 3, the ordinate being relative elemental growth rate expressed as millimeters per millimeter per hour. The curve depicts the detailed distribution of momentary longitudinal growth rates along the growing tip.

Longitudinal growth of this cell is distributed highly asymmetrically. The rate is greatest at the extremity of the tip, if a slight extrapolation to a value of  $x = 0$  is allowed. Certainly there is no evidence of a maximum rate displaced some distance from the tip, as is uniformly the case in multicellular roots. The growth rate falls smoothly as distance from the apex increases, reaching zero at a distance of about 1.8 mm.; this is the span of the growing zone of this cell. The half-maximum rate is reached at about 0.4 mm. from the cell tip, as was seen earlier.

*Growth in Girth.*—From measurements on the same photographs, the rate of change of cell diameter with increasing distance from the tip can be found. This is plotted in Fig. 4,  $\Delta D/\Delta t$  being the increment in cell diameter in 15 minutes, and  $x$  the distance from the tip as before. The relation is unexpectedly complex. At the extremity of the tip  $\Delta D/\Delta t$  is high and only determinable by extrapolation. At the locus of the first marker (initially only 0.018 mm. from the cell tip) the rate is falling steeply, next it passes through a minimum when  $x$  is about 0.2 mm., then rises through a gradual maximum, and declines toward zero as the end of the growth zone is reached. The precision of the diameter measurements on which these figures are based is not great, but similar determinations on succeeding pairs of the serial photographs (and on other cells) confirm the relation shown in Fig. 4. When data from later pictures are used, the extreme left portion of the curve is not fully represented, since all the markers have by then progressed to greater distances from the cell's apex.

One meaning of the curve in Fig. 4 is that the cell's diameter, and hence its circumference, is increasing at all points within the limits of the growing zone. Nowhere does the membrane grow solely by longitudinal extension; at every point it is expanding simultaneously along axes that are longitudinal and tangential (circumferential) with respect to the cell. This conclusion could perhaps be drawn from simple inspection of the tapered shape of the growing zone. But what is not at all apparent therefrom is the complex distribution, along the growth zone, of varying rates of circumferential growth.

It is useful to express these changes in cell diameter as relative elemental growth rates of the cell's circumference. At any distance from the cell apex the circumference is a circle that increases with increasing distance from the tip, until the limit is reached at the base of the growth zone. From the radial symmetry of the cell it may be assumed that, at a given axial distance from the tip, all portions of the circumference contribute equally to circumferential

growth. Then for any value of  $x$  the relative elemental growth rate of the circumference,  $C$ , will be approximated by  $\Delta C/C/\Delta t$ , or simply  $\Delta D/D/\Delta t$ . Therefore if each ordinate value of the curve in Fig. 4 is divided by the length of the cell diameter at that point, the corresponding relative elemental growth rate of the circumference is obtained.

Such rates expressed as millimeters per millimeter per hour are plotted against distance from the tip in Fig. 5. The resulting curve is complex, like its parent in Fig. 4: the high growth rate near the apex falls steeply to a minimum at about 0.2 mm. from the tip, then rises to a plateau that drops off toward zero at the basal end of the growing zone.

*Comparison of Longitudinal and Circumferential Growth Rates.*—Consider a small area of the growing membrane to be in surface view initially a minute square. After a time this square has moved to a position farther from the cell

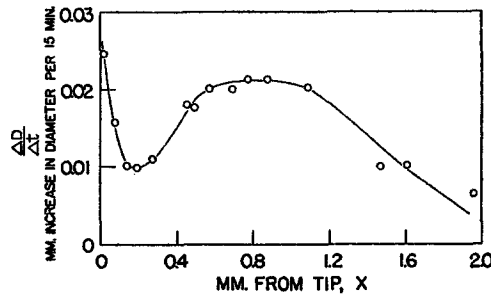


FIG. 4. Rate of increase in cell diameter plotted against distance from the cell tip.

tip, and while so doing it has enlarged in both its dimensions. Is it a square any longer, or is it a rectangle? And if the latter, which side of the rectangle is now longer? More generally, we would like to know the *relative* rates of growth in two dimensions of a very small area of the cell surface.

We may recall that a relative elemental growth rate expresses the momentary rate of linear enlargement of an infinitely small length of the growing object. The curves of Fig. 3 and Fig. 5 present such rates of enlargement of the cell surface in two directions at right angles to each other, longitudinal and circumferential respectively. The ratio of longitudinal to circumferential growth rates for any point will be  $d(\Delta x/\Delta t)dx/\Delta D/D/\Delta t$ . This is obtained for any value of  $x$  by reading the appropriate ordinate value from the curve of Fig. 3 and dividing it by the corresponding ordinate value from the curve of Fig. 5. Resulting values of the ratio are plotted against  $x$  in Fig. 6. This curve shows the changing relation of longitudinal to circumferential growth rate at points along the growing zone.

It will be seen that in the distal half of the growing tip longitudinal growth is



more rapid than circumferential. The ratio rises to a sharp peak at about 0.2 mm. from the cell apex, reflecting the position of the minimum in the curve of Fig. 5. Farther from the apex the ratio lessens, and at distances beyond about 1.0 mm. the ratio is numerically less than unity. This means that in the proximal half of the growing zone growth of the membrane is *relatively* faster in circumference than longitudinally, though both rates have by then fallen to a small fraction of their values at the cell apex.

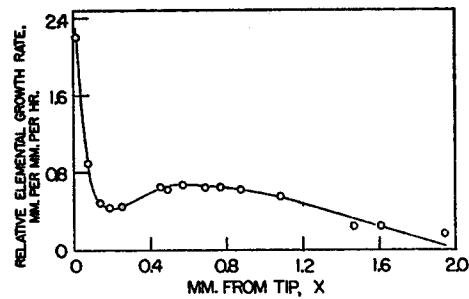


FIG. 5. Relative elemental growth rate in circumference as a function of distance from the cell tip.

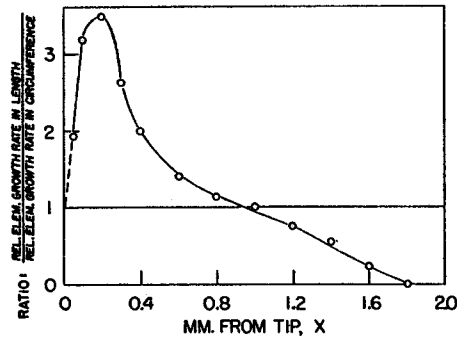


FIG. 6. The ratio of longitudinal to circumferential relative elemental growth rate plotted against distance from the cell tip. Component values taken from Figs. 3 and 5.

The course of enlargement of a small unit area of the membrane is therefore complex. If, as above, we visualize this area as initially a small square close to the cell's apex, it will first grow faster longitudinally and will become a rectangle whose greater dimension is along the cell's long axis. Thereafter growth along both axes becomes slower, but the rectangle will pass through a final phase of *relatively* faster enlargement of its transverse axis, thus acting to reduce the difference between the lengths of its sides.

The high rates of growth occur near the tip, and this is where longitudinal growth rates are specifically much greater than circumferential growth rates. Hence a small area of membrane passing the length of the growth zone will actually increase in length much more than it does in width. (This fact can be shown in a different way by following in a long series of photographs the *spacing* between two markers initially close together, and by measuring the average diameter associated with this segment of the cell in successive pictures. This procedure is an alternative method of approximately determining respective relative elemental growth rates; its use confirms the relations shown in Figs. 3 and 5.) We roughly estimate that a very small square of membrane considered initially near the cell apex will have increased in length about 9 times and in width about 4 times in passing through the growth zone.

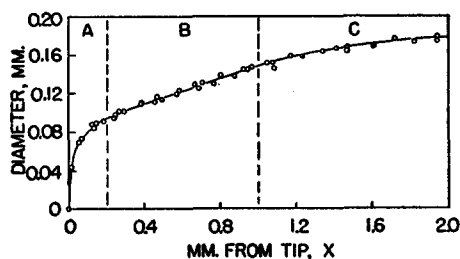


FIG. 7. Measured diameter of the tip at points along the growth zone. Data from measurements on all six photographs in Fig. 1. *A*, *B*, and *C* mark phases of the cell's profile noted in the text.

*Shape of the Growing Tip.*—The cell maintains nearly constant for hours its characteristically shaped tip, even in the face of continuous growth. Hence the tip's form is not at all static, but is determined by the dynamics of its own growth. This shape may be termed the cell's "standing profile," emphasizing that it persists in form despite changing substance and position. Measurements of growth of the cell membrane in the two dimensions of its surface have been given above, and from these it should be possible to reconstruct this time-independent profile.

To the eye the profile of the growing tip appears generally tapered (Fig. 1), but when examined in detail exhibits a subtle and characteristic configuration. Fig. 7 gives a plot of measurements of this cell's diameter against distance from its apex; by relative exaggeration of the ordinate scale the figure brings out what may also be seen in a large scale drawing of the cell tip's profile. There are three distinguishable phases in the plot of Fig. 7:

*Phase A.*—From the cell's apex to a distance about 0.2 mm. distant the diameter is rapidly increasing, but at a decreasing rate (per unit distance).

*Phase B.*—For values of  $x$  from about 0.2 mm. to 1.0 mm. the diameter

is almost a linear function of  $x$ ; this is the phase of "straight taper," and this section of the cell is almost literally a truncated section of a cone.

*Phase C.*—At greater distances than about 1.0 mm. from the apex the diameter again increases at a decreasing rate, and reaches its limiting maximum value at or near the end of the growth zone.

Thus the shape of the growing tip is by no means simply tapered, or bullet-shaped, or part of an ellipsoid of revolution. Its form is highly characteristic, and must be determined from point to point by the momentary rates of growth of the membrane in the two dimensions of the cell surface. Such rates are given by the curves of Figs. 3 and 5, and any singularities in these curves might be expected to be reflected in the cell's shape. This is so. For instance, phase B

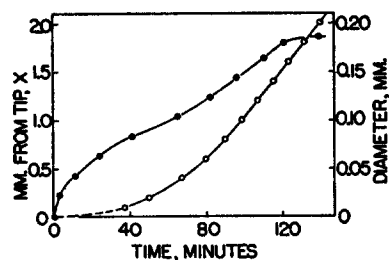


FIG. 8

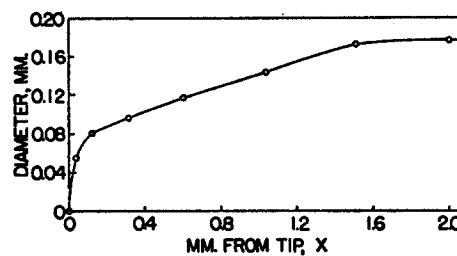


FIG. 9

FIG. 8. Computed time courses of (1) longitudinal displacement of a marker (open circles, left-hand ordinate), and (2) growth of the cell diameter (solid circles, right ordinate).

FIG. 9. Standing profile of the cell reconstructed from the data of Fig. 8 (see text).

(the region of straight taper) begins at about the peculiar minimum in the curve of Fig. 5 and coincides with the broad maximum in that curve at distances between 0.2 and 1.2 mm. from the tip.

For a complete reconstruction of the cell profile we ideally need the full time course of a marker passing from near the cell apex to the marker's exit from the growth zone, with simultaneous measurements of its position on the  $x$ -axis and the  $D$ -axis. This is experimentally difficult since a series of pictures taken over several hours would be required. But alternatively we may estimate  $x$  and  $D$  as functions of  $t$  from the data represented in Figs. 2 and 4. This may be done by regarding  $\Delta x/\Delta t$  and  $\Delta D/\Delta t$  as rough differentials, taking their reciprocals, and calculating values of  $t$  for each value of  $x$  and  $D$  by numerical integration (*cf.* Erickson and Sax, 1956, p. 496).

Fig. 8 shows the time course of longitudinal displacement of a single marker so computed, and also the form of the corresponding time curve for growth of the cell in diameter. (Differentiation of these curves would evidently again

yield the curves of Figs. 2 and 4 respectively.) These integral plots are very rough approximations, but they do permit a test of the idea that the growing tip is shaped by the respective growth rates of the membrane in the two dimensions of its surface.

Thus from the two curves of Fig. 8 can be read off values of  $x$  and  $D$  that correspond in time. When time is in this way eliminated as a variable,  $D$  may be plotted against corresponding values of  $x$  and the resulting curve (Fig. 9) should approximate the cell's standing profile shown in Fig. 7. This it does; in Fig. 9 the characteristic "phases" of the cell's curvature are seen. While errors must have been compounded in these calculations, reconstruction of the cell tip's peculiar shape shows that the shape is determined by, and derivable from, the longitudinal and circumferential growth rates of the membrane at every point. The argument is in a sense circular, but the author welcomes this homely evidence that the cell's special shape is not easily lost in a mathematical shuffle.

#### DISCUSSION

Elongation of the cell tip of *Phycomyces* is the sum of a series of graded growth increments occurring along the whole length of the growing zone, the size of an increment being related to its distance from the cell's apex. As here measured, there is no evidence that these increments occur discontinuously in either time or space.

The absolute magnitude of the maximum growth rate occurring at the extremity of the tip is noteworthy. By extrapolation of the curve in Fig. 3, a maximum relative elemental growth rate of at least 2.4 mm./mm./hr. is obtained. In other words the infinitely small terminal segment at the cell's apex is increasing in length by 240 per cent per hour. This extremely high figure is believed to be the highest yet reported; it exceeds the maximum for the mature (spore-bearing) sporangiophore of *Phycomyces* calculated by Erickson and Sax (1956), which is significantly not a case of tip growth. Comparable values for roots given by these authors are even lower, and in the case of *Nitella* internode cells studied by Green (1954) maximum relative elemental growth rates are of the order of only 5 per cent per hour. It is possible that the apical regions of cells with tip growth may have the highest relative elemental rates of elongation known.

We do not know what makes a high growth rate at one region of the cell and a lower one at another. We do know from Fig. 3 that relative rates of growth are distributed along the growing tip in an orderly way; also we know that the spatial pattern of distribution is maintained in the face of new growth and advance by the growing tip. Whatever the metabolic background may be for a graded distribution of local growth rates, tip growth seems characterized by an exceedingly high local concentration of intracellular "activity" at the cell's apex.

It is striking that the tip's growth in length is also at every point accompanied by growth in girth. The cell as a whole might appear to be "polarized" or unidirectional in its growth, in so far as the net addition of wall per unit time is a cylindrical section of constant diameter displaced from the bottom of the growth zone. But the growth in area that forms this cylinder as an end-product is in reality taking place all along the growing tip, and a unit area of the tip's membrane is everywhere increasing in both of the two dimensions of the cell surface. Thus the membrane is at any point directionally polarized in its surface growth only to the extent indicated by the ratio between its longitudinal and circumferential growth rates. As shown in Fig. 6, the ratio changes with distance from the tip.

The highest value of this ratio is about 3.5, occurring at a point 0.2 mm. from the cell's apex. At the apex itself, extrapolation of the respective curves in Figs. 3 and 5 suggests that relative elemental growth rates are equal in the two dimensions concerned, so that their ratio is unity. This supposition is indicated in Fig. 6 by the dotted line extrapolating the curve to the ordinate axis. It is reasonably implied that at the very apex of the cell the membrane is growing without directional preference or restraint. At no other spot along the growing cell is this true, save where the curve of Fig. 6 passes through an ordinate value of 1 and directional preference thereafter shifts in favor of circumferential growth (at distances greater than 1 mm. from the tip).

The growth of many plant cells is not restricted to the tip, but occurs over their entire area. One such case carefully studied by Green (1954) is *Nitella*, also a multinucleate cell that is subject to little or no constraint from its neighbors. Here the cylindrical internode cell elongates for days, and elongation is invariably accompanied by increase in diameter. For a population of *Nitella* cells, Green and Chapman (1955) found that the ratio of relative elemental growth rate in length to that in circumference was reasonably constant and had a value of about 5. They suggest that this five-to-one ratio characterizes the directional aspects of a unitary submicroscopic "growth event" that is compounded in time and space to produce the cell's manifest enlargement and the directional preference of its growth.

If this inference is correct for *Nitella* it surely fails for tip growth in *Phycomyces*. Fig. 6 shows that here the comparable growth ratio rises from a presumptive value of 1 at the cell apex to a maximum of 3.5 farther along the cell, then falls and actually becomes less than 1; such growth cannot be considered unitary in any meaningful sense. Green and Chapman's quantal growth event may be a valid mathematical abstraction rather than a physical reality.

What does appear significant is that in the case of both of these cells, so radically different in their absolute rates and patterns of growth, enlargement of the cell membrane always occurs simultaneously along both longitudinal and circumferential axes, albeit preferentially. This fact has not been ade-

quately considered in speculations about the submicroscopic mechanisms of growth. Bidimensional enlargement of an area of growing membrane must relate intimately to the disposition and behavior of its contained microfibrils.

We do not understand why plant cells so generally assume an approximately cylindrical form, except that we know they reach that form by *growth*. And the tubular shape, unlike the soap bubble, can only result from enlargement that is consistently *unequal* in the two dimensions of the surface. The exact pattern and location of a cell's growth seem not decisive: thus growth in both *Nitella* and *Phycomyces* generates a tube, although the former enlarges throughout its surface and the latter only at the tip. The common feature is the *directional preference* in membrane growth. Whatever determines this preference must be some antecedent force, activity, or structure in the expanding wall. There are at present only two clear possibilities: (1) existing oriented wall structure; (2) directionally unequal wall stress. It is well known that the walls of growing tubular cells are anisotropic, but it is not clear whether this is a cause or a consequence of directionally oriented growth. Similarly, it is recognized that in a cylindrical structure under internal pressure the circumferential wall stress is twice the longitudinal stress. Either of these two correlates might be causally secondary or irrelevant, but this is not proved.

Florey (1956) has pointed out, in considering transitions between amorphous and crystalline states of polymers, that stretching promotes crystallization and that crystallization in a polymer oriented by elongation diminishes the stress on it. Thus in model *in vitro* systems there is an interaction between oriented stress and the physical state of long polymer molecules. The *in vivo* site of formation and arrangement of crystalline microfibrils is the growing membrane. Heterogeneous as this membrane is, there can be small doubt that its mesh of polysaccharide microfibrils shares the tensile stresses on the wall. Since these stresses are directionally unequal (except in a cell that is growing as a sphere), it is possible that they participate in the origin of anisotropic structure and of anisometric expansion. It may be significant that among growing plant cell membranes statistically isotropic structure and the spherical shape are perhaps equally rare.

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