SPIRAL GROWTH AND SPIRAL STRUCTURE I.

SPIRAL GROWTH IN SPORANGIOPHORES OF PHYCOMYCES

by

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INTRODUCTION

It is now some seventeen years since the first observation of spiral growth in *Phycomyces* was announced by OORT (1931) and though we now know a great deal about the phenomenon, thanks very largely to the work of CASTLE, the explanation still escapes us. Several attempts have indeed been made to define the causal mechanism (CASTLE 1936, POP 1938, HEYN 1936, 1938) but each of these is too limited, as pointed out by CASTLE, to explain all the peculiarities which his work has revealed. The factors which have hitherto been used as the basis for these various explanations centre without exception around the cell wall, the underlying assumption, expressed or implied, being always that the anisotropy of the elastic properties of the wall, arising from the fine structure, is of supreme importance. As with most fungi, the wall of the sporangiophore of *Phycomyces* is composed of chitin, whose long molecular chains of glucosamine residues (VAN ITERSON *et al.* 1936, HEYN 1936, see also MEYER 1940) are arranged to lie parallel to each other in "micelles" pointing more or less accurately along a common direction and the whole structure resembling therefore the corresponding organisation in cellulose walls. In the growth zone of the sporangiophore this direction is said to be roughly transverse (OORT 1931) but difficulties associated with the nature of the wall, into which we need not go, make it impossible as yet to define this direction in more specific terms. In the light of such a structure, explanations have been offered along three lines. *a.* Protoplasmic streaming has been considered as aligning chain molecules as they are being built into the wall. This is clearly an attempt to explain spiral *structure* not spiral growth. *b.* Slip planes are said to be present in the chitin structure and spiral growth is considered as due to submicroscopic displacement along these planes (HEYN 1936, 1939). Unfortunately, this otherwise elegant suggestion fails to allow for any variation in the degree of spiral growth. *c.* The most promising suggestion seems to be that of CASTLE (see *e.g.*, CASTLE 1942) in which an interplay of the forces causing growth with the elastic properties of the wall, as governed by its spiral structure, is regarded as fundamental, though the exact expression given to this interplay leaves much to be desired. CASTLE himself has rejected the first two hypotheses on the clearest possible grounds and concludes: "It appears most plausible that these directional properties are determined by the structure of the wall itself". The interpretation of spiral growth to be attempted here falls into the third group.

In none of the hypotheses presented up to the present has there been any serious attempt to give a *quantitative* explanation: it has been regarded as sufficient to give merely an indication how spiral growth *of some undefined degree* might arise. It is the purpose of the present paper to examine a phenomenon well established in physics, but whose significance has been completely overlooked from the present point of view. The hypothesis to be presented is capable of critical *quantitative* checking though in view of our present lack of knowledge of the organisation of the wall in the growth zone of the sporangiophore and of our equally complete lack of data on the elastic properties of this wall, anything approaching accuracy in checking is hardly possible at this time. Nevertheless, by carrying over corresponding data from the closely related polysaccharide cellulose, it will be seen that there are good grounds for believing the present explanation to be on the right lines. The theory is presented at this time, however, chiefly because it does point to the data which are required for complete analysis, however difficult their determination seems at present to be. It is not suggested for a moment that the present paper constitutes anything more than a very reasonable hypothesis or that the striking agreement with the work on cellulose bears witness to anything but its feasibility. Nevertheless, the remarkable way in which a very complicated phenomenon is brought into line with the known behaviour of spirals makes the whole picture rather convincing.

Finally, the present writer finds himself so completely in agreement with CASTLE (1942) that spiral growth as found in *Phycomyces* is probably the elementary phenomenon underlying spiral growth in tissues that the opportunity will be taken of examining one such case — spiral grain in soft woods — in an attempt to show how this might receive explanation along similar lines. This will follow, however, in a later paper; the present work will involve merely the statement of the principles and their application to the simpler problem in the sporangiophore.

THE COURSE OF SPIRAL GROWTH

It will be as well first to point out the relevant facts concerning spiral growth as revealed by the elegant methods used by CASTLE and culminating in a very exact and detailed study (CASTLE 1942) from which most of the data to be used here are drawn. The description of events is given in terms of CASTLE's (1942) modification of ERRERA's (1884) classification of stages of growth. At all growing stages, growth occurs solely at or near the tip of the sporangiophore in what may therefore be called a growth zone, whose extent from the tip downwards varies from stage to stage of growth. From the first development of the sporangiophore up to the time when the sporangium begins to appear as a terminal swelling, it elongates rapidly through the agency of a terminal growth zone about 1 mm long. During this elongation the tip frequently rotates around the longitudinal axis of the sporangiophore. This rotation had been overlooked until detected by CASTLE (1942) who states that out of fifteen cases examined, thirteen showed this rotational component of growth, though not all to the same degree. It will be clear from Fig. 1 that if $\Delta\phi$ is the angle in degrees through which a point on the wall moves while being raised a distance ΔL by elongation of the sporangiophore, then the "angle of growth", Θ, may be determined by the relation

$$\Theta = \tan^{-1}\frac{\pi a \Delta\phi}{180\,\Delta L}.$$

Θ turns out to be about 10° in these Stage I sporangiophores and lies along a left-hand spiral as shown in Fig. 1; *i.e.*, looking down on the tip, any point of it rotates in a clockwise manner. In Stage II, the sporangium begins to swell and both elongation and rotation cease; this is followed by Stage III in which the sporangium is fully grown and no elongation or rotation is observed. This stage lasts from two to three hours. Elongation then begins again (Stage IV) and continues for many hours, and rotation of the tip reappears simultaneously. The growth zone is now 1.5 to 2 mm long. The remarkable fact is, however, that during about the first hour of this stage (Stage IVa) the rotation is right-handed, instead of left-handed as it was in Stage I, with the angle of spiral growth somewhere between 7° and 15°. This rotation, however, gradually slows down to zero and then reverses itself, becoming again left-handed with an angle of spiral growth which increases up to a maximum between 7° and 12°.

Two general points therefore emerge. In growing sporangiophores we have first left-handed, then right-handed and again left-handed rotation and any attempt to explain spiral growth must also explain this regular alternation. This appears to be by far the most searching point in the whole story. As a second point of smaller importance, though of equal significance, the angle of spiral growth can vary from cell to cell. This rules out immediately any explanation based on structural features peculiar to the crystalline fraction of chitin. It may perhaps be added, however, that the angle of growth remains remarkably constant in any one sporangiophore except during the change in sign. With these points in mind, discussion of the present hypothesis can now be made. Further details concerning spiral growth pertinent to the present issue, in so far as they can be used to check the validity of the hypothesis, will be considered as the occasion arises.

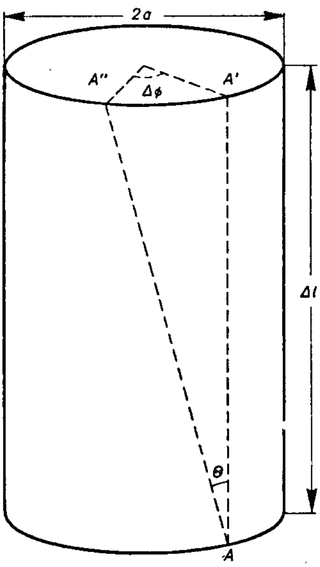

Fig. 1. Diagrammatic representation of the relation between the angle of growth, Θ, and the rotation of any point in the wall per unit elongation.

THEORETICAL CONSIDERATION

In applying theoretical quantitative considerations to morphological changes in any plant organ, one of the prerequisites is usually a precise mathematical formulation of shape. This is difficult to achieve with the sporangiophores, particularly since the shape varies with the maximum diameter (CASTLE 1936a); and for preliminary investigations the mathematical treatment involved presents difficulties which, if not insuperable, at least are best avoided in such exploratory studies. For present purposes, therefore, the sporangiophore will be considered as a right circular cylinder, bounded at one end by a flat face. We shall further consider the chitin chains to lie at an angle 90°-α to the directrix of the cylinder; this does not introduce anything undesirable since α may vary from 0° to 90°. The sporangiophore is thus considered as a hollow cylinder wound with a series of spirals all with the same inclination. This is not to suggest that all the chitin micelles lie at the same angle — undoubtedly some, perhaps considerable, dispersion will occur — but rather to replace these micelles by a hypothetical set, all lying at the mean angle of the real set, and with their elastic properties therefore depending in part on the dispersion of the real set. The cell is being extended by internal turgor forces (CASTLE 1937) and we can therefore consider the spiral windings as loaded at the end nearer the apex with a force which will depend on the turgor pressure and on the diameter of the sporangiophore. If we can consider the wall as built of a series of spiral windings, one single spiral element with its appropriate load can be examined and the manner in which it behaves should therefore tell us something of the behaviour of the whole cell. It is always to be remembered that this represents a further simplification of the conditions actually obtaining in the wall. The spiral elements are certainly not so independent of each other as this view would suggest. Nevertheless, fibrils can be made to appear so readily that the mechanical connection between them must be very weak.

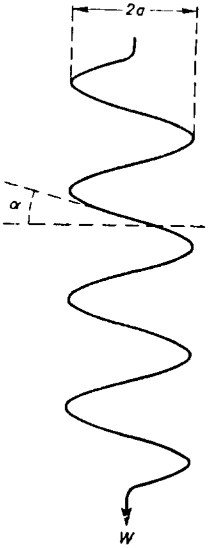

Fig. 2. Diagrammatic representation of a spiral spring under axial load.

The physical features associated with spirals under axial load are well understood; it is not proposed to give any formal treatment, for the details are to be found in standard text-books (POYNTING AND THOMSON 1934). Very briefly, we may imagine a spring, Fig. 2, of which the winding makes an angle α with the horizontal, loaded axially with a weight W. This will extend, and the extension can be traced to two sources *a.* the *bending* of the wire and *b.* the *twisting* of the wire around its own axis. If the length of the spiral winding is l, the radius of the spring a and the load W, then the elongation ΔL is given by

$$\Delta L = Wla^2 (\cos^2\alpha/nC + \sin^2\alpha/qD)$$

where n is the torsional rigidity and q the YOUNG's modulus of the wire, and C and D factors which depend on the shape of its cross section. At the same time, the spring will twist about its own axis. This again arises from both the bending and the twisting of the wire and its value is given by

$$\Delta\phi = Wla\cos\alpha\sin\alpha\,(1/nC - 1/qD)$$

and is therefore a maximum when $\alpha = 45°$. For our purpose it is better to express the rotation in terms of length increase thus:

$$\frac{\Delta\phi}{\Delta L} = \frac{\cos\alpha\sin\alpha\left(\frac{1}{nC} - \frac{1}{qD}\right)}{a\left(\frac{\cos^2\alpha}{nC} + \frac{\sin^2\alpha}{qD}\right)} = \frac{\cos\alpha\sin\alpha\left(1 - \frac{nC}{qD}\right)}{a\left(\cos^2\alpha + \frac{nC}{qD}\sin^2\alpha\right)} \qquad (1)$$

thereby eliminating both l and W and expressing the rotation $\Delta\phi$ corresponding to an elongation ΔL. We thus see that as the spiral elongates the free end will rotate unless some external restraint is put upon it, except in the case when $1/nC = 1/qD$. This is the principle underlying the present attempt to explain spiral growth in cells. It is suggested that this phenomenon may result merely from the elongation of a cell wound with a series of spirals. Such a suggestion is naturally of little value unless it can be tested against known facts of spiral growth and it is fortunate therefore that the equation lends itself to such checking very readily. The implications of the equation can therefore now be studied in terms of the known facts of growth.

THE PROPOSED EXPLANATION OF SPIRAL GROWTH

We notice first that these considerations apply strictly to the case of a spiral spring loaded statically to equilibrium. In the elongating cell equilibrium is not reached. There is, however, clear evidence that the wall is stretched elastically (CASTLE 1937) and all we need to add to the present theory is that as the walls of the growth zone are extended the tensions are released by interpolation of new wall particles (in which the chitin crystallites must be aligned in the same direction as those already present, since no change in net orientation occurs), or by some other process, when the internal pressure will cause further elongation. We have here, then, a series of spirals which are kept in continuous elongation by the insertion of new elements. The spiral remains the same length since, as the growth zone elongates basifugally, an equivalent portion at its base is in effect removed by the deposition of a tougher "secondary" layer. Thus the tip continues to rotate at a rate which is predictable from the above equation.

Before proceeding to the rough quantitative tests which can be made, it will be as well to examine first the degree to which the equation is satisfactory in a qualitative sense, and the following points are therefore to be noted.

a. It is observed that rotation accompanies elongation and ceases when elongation ceases. This is clearly contained in the present hypothesis since the same mechanism causes both elongation and rotation. The apparent anomaly that the rate of rotation changes during the change from right- to left-hand spiralling in Stage IV will be explained later. During steady right- or left-hand spiralling, further, the rate of rotation under constant conditions is proportional to the rate of elongation. This is clearly contained in the formula since under these conditions $\Delta\phi/\Delta L$ is constant.

b. The value of α is known to be small since the chitin chains are said to be oriented more or less transversely; it is further very probable that n, which depends on secondary valences, will be small compared with q, depending as it does on primary valences (see below for further discussion of this point). Hence, since C and D are obviously of the same order of magnitude, $(nC/qD.\sin^2\alpha)$ will be small compared with $\cos^2\alpha$ and therefore the value of $\Delta\phi/\Delta L$ *i.e.*, the rotation per unit elongation, will be largely dependent on $(1 - nC/qD)$. Any change in the environment which affects this term should therefore have a corresponding effect on the rate of rotation per unit elongation. No short term changes in the environment are likely to affect either C or D since these depend only on the shape of the chitin elements in transverse section, so that changes are to be expected only in n or in q. The effect, for instance, of temperature has been studied in some detail (CASTLE 1936b) and it is found that, so long as temperatures do not exceed 27° or 28° C, increase in temperature increases markedly the rotation per unit elongation. This effect arises specifically in the growing region and is regarded as an effect on the wall itself (CASTLE 1934, 1936). Now in a substance like chitin, where n depends on secondary valences and q on primary valences, we might expect q to remain more or less constant except at high temperatures and n to decrease with increase in temperature. This change in n has actually been observed in cellulose (CLAYTON AND PEIRCE 1928–1929) and we may be reasonably sure that, though experimental evidence is lacking, the same will be true of chitin. Hence $(1 - nC/qD)$ will increase, and hence $\Delta\phi/\Delta L$ increase, as temperature rises just as is actually observed. Further, it is found that at temperatures round 27°–28° C the rate of spiralling begins to decrease again (CASTLE 1936). It would seem therefore significant that according to CLAYTON AND PEIRCE (1928–1929) if the temperature of cotton cellulose is raised much above room temperature at fairly high regain (water content) the value of n begins to increase again. If we can carry this result over to chitin, then it would mean that the factor $(1 - nC/qD)$ would decrease and therefore correspond to the decreased rate of spiralling observed.

c. It is found by CASTLE (1938) that the application of torque to the spore mass around an axis running longitudinally down the sporangiophore will reduce the rate of rotation and even cause rotation to cease altogether. This is clearly implied in the suggestion presented here and furnishes further qualitative and even roughly quantitative checks. It is found that the couple required to prevent rotation increases rapidly as the diameter of the sporangiophore increases. According to the present hypothesis, the couple C required to stop rotation may be expressed in the form:

$$C \, \Delta\phi = W \Delta L^{*}$$

Since in the sporangiophore $W \propto a^2 P$ (P being the turgor pressure) then

$$C = KPa^2 \Delta L / \Delta\phi = K' a^3$$

K, k′ being constants if we assume n, q, C, D and P to remain constant. This may be checked against experimental results as in Table I. Several points are to be remembered in assessing the correspondence here between observed and calculated figures. Since the larger cells show a greater degree of curvature in the growth zone (CASTLE 1936), the figures for cell diameter are progressively increasing overestimates of the average diameter in the growth zone; further, it is not certain that factors such as P are independent of cell diameter; and it is very possible that wall structure is not independent of cell diameter. It would seem therefore that the agreement is encouraging. Furthermore, we can determine the *order* of the torque required to stop rotation in cells of any chosen diameter. This calculation must of necessity be rather rough since we do not know what effect torque will have on the wall, since elongation does not cease though it is markedly diminished. We must assume that torque affects elongation only as it reduces to zero that part of the elongation associated geometrically with the twisting of the cell. Expressed analytically, this implies that

TABLE I

VARIATION WITH DIAMETER OF THE SPORANGIOPHORE OF THE TORQUE REQUIRED TO STOP ROTATION

Cell radius	Torque	Relative torque	
(μ)	(obs.)	(obs.)	(calcd)
32	0.03	1.0	1.0
43	0.03	1.0	2.5
45	0.08	2.7	2.8
50	0.14	4.7	3.8
65	0.17	5.7	8.3

$$C = Wa \sin\alpha$$

Remembering that in the original spring model the load W exerts its effects through the

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* Strictly speaking this relation cannot be true, for the couple which stops rotation does not also stop elongation, though elongation is slowed down considerably. The relation offers a ready illustration of the point at issue, however; a closer approximation is made later (p. 161).

torque Wa, it can readily be shown that here $W = \pi a^2 P/3$. We can use this *whole* load on the sporangiophore wall since we are now considering *all* the spirals in the wall. Hence, taking $a = 0.005$ cm, $P = 8$ atm (CASTLE 1937) and $\alpha \doteq 10°$ as the limit to what might be called "transverse" orientation (see below) then

$$C = (\pi/3)\,(0.005)^3 \cdot 8 \cdot 10^6 \cdot \sin 10° \text{ dyne cm} = 0.18 \text{ dyne cm}$$

This compares very favourably with the value 0.14 found by CASTLE.

The more searching tests of the hypothesis can now be made. The chitin elements dealt with in the above discussions may probably be connected with the fibrils, composed of micelles analogous to those in cellulose and, like them, may be considered as roughly circular in section. Hence C and D may be written as

$$C = \pi\, b^4/2$$

$$D = \pi\, b^4/4$$

where b is the diameter of a fibril. Equation (1) then becomes

$$\frac{\Delta\phi}{\Delta L} = \frac{\cos\alpha \sin\alpha \left(1 - \frac{2n}{q}\right)}{a\left(\cos^2\alpha + \frac{2n}{q}\sin^2\alpha\right)} \qquad (2)$$

Thus if α can be estimated, then the value of n/q can be determined. This will enable not only the decision to be made whether or not the derived value is a feasible one, but also the final step to be taken in the argument by explaining the change from left- to right- and back to left-hand spiralling in Stage 4. Unfortunately, the only reference available concerning the orientation of chitin here is that the chains are more or less transverse (OORT 1931), though CASTLE (1942) seems prepared to find them lying along a spiral. In actual fact, the optical work which has been done on the wall suffices only to indicate that the chains are inclined to the transverse at angles considerably less than 45°. It is not clear in the literature even whether the spiral is left- or right-handed.

It is stated by OORT AND ROELEFSON (1932) that on the whole the spiral is left-handed*, and on the drawing they give (which shows, however, a right-hand spiral) the angle drawn is about 8° for what that is worth. We are compelled therefore again for the moment to fall back on the analogous case of cellulose. We have two recorded cases (ASTBURY AND PRESTON 1940, PRESTON 1947), one of them a primary wall (PRESTON 1947), in which the inclination of the cellulose chains to the transverse plane is about 10°. Assuming this value therefore, as a rough limit to what might be called "transverse", the following consideration can be made. Taking first the data of OORT (1931) we may calculate from the angle of spiral growth (5.8°) that

$$\tan(5.80) = \frac{\sin 10° \cdot \cos 10° \cdot \left(1 - \frac{2n}{q}\right)}{\cos^2 10° + \frac{2n}{q}\sin^2 10°}$$

whence $n/q = 0.2$.

Unfortunately there are few estimates of n/q even for cellulose. Values for q are recorded frequently, but so far as the writer is aware only one reasonably accurate value

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* In the English sense.

References p. 165.

of n is available. In a careful survey of cotton hairs, CLAYTON AND PEIRCE (1928–1929) record values from which n/q can be calculated as 0.155, a figure which, applying as it does to the spiral organisation of cellulose found in cotton, may be taken as referring to cellulose with a moderate degree of angular dispersion. The value is remarkably close to the estimate obtained above for chitin and while it is to be recognised that the elastic constants of biological material can vary between wide limits, it is nevertheless satisfactory that the agreement is so close; in any case it establishes that the value of n/q required to give the observed rate of rotation is feasible. It is further to be noted that since n/q is less than unity then the spiral growth is left-handed (if the structural spiral is left-handed and since the spiral coils up on itself). This is the commonly observed direction of rotation. This value can now therefore be applied to CASTLE's (1942) data; in Stage I sporangiophores the angle of spiral growth is 10°. Hence

$$\tan 10^\circ = \frac{\sin \alpha \cos \alpha \ (0.6)}{\cos^2\alpha + 0.4 \sin^2\alpha}$$

for which one solution is $\alpha = 16.5^\circ$ (the other value being the corresponding steep spiral giving the same rotation). This is rather higher than the average of 10° we have noted for cellulose primary walls, but well within the range of angles known to occur (PRESTON 1947); it may, therefore, be regarded as reasonable.

Now comes perhaps the most telling feature of the present considerations — the explanation of the reversal of spiralling. In order to provide a complete vindication of the hypothesis presented here, not only must the reversal of spiralling receive explanation, but the stage of growth at which the reversal is most likely to occur must also be predicted. Now it is clear from (2) that the rotation of an extending spiral is proportional to $(1 - 2n/q)$ and it has been seen that since $2n/q$ is less than unity, this implies sinistral spiralling. It is therefore equally clear that if at any time $2n/q$ becomes greater than unity then the rotation will become right-handed. In other words, if q, for instance, changes to a sufficiently low value, or if n increases sufficiently, then the rotation will become right-handed. Considering first changes in q, we note that there are several ways in which change could be effected, the simplest and most obvious, and certainly the most probable, being change in the *angular dispersion* of the chitin crystallites. As the crystallites become arranged more at random the value of q parallel to the mean direction of the crystallites will clearly diminish. There is abundant evidence in the literature that this is true for cellulose (see *e.g.*, MEYER AND LOTMAR 1936) and there seems no reasonable doubt but that the same will hold for chitin. Although corresponding figures are lacking for n it seems equally clear that its value will increase as the dispersion increases. Thus the value of n/q will be greater the greater the dispersion of the constituent crystallites. In order to explain a change in the direction therefore of rotation it is sufficient to invoke a change in angular dispersion, providing such a change can produce a sufficiently great change in n/q; and the enormous changes found in q as dispersion changes in cellulose leaves little doubt but that concomitant changes in n/q can be sufficient for present purposes.

Turning now, therefore, to the second point, concerning the period at which we might expect changes in rotation rate and even direction, it is now a familiar concept that as the wall of a growing cell is first laid down the micelles of which it is composed, while lying in general along a line more or less transverse to the length of the cell, are dispersed about this line; and as the cell continues to grow these micelles, under the influence of the strain imposed on the wall, come to lie more and more nearly parallel to each other with little or no change in mean direction. There is, in fact, some evidence that this change does occur (MAJUMDAR AND PRESTON 1941, MAAS GEESTERANUS 1941). If the cell ceases temporarily to grow, then the micelles being laid down will retain for the time being their orginal angular dispersion. Hence n/q may well increase as a cell ceases growth. Now the only phase in which temporary cessation of growth occurs in the sporangiophore of *Phycomyces* is during the enlargement of the sporangium, and therefore when growth recommences the wall now has a greater n/q than before growth ceased and the growth spiral is correspondingly right-handed. Further, since the wall is now being stretched, both longitudinally and laterally, the angular dispersion of the micelles already laid down will now be decreased, n/q will decrease (and therefore rotation will slow down) until $n/q = 1$ when rotation will momentarily cease; as n/q then decreases further to the value it had before the sporangium began to swell (*i.e.*, when wall conditions again become stable) the rotation will become again left-handed. The change in sign of the growth spiral thus receives complete explanation.

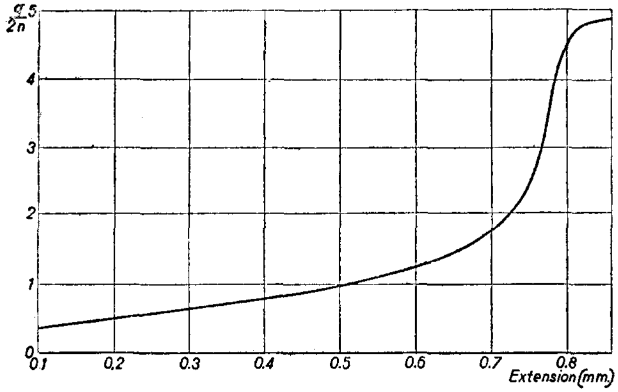

Fig. 3. Relation between n/q and elongation as determined from growth data on Stage IV sporangiophores in CASTLE (1942).

It is difficult at the moment to give any quantitative check of this possibility. Obviously we require to know more about the wall of the growth zone at this critical time. We can, however, show that there is nothing in the available data that is out of harmony with this suggestion. Thus we note that equation (2) can be written

$$\frac{q}{n} = \frac{a \sin^2 a + \cos a \sin a}{\cos a \sin a - a \dfrac{\Delta \phi}{\Delta L} \cos^2 a}$$

Using this equation, q/n can be calculated at various time points during the change from right-handed to left-handed spiralling, using the figures given graphically by CASTLE (1942). The resultant values are given in Fig. 3. Up to an elongation of 0.6 mm the value of q/n slowly rises and then the wall suddenly stiffens up to an elongation of 0.7 mm. This is what might be expected as the micelles are pulled into the parallel position.

DISCUSSION

In assessing the merits of the suggestions made in this paper it is imperative that the assumptions made should be clearly recognised, since it is only insofar as they are justifiable in the light of present knowledge of cell growth, or at any rate are such as can be tested experimentally, that the theoretical considerations made here have any merit. It must be admitted in the first place that they do represent a simplification, possibly a gross over-simplification, of the state of affairs actually involved during growth, and it can be said only, perhaps, that they express a very complicated set of phenomena in a way which, though unduly simple, is nevertheless in terms of the correct and relevant parameters.

It has been assumed that the chitin chains in the growth zone are oriented uniformly at an angle (here taken as 10°) which is relatively constant over the growth zone and invariate during the growth of the sporangiophore. This raises a point which has been discussed repeatedly in the parallel case of cellulose. It might be expected that, under the considerable extension which the wall undergoes, the chitin spiral would be pulled out steeper with time. This is known not to occur in cellulose walls and it seems, in fact, very doubtful whether mere mechanical forces have any part to play in orientation in spite of the contrary opinion recently expressed by PICKEN *et al.* (1947). It would be of material importance if the same could be shown true in the present case in which the cell grows free of all external restraint. In point of fact, the uniformity of the birefringence over the growth zone at all periods of growth, and the lack of change in this property as the sporangiophore grows, would argue strongly in favour of the assumption. Yet at the same tine there is the apparent paradox that the analogy made here with spiral springs demands that some change in the spiral angle should occur. It is possible, however, to resolve this paradox in either of two ways. It is possible to conceive of a series of infinitesimally small changes in spiral angle as elongation proceeds, each change followed by a return to the original angle as new material is laid down in the wall. If this sequence does obtain, then one might expect growth to occur discontinuously and it is therefore notable that CASTLE (1940) with this point in mind has actually observed discontinuities of the type expected. It seems equally possible that new wall material is deposited only locally, *e.g.*, in the extreme tip of Stage I sporangiophores where the chains are then oriented in a very flat spiral and the spiral angle changes as the sporangiophore grows, but only insofar as there is any disparity between the relative girth increase and the length increase in a section of the wall as it passes progressively down the growth zone. One could obviously test this possibility by making the relevant determinations and it seems hardly safe to speculate at this time. This type of localised growth is implied in the older work of NOLL on filamentous algae. In either case the present interpretation could hold but it is obviously imperative that the precise condition of the wall in the growth zone should be elucidated. It may further be emphasized at this point that no account has been taken here of the changes in diameter along the growth zone; the zone has been considered as a right circular cylinder. It is not to be denied that changes in girth will have a part to play in the determination of spiral growth and its omission is perhaps the weakest part of the present thesis. Such an omission would, however, seem inevitable at this stage.

As regards the assumption that the spirally arranged fibrils in the wall of the growth zone may be considered as simple entities with no appreciable effect upon each other, little need be added to what has been said. There can be no doubt that interfibrillar material (possibly protein) will interfere to a greater or less degree with the twisting of the elements demanded in the above considerations. The major effect will be, however, to replace the elastic constants of the fibrils, which appear in the relations expressed above, by other, similar constants involving also the non-crystalline material; the principles will remain the same. There is, however, the further point that, if the fibrils cannot be considered even approximately as independent mechanical units, then the change in sign of spiral growth, interpreted here as change in angular dispersion, might possibly receive explanation along other lines. If the unit is not the spiral fibril, it might in some way, for instance, involve a function of wall thickness and in that case the change in sign could be associated with change in C and D.

The quantitative agreement between the values of n/q for chitin and the values for cotton is, of course, quite fortuitous as is also the close agreement between the calculated and observed values of the torque necessary to stop rotation. The major point at issue is, however, that by choosing reasonable values of C/D and α the value of n/q required to give the observed rate of spiralling is feasible for structures like chitin; and this is sufficient for a preliminary theoretical investigation.

In general therefore it may be concluded that the present hypothesis has succeeded in yielding a formula whereby the course of spiral growth can be made intelligible and, though some modification will be needed, there can be no doubt but that it represents the closest approximation yet made. It does point clearly to the further work that is necessary for a full understanding of the process. At the very least the formula developed can be regarded as of a type which cannot be far removed from the real one — even if it turns out to be no more than an empirical expression of a very complex phenomenon.

SUMMARY

An explanation is suggested of spiral growth in sporangiophores of *Phycomyces* in terms of wall structure. It is pointed out that the growth of the cell resembles the extension of a rather flat spiral spring loaded axially at one end. Like the cell, the spring rotates as it extends. An equation is derived from which the rotation per unit elongation may be obtained and it is shown that the relation gives satisfactory qualitative and rough quantitative agreement with the facts of spiral growth. In particular it is possible to explain the observed reversal of spiralling.

RÉSUMÉ

Une explication est proposée concernant la croissance en spirale des sporangiophores du *Phycomyces*, basée sur la structure de la paroi. On remarque que la croissance de la cellule ressemble à l'extension d'un ressort en spirale assez plate, chargé axialement à une extrémité. De même que la cellule, le ressort subit une rotation lorsqu'il s'allonge. Une équation est établie, permettant de calculer la rotation par unité d'élongation, et on montre que cette équation est en accord qualitatif suffisant, et en assez bon accord quantitatif avec le phénomène de la croissance en spirale. En particulier, cette équation explique la réversibilité de la forme en spirale.

ZUSAMMENFASSUNG

Eine Erklärung des Spiralwuchses bei Sporangiophoren von *Phycomyces* als Funktion der Wandstruktur wird vorgeschlagen. Es wird deutlich gemacht, dass das Zellwachstum der Ausdehnung einer ziemlich flachen Spirale gleicht, die an einem Ende axial belastet ist. Wie die Zelle, rotiert auch die Feder wenn sie sich ausdehnt. Eine Gleichung wird abgeleitet, aus der die Rotation per Ausdehungseinheit erhalten werden kann, und es wird gezeigt, dass diese Beziehung eine befriedigende qualitative und rohe quantitative Übereinstimmung mit den experimentellen Daten des Spiralwuchses ergibt. Insbesondere ist es möglich die wahrgenommene Umkehrung als Spiralung zu erklären.

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Received March 12th, 1948