NOTE ON SPIRAL GROWTH AND SPIRAL CELL WALL STRUCTURE IN SPORANGIOPHORES OF *PHYCOMYCES*

by

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Recently a very attractive hypothesis has been postulated in this journal by R. D. PRESTON (1948) on the spiral growth of *Phycomyces* sporangiophores, which would be governed by the spiral structure of the primary cell wall in the growth zone of these cells. The rotation of the sporangium, or of the tip in young sporangiumless cells, is compared with the rotation of the top of a flat spiral wire which is being extended by some pulling force.

Although this line of interpretation might not be too far removed from the truth, the present author is of the opinion that in applying this hypothesis to this object certain facts have been overlooked.

The usually predominating *left*-handed* spiral of growth is explained by PRESTON by *left*-handed structural spirals in the (primary) cell wall of the growth zone, thereby however neglecting two facts, *viz.*:

a) the optical work of OORT AND ROELOFSEN (1932) indicates a flat *right*-handed structural spiral;

b) a *left*-handed spiral does not fit his spring-elongation theory in explaining a clockwise rotation of the sporangium, as elongation of such a spiral would cause a counter-clockwise rotation.

As to a) the following may be remarked. PRESTON (*l.c.*, p. 161) states:

"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 (1)** is left- or right-handed.

It is stated by OORT AND ROELOFSEN (1932) that on the whole the spiral (2)** is *left*-handed, and on the drawing they give (which shows, however, a right-hand spiral) (3)** the angle drawn is about 8° for what that is worth".

Here the results of OORT AND ROELOFSEN (*l.c.*) are evidently misinterpreted, because in Fig. 1 of their publication, reproduced here again as Fig. 1, the right handed spiral (spiral no. 3 of PRESTON), marked nγ, in cell-wall layer 1, represents only the spiral of the *highest refractive index* and neither the spiral of the chitin chains (spiral no. 1 of PRESTON) nor the spiral of growth (spiral no. 2 of PRESTON).

* Left-handed in the English sense, *i.e.*, in descending a spiral the axis will be on the left hand. With a left-handed spiral of growth the sporangium rotates clockwise when looking down on it.

** Numbered by present author.

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In summarizing, OORT AND ROELOFSEN (*l.c.*) stated:

"In der primären Wand (Schicht 1 ist in der Wachstumzone allein vorhanden), stimmt die Richtung der grössten Dehnbarkeit, der Spaltbarkeit, einer feinen Streifung und von $n\beta$ mit der Wachstumsrichtung überein. Diese verläuft meistens in einer steilen Rechts-*, bisweilen auch Linksspirale. $n\gamma$ steht senkrecht auf dieser Richtung und verläuft ungefähr tangential".

So here it was pointed out, that the spiral of growth (Wachstumsrichtung) was left-handed whereas $n\gamma$ was right-handed. A mistake, as supposed by PRESTON, was therefore excluded. OORT AND ROELOFSEN (*l.c.*) did not venture to take a decision concerning the direction of chitin strands, but mentioned (p. 905) the following theoretical possibilities:

1. the strands run parallel to $n\gamma$ and consist of rodlets, also lying roughly parallel to $n\gamma$;

2. the strands run perpendicular to $n\gamma$, but consist of piled-up platelets and therefore their textural birefringence is negative.

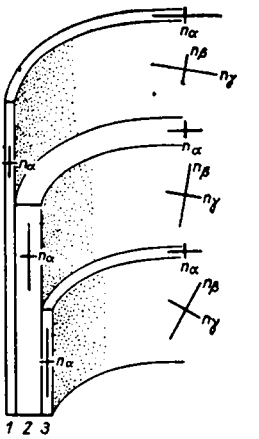

Fig. 1. Schematic representation of the cell-wall layer swith refractive indexes inserted

Now possibility 2 is very unprobable and actually impossible with a view on the orientation of the indices of birefringence in transversal and radial sections of the primary cell wall. The only objection against assumption of possibility 1 is, that the preferred line of burst ("Spaltbarkeit" in citation above) was seen to be perpendicular to $n\gamma$, whereas one would expect it parallel to $n\gamma$ and to the strands of chitin rodlets.

However before the sporangiophore is brought to burst by pressing on the basal portions, the top shows torsions accompanying the elastic elongation and the direction of the burst-line can very easy be wrongly interpreted. Keeping in mind that further investigations on this point are required, one may assume for the present possibility 1.

Concerning consideration b, mentioned above, it may be pointed out that a clockwise rotation of the top is shown, when a right-handed spiral of, for instance, steel wire is elongated, as can be seen from the difference in position of the tops in Figs 2 and 3, which actually represent drawings of models. PRESTON (*l.c.*, p. 162) states: "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".

With a steel wire n/q certainly will be less than unity, but it is observed that the spiral does not coil up on itself. Such would only happen if the rotation is *not* due to elongation of spirals, but only to growth in length of the strands constituting the spirals. Such growth is also assumed by PRESTON (*l.c.*, p. 159) when he states "We have here, then, a series of spirals which are kept in continuous elongation by the insertion of new elements".

Considering the optical facts as elucidated by OORT AND ROELOFSEN (*l.c.*) (essentially confirmed by CASTLE, 1938) and making use of the spiral-elongation-theory of

* Right and left here contrary to the English sense.

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PRESTON, corrected as to the direction of the rotation, furthermore assuming that the chitin strands in the primary and the secondary wall run approximately parallel to $n\gamma$, as drawn in Fig. 1, the spiral growth can be easily explained as follows.

A. The *usual clockwise* rotation of the sporangium, in accordance with a left-handed spiral of growth, may be due to one or more of the following causes.

1. The flat *right*-handed chitin-strand spirals in the cell wall of the upper parts of the growth zone are elongated by turgor-tension, become steeper and cause a clockwise rotation, as explained by PRESTON's theory, see Figs. 2 and 3. In the meantime they become located in lower parts of the growth zone.

2. These spirals not only elongate, but also acquire a larger radius because the sporangiophore in the growth zone is not tubular, but somewhat cone-shaped. As demonstrated by Fig. 4, such enlargement of right-handed spirals also causes clockwise rotation of the top.

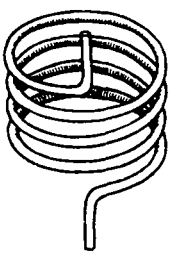

Fig. 2. Model of spiral steel wire

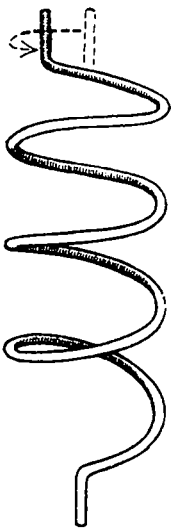

Fig. 3. Spiral of Fig. 2 elongated

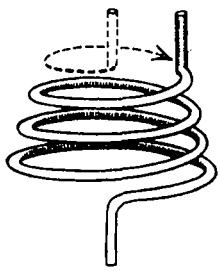

Fig. 4. Spiral of Fig. 2 enlarged coneshaped

3. When the spirals are elongated (or widened in radius) as supposed under 1 (or 2) the widening spaces between the "primary" chitin strands considered, very probably will be filled up, at least partly, with new cell-wall material. When the chitin-material is supposed to consist of strands, then what happens is an increase of the number of strands. As long as this intussusception of new "secondary" strands does not exceed the task of filling the required space, no additional rotation is originated. Only, if this would not take place, the rotation would be diminished by increasing elastic resistance, but in case *more* "secondary" strands are intussuscepted, a clockwise rotation will result of it. This would make the sporangiophore both wider and longer, dependent on the steepness of the structural spirals. It would therefore diminish the rotational forces due to 1 and 2.

B. *Counter clockwise* rotation of the sporangium may be due to one or more of the following reasons:

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1. PRESTON's theory concerning the reversal of the growth spiral when 2 n becomes greater than q.

2. Domination of the clockwise rotation by the counter-clock-wise rotational effect, caused by the growth in length of the strands of chitin chains constituting the spirals. Depending on how one supposes that the interpolation of chitin units in the chains takes place, one may speak of growth of the chains or of slipplanes between the chains, or between the strands (HEYN, 1939). This process, whatever it may be, may be located for instance at the apical ends of the chains in the topmost part of the growth zone, or distributed over the entire growth zone. Due to this process "the spirals will coil up on themselves" and as they are right-handed a right-handed rotation of the sporangium will occur. Actually this counter-clockwise rotational influence will be constantly present during periods of clockwise rotation, but in insufficient degree to compensate the clockwise rotation.

The present author is inclined to believe that this process in fact causes the small counter-clockwise rotation occurring at the onset of growth after the sporangium has been formed (stage IVa of CASTLE, 1942). In stage III (CASTLE) the former growth zone has probably been stiffened by the deposition of (primary or secondary) cell wall material. In that case a new growth zone must be generated. In the initial phase of this, when no widening of the cell radius comes into question, intussusception is excluded, as well as all growth due to plastic elongation. Then growth in length of the chitin strands themselves is the only means of starting sporangiophore growth. The high quotient $\frac{\text{rotation}}{\text{elongation}}$ in this stage, as found by CASTLE (*l.c.*), is in accordance with this assumption.

3. During a period of lowering of the turgor-tension the effect of the factors mentioned under A 1 and 2 will be reversed.

4. When temporary the secondary cell wall, which, as Fig. 1 shows, is probably constituted of steep left-handed structural spirals, is deposited in the growth zone, or at least in a zone which later on resumes growth, the factors mentioned under A 1 and 2 may be reversed if the secondary wall dominates the primary wall. (This may also explain the counterclock wise rotation in stage IVa).

SUMMARY

It is pointed out that the theory of PRESTON (*l.c.*) explaining spiral growth of *Phycomyces* sporangiophores by elongation of chitin strand spirals in the primary cell wall is fully in accordance with the known facts about its physical structure as described by OORT AND ROELOFSEN (*l.c.*). More possibilities causing spiral growth and temporary reversal of the spiral growth direction from left to right are however mentioned.

RÉSUMÉ

L'auteur démontre que la théorie de PRESTON (*l.c.*) expliquant la croissance en spirale des sporangiophores du *Phycomyces*, basée sur l'allongement des spirales de fascicules de chitine dans la paroi primaire, est en accord complet avec les faits décrits sur la structure physique par OORT ET ROELOFSEN (*l.c.*).

En outre, il propose quelques circonstances qui pourraient causer aussi cette croissance en spirale et son changement de direction temporaire (de gauche à droite).

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ZUSAMMENFASSUNG

Es wird gezeigt, dass die Theorie von PRESTON (*l.c.*) die das Spiralwachstum des Sporangiophoren von *Phycomyces* durch die Verlängerung der spiralformigen Bündel von Chitin in der primären Wand erklärt, vollkommen mit den von OORT UND ROELOFSEN (*l.c.*) beschriebenen Tatsachen über ihre physikalische Struktur übereinstimmt.

Es werden ausserdem noch andere Umstände erwähnt, die ebenfalls dieses Spiralwachstum und seine zeitweilige Richtungsänderung von links nach rechts bewirken könnten.

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