A geometrical model of *Chara* rhizoid growth

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Abstract

The applicability of the Kirchoff-Love Hypothesis to the growth of the *Chara* rhizoid, approached as the constant deformation of the shell, was investigated. It is shown that the observed distribution of cell wall growth velocity may be, under certain assumptions, the result of the changing curvature of the growing surface.

Key words: rhizoid, cell wall, growth, model

INTRODUCTION

A growing rhizoid may be viewed as the continuous deformation of its shell. The Kirchoff-Love Hypothesis is frequently used in thin-shell mechanics (Fung 1965). It states that every element of the shell that is linear and perpendicular to the mean surface before deformation remains linear and perpendicular after deformation, retaining at the same time its length. Acceptance of this hypothesis makes it possible to reduce the problem of deformation of a layer to the problem of deformation of its mean surface. We thus obtain in the place of a three-dimensional problem in the theory of elasticity — a two-dimensional problem with boundary conditions.

In a paper by Hejnowicz et al. (1977), the relative, elementary growth rate of a cell wall on the *Chara* rhizoid apex was determined in the meridional and equatorial directions. The static turgoric stresses in orthogonal directions were also calculated, based on measurements of the cell wall curvatures and on the Laplace formula. It was found that the elementary growth rate is greatest where the stresses are smallest because of the largest curvature, that is, on the

rhizoid apex. The high degree of symmetry in the distribution of stresses and the relative elementary rate suggests that there are deeper ties between these two physical quantities.

The objective of this paper is to find the geometrical relationship between the distribution of stresses in a rhizoid cell wall and the distribution of the growth rate of this wall and to test the applicability of the Kirchhoff-Love Hypothesis to cases of rhizoid growth treated as the continuous deformation of the shell.

RESULTS

Chara rhizoid growth is an example of stationary apical growth. The shape of a rhizoid that grows in such a manner can be modelled, e.g. by using a rotational semiellipsis with a ratio of semiaxes of $1:1:a$ ($a > 1$). During "growth" the semiellipsis representing the surface of the rhizoid moves with a constant speed within the cylinder (Fig. 1). The model rhizoid is therefore

Fig. 1. A model of a growing rhizoid — an axial section through a cylinder filled with semiellipses. The trajectory of point A orthogonal to the semiellipses is marked (dashed line)

made up of two parts: an ellipsis one and the cylindrical part the lies under it. In an axial section, the rhizoid is always represented by a semiellipsis that "turnes into" two straight lines forming the sides of the cylinder. During growth, transformation from one semiellipsis to another occurs. We obtain in this manner a family of semiellipses filling up the area between the sides of the cylinder.

The assumption of a constant shape of the growing rhizoid says nothing about the distribution of the growth velocity on the surface. For example, theoretically growth could occur only at the point of junction between the semiellipsis with the cylinder.

Each point located on the semiellipsis (e.g. point A on Fig. 1) moves during growth over a specific curve, entirely determined by the distribution of the growth velocity. In order to test the applicability of the Kirchoff-Love Hypothesis, let us choose a family of curves orthogonal to the family of semiellipses. Which ever vector that is perpendicular to the semiellipsis at a given moment, will remain perpendicular to it at successive moments of time. Let us check if the so-designated manner of movement of the same point on a "growing" semiellipsis gives a "growth" velocity distribution that is comparable with the distribution obtained *in vivo* by Hejnowicz et al. (1977).

The equations for both families of curves are as follows:

family of semiellipses

$$z = a \sqrt{1-x^2} + v \cdot t$$

family of orthogonal curves

$$z = \frac{1}{a} \left[\sqrt{1-x^2} - \ln \left| \frac{1+\sqrt{1-x^2}}{2} \right| \right] + d.$$

Since it was assumed that the elongation growth rate of the rhizoid is a unit value, then time "t" is a parameter of the family of semiellipses. A parameter of the family of orthogonal curves is "d".

The rate at which the chosen point recedes from the apex can be determined by measuring the length of the arch between the apex and the chosen point at successive time intervals. The alorythm permitting description the movement of the chosen point along the semiellipsis is as follows:

- 1) Choose a parameter "d" that corresponds to the trajectory of the point whose movement is to be studied.
- 2) Calculate using Newton's method the point of intersection of the orthogonal curve with the parameter "d" with the semiellipsis at time $t = 0$.
- 3) Calculate the length of arch s ($t = 0$) found between the apex and the point of intersection using an elliptical integral.
- 4) Return to point 2 and repeat the calculations for a new time $t = t + 1$.

5) The values obtained above are used to calculate the velocity of the point as it recedes from the apex:

$$V(s) = \frac{s(t+1) - s(t)}{t}, \text{ where } t \text{ is a unit increment of time.}$$

Figure 2 shows a comparison of the distribution of the velocity of the rhizoid surface growth rate obtained *in vivo*, (Hejnowicz et al. 1977) with the model distribution. Significant similarity of both curves is evident. This indicates that the hypothesis about the role of orthogonal curves in apical growth is not groundless. At the same time, it is seen that this manner of deformation of the shell (growth) fulfils the assumptions of the Kirchhoff-Love Hypothesis.

Fig. 2. Velocity curves for the movement of a point away from the apex as a function of the distance from the apex measured along the meridian. A — based on Hejnowicz et al. (1977), the outline in the upper right hand corner shows the rhizoid apex; B — on the basis of the model with parameters $a = 2$, $d = 4$; C — on the basis of the model with parameters $a = 3$, $d = 4$

DISCUSSION

Let us consider the following diagram of rhizoid growth occurring under conditions of constant turgor and at a given distribution of stresses in the cell wall:

increase of the volume -----> increase in the
 of a cell <----- surface of the cell wall

The arrows symbolise a feedback mechanism.

Growth in agreement with the above diagram in the case of a cell wall with only elastic properties would be impossible because of the rapidly attained state of mechanical balance in the cell wall-cytosol system. Closer to the nature of cell wall growth seems to be the analogy with the revolving shell made from a viscoelastic solid substance subjected to constant internal pressure. In such a case, so-called creeping of material must occur, and its velocity would be dependent on the viscoelasticity which changes as a function of the distance from the apex and on the changing of extension stresses (dependent on the curvature of the surface). The growth of the rhizoid may thus be imagined to be (this is a gross approximation) the controlled, slow "outflow" of the cytosol surrounded by a viscoelastic cell wall. It seems that growth understood as a process occurring under so determined conditions of constant mechanical imbalance requires a smaller number of parameters necessary to direct it. The family of curves orthogonal to the surface of a growing rhizoid described in this paper may correspond thus to the "lines of flow of outflowing cytosol". Let us assume that the flow of vesicles containing the structural materials for the cell wall (and other structures) is in agreement with these "lines of flow". Assuming that the flow of vesicles per unit time is equal in each point of the cross section of the subapical part of the rhizoid, then in the apical part we obtain a distribution of vesicles similar to the so-called Szpitzkörper, a body made up of vesicles and observed in the apex of the rhizoid (Brunswik 1924).

It has frequently been suggested that the role of the main factor regulating the growth of the cell wall could be played by the cytoskeleton (Bershadsky and Vasiliev 1989). It is therefore possible that apical growth may be regulated through either directional supply of vesicles containing structural materials for the cell wall, or through another mechanism related to that part of the cytoskeleton which adheres to the internal side of the plasma membrane. In the first of these cases, the pattern of the bundles of the cytoskeleton supplying the vesicles could coincide with the pattern of the family of curves orthogonal to the surface of the growing rhizoid. If it were possible to additionally show the existence of an inverse proportion between the velocity of the directional supply of vesicles (occurring most frequently with a saltatio motion), and, for example, the stress of the cytoskeleton stretched out on

plasma membranes, this would be sufficient for the construction of a model for the regulation of apical growth. It cannot be excluded that the "lines of flow" coincide with the pattern of cytoskeleton bundles, which, from the point of view of energetics, would be very favourable.

The two orthogonal families of curves described in this paper may be treated as a convenient coordinate system for the description of the growth of rhizoids. Such a description using a growth tensor will be the subject of a subsequent paper.

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Geometryczny model wzrostu ryzoidu Chara

Streszczenie

Sprawdzono stosowalność hipotezy Kirchoffa-Love'a w przypadku wzrostu ryzoidu *Chara* traktowanego jako zachodzące w sposób ciągły odkształcenie powłoki. Pokazano, że obserwowany rozkład prędkości wzrostu ściany komórkowej może być, przy pewnych założeniach, konsekwencją zmiennej krzywizny rosnącej powierzchni.