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Spatial variations of growth within domes having different patterns of principal growth directions

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Abstract

Growth rate variations for two paraboloidal domes: *A* and *B*, identical when seen from the outside but differing in the internal pattern of principal growth directions, were modeled by means of the growth tensor and a natural coordinate system. In dome *A* periclinal trajectories in the axial plane were given by confocal parabolas (as in a tunical dome), in dome *B* by parabolas converging to the vertex (as in a dome without a tunica). Accordingly, two natural coordinate systems, namely paraboloidal for *A* and convergent parabolic for *B*, were used. In both cases, the rate of growth in area on the surfaces of domes was assumed to be isotropic and identical in corresponding points. It appears that distributions of growth rates within domes *A* and *B* are similar in their peripheral and central parts and different only in their distal regions. In the latter, growth rates are relatively large; the maximum relative rate of growth in volume is around the geometric focus in dome *A*, and on the surface around the vertex in dome *B*.

Key words: apical dome, growth variation, growth tensor

INTRODUCTION

Principal directions of growth (*PDG*) can be determined in symplastically growing plant organs (Hejnowicz and Romberger 1984). They are indicated by eigenvectors of symmetric part of the growth tensor. We can associate these directions with each point within the organ, thus there is a pattern of *PDG* trajectories. Trajectories of *PDG* are mutually orthogonal

(Hejnowicz 1984). In practice, their pattern can be recognized from the cell-wall network (under the condition that the growth is not isotropic) because the line elements oriented along *PDG* and thus mutually orthogonal, preserve orthogonality during growth. The curvilinear coordinate system, for which coordinate lines are tangent at any point to the trajectories of *PDG* is called a natural coordinate system (Hejnowicz 1984). This system is the most appropriate for dynamic descriptions and analysis of the growing organ.

In an apical dome there are three *PDG*: periclinal, anticlinal and latitudinal (Fig. 1a). How do the trajectories of these directions run, if the dome maintains a steady-state shape during growth? Since *PDG* appear in the cell-wall pattern, the periclines and anticlines can be drawn from these patterns but sometimes they are not well visible in some regions of the organ. From the inspection of the surface layer of cells in the dome it appears that at a given point on the surface, the anticlinal trajectory is normal, and that the two remaining are tangent to the surface. If the dome is a figure of revolution around the axis, and if the tip of the dome does not rotate during growth, the periclinal trajectory on the surface is represented by the dome profile, whereas the latitudinal trajectories are always circular. Such a pattern certainly occurs at the surface, but what happens inside? If the dome grows symplastically then the trajectories of *PDG* must be continuous, and the pattern of trajectories, known at the surface, can be extrapolated into the dome interior (Hejnowicz 1984), However, we can obtain two different patterns in this way, with two types of periclinal trajectories: *A* — converging to the segment on the dome axis (as the periclines in the axial plane of the tunical dome), *B* — converging to one point at the vertex (as in the dome without a tunica). We denote these cases as *A* and *B*, respectively. It can be expected that domes *A* and *B* with the two different patterns of *PDG* have different variations of growth rates inside. The question is: how different are the distributions of growth rates within domes *A* and *B*, if the domes are identical from the outside, i.e., they have the same shape, size, and the same rate of growth in area on the dome surface? In the present paper an attempt is made to answer this question by relating it to a paraboloidal-dome-shaped meristem.

RESULTS

THE NATURAL COORDINATE SYSTEMS FOR A PARABOLOIDAL DOME

Let us consider a paraboloidal dome of the apex, assuming that its shape is a steady-state during growth. The outline of the axial longitudinal section of the dome can be described by $x^2 = 2pz$, where p is the parameter of the parabola (Fig. 1a). Two natural coordinate systems can be

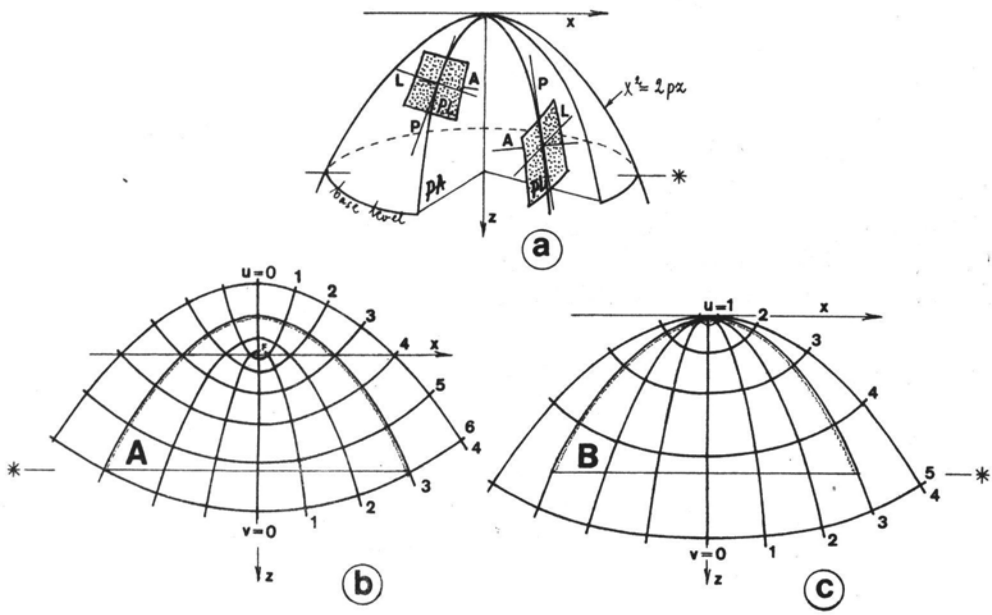

Fig. 1. A paraboloidal apical dome with two patterns of trajectories of principal growth directions in the axial plane: a) three-dimensional drawing showing spatial orientation of principal directions *P*, *A*, *L* — periclinal, anticlinal and latitudinal respectively for two chosen points; the axial plane *PA* and planes *PL*, fixed by directions *P* and *L*, are marked (the maps on Figs. 2, 3 and 4 were made for these planes), b) pattern *A* of trajectories given by the paraboloidal system, c) pattern *B* of trajectories given by the convergent parabolic system. In both natural systems the surface of the dome is represented by $v_s = 3$. The base of the dome is on the level indicated by the asterisk

proposed for this dome, one is paraboloidal coordinate system (*A*), the other, a convergent parabolic system (*B*) (see Fig. 1b, c). The first represents pattern *A*, the second, pattern *B* of *PDG* in the axial plane. The dome for which the paraboloidal system is natural, is denoted by *A*, the second is best described by a convergent parabolic system, *B*.

Paraboloidal coordinate system

This system was already used in previous models (Hejnowicz et al. 1984a, b). The traces of the coordinate surfaces in the axial plane x, z are confocal parabolas (Fig. 1b). They represent periclinal and anticlinal trajectories, while the latitudinal trajectories are circles (they are not marked) because the z is a symmetry axis. The equations defining transformation between rectangular and paraboloidal coordinates, and the scale factors (Spiegel 1959) are as follows:

$$x = uv \cos \varphi, \quad y = uv \sin \varphi, \quad z = \frac{1}{2}(u^2 - v^2), \tag{1}$$

where $u \geqslant 0$, $v \geqslant 0$, $0 \leqslant \varphi < 2\pi$,

$$h_u = h_v = \sqrt{u^2 + v^2}, \quad h_\varphi = uv.$$

For $\varphi = 0$, we have: $u = \sqrt{\sqrt{x^2+z^2}+z}$ and $v = \sqrt{\sqrt{x^2+z^2}-z}$. The surface of dome *A* is represented by one of the surfaces v. Let us denote it as v_s. The focus *F* divides the axis of the dome into two parts. The dimension of the upper part from *F* to the tip increases if the dome becomes wider. The relation between v_s and p for the parabola which represents the surface of the dome is $v_s = \sqrt{p}$.

Convergent parabolic system

The system was constructed especially for the modeling of dome growth. The traces of the coordinate surfaces on the x, z plane are shown in Fig. 1c. They are parabolas converging to the origin (perclinal trajectories) and ellipses (anticlinal trajectories). The latitudinal trajectories are circles, as previously. The equations for the transformation and scale factors are:

$$x = v^2 \sqrt{m-1} \cos\varphi, \quad y = v^2 \sqrt{m-1} \sin\varphi, \quad z = \frac{1}{2} v^2 (m-1),$$

where $u \geqslant 0$, $-\infty < v < \infty$, $0 \leqslant \varphi < 2\pi$, (2)

$$h_u = \frac{4u^3}{v^2 \sqrt{m(m-1)}}, \quad h_v = \frac{v(m-1)}{\sqrt{m}}, \quad h_\varphi = v^2 \sqrt{m-1},$$

where $m = \frac{1}{v^2} \sqrt{4u^4 + v^4}$.

For $\varphi = 0$ and $z \geqslant 0$, we have: $u = \sqrt[4]{\frac{1}{2} x^2 + z^2}$, $v = \sqrt{\frac{x^2}{2z}}$. The tip of dome *B* is represented by the origin of the coordinate system, the surface of the dome is represented by the surface v_s and, as previously, we have $v_s = \sqrt{p}$.

GROWTH TENSOR IN ANY COORDINATE SYSTEM WITH ROTATIONAL SYMMETRY

The growth tensor was defined as the covariant derivative of the field $\bar{V}$, of displacement velocities of material points in the organ (Hejnowicz and Romberger 1984). This tensor expressed in physical components allows full characterization of the growing organ. Among other things, in a natural coordinate system, diagonal elements of the matrix of the growth tensor represent principal growth rates, i.e., relative elemental rate of growth in length, $RERG_l$, in *PDG*. The sum of these elements (in the physical components) gives the relative elemental rate of growth in volume, $RERG_{vol}$.

The growth tensor can be obtained directly in physical components from the dyadic $\bar{\nabla}\bar{V}$ (Hejnowicz and Romberger 1984). This method will be used to calculate the general form of the matrix of physical components of the growth tensor for any curvilinear coordinate system with rotational symmetry.

Let us consider the system (u, v, φ) with rotational symmetry (as it is in paraboloidal and convergent parabolic systems). In this system $\bar{e}_u$, $\bar{e}_v$, $\bar{e}_\varphi$ represent the unit base vector and vector $\bar{V}$ is given by the components: V_u, V_v, V_φ. Because the differential operator in each curvilinear system has the form (Spiegel 1959):

$$\bar{\nabla} = \frac{\bar{e}_u}{h_u}\frac{\partial}{\partial u} + \frac{\bar{e}_v}{h_v}\frac{\partial}{\partial v} + \frac{\bar{e}_\varphi}{h_\varphi}\frac{\partial}{\partial \varphi},$$

where h_u, h_v, h_φ are the scale factors, hence dyadic $\bar{\nabla}\bar{V}$ can be written as:

$$\begin{aligned}\bar{\nabla}\bar{V} &= \left(\frac{\bar{e}_u}{h_u}\frac{\partial}{\partial u} + \frac{\bar{e}_v}{h_v}\frac{\partial}{\partial v} + \frac{\bar{e}_\varphi}{h_\varphi}\frac{\partial}{\partial \varphi}\right)(V_u\bar{e}_u + V_v\bar{e}_v + V_\varphi\bar{e}_\varphi) = \\ &= \frac{1}{h_u}\frac{\partial}{\partial u}(V_u\bar{e}_u)\bar{e}_u + \frac{1}{h_u}\frac{\partial}{\partial u}(V_v\bar{e}_v)\bar{e}_u + \frac{1}{h_u}\frac{\partial}{\partial u}(V_\varphi\bar{e}_\varphi)\bar{e}_u + \\ &+ \frac{1}{h_v}\frac{\partial}{\partial V}(V_u\bar{e}_u)\bar{e}_v + \frac{1}{h_v}\frac{\partial}{\partial v}(V_v\bar{e}_v)\bar{e}_v + \frac{1}{h_v}\frac{\partial}{\partial v}(V_\varphi\bar{e}_\varphi)\bar{e}_v + \\ &+ \frac{1}{h_\varphi}\frac{\partial}{\partial \varphi}(V_u\bar{e}_u)\bar{e}_\varphi + \frac{1}{h_\varphi}\frac{\partial}{\partial \varphi}(V_v\bar{e}_v)\bar{e}_\varphi + \frac{1}{h_\varphi}\frac{\partial}{\partial \varphi}(V_\varphi\bar{e}_\varphi)\bar{e}_\varphi.\end{aligned}$$

First the components are differentiated partially, then all terms are grouped with respect to the so-called unit dyadics, $e_i\,e_j$, for $i, j = u, v, \varphi$ (Spiegel 1959). Thus the sum is obtained which can be expressed as:

$$\begin{aligned}\bar{\nabla}\bar{V} = {} & T_{uu}\,\bar{e}_u\bar{e}_u + T_{uv}\,\bar{e}_u\bar{e}_v + T_{u\varphi}\,\bar{e}_u\bar{e}_\varphi + \\ & + T_{vu}\,\bar{e}_v\bar{e}_u + T_{vv}\,\bar{e}_v\bar{e}_v + T_{v\varphi}\,\bar{e}_v\bar{e}_\varphi + \\ & + T_{\varphi u}\,\bar{e}_\varphi\bar{e}_u + T_{\varphi v}\,\bar{e}_\varphi\bar{e}_v + T_{\varphi\varphi}\,\bar{e}_\varphi\bar{e}_\varphi,\end{aligned}$$

where T_{ij} for $i, j = u, v, \varphi$ are the components of the dyadic. An array of dyadic components, in the form of a 3 by 3 matrix, can be written. This matrix is identical with the sought matrix of the growth tensor in physical components. It has the following form:

$$\left\{\begin{array}{ccc} \frac{1}{h_u}\left(\frac{\partial V_u}{\partial u} + \frac{1}{h_v}\frac{\partial h_u}{\partial v}V_v\right) & \frac{1}{h_u}\left(\frac{\partial V_v}{\partial u} - \frac{1}{h_v}\frac{\partial h_u}{\partial v}V_u\right) & \frac{1}{h_u}\frac{\partial V_\varphi}{\partial u} \\ \frac{1}{h_v}\left(\frac{\partial V_u}{\partial v} - \frac{1}{h_u}\frac{\partial h_v}{\partial u}V_v\right) & \frac{1}{h_v}\left(\frac{\partial V_v}{\partial v} + \frac{1}{h_u}\frac{\partial h_v}{\partial u}V_u\right)\times & \frac{1}{h_v}\frac{\partial V_\varphi}{\partial v} \\ \frac{1}{h_\varphi}\left(\frac{\partial V_u}{\partial \varphi} - \frac{1}{h_u}\frac{\partial h_\varphi}{\partial u}V_\varphi\right) & \frac{1}{h_\varphi}\left(\frac{\partial V_v}{\partial \varphi} - \frac{1}{h_v}\frac{\partial h_\varphi}{\partial v}V_\varphi\right) & \\ & \frac{1}{h_\varphi}\left(\frac{\partial V_\varphi}{\partial \varphi} + \frac{1}{h_u}\frac{\partial h_\varphi}{\partial u}V_u + \frac{1}{h_v}\frac{\partial h_\varphi}{\partial v}V_v\right) & \end{array}\right\}$$

As was mentioned before, the principal growth rates are given by diagonal elements in (3). The element in the upper left hand corner, T_{uu}, represents $RERG_l$ in the periclinal direction ($RERG_{l(per)}$), the element in the bottom right hand corner, $T_{\varphi\varphi}$, represents $RERG_l$ in the latitudinal direction ($RERG_{l(lat)}$), the element in the center, T_{vv}, represents $RERG_l$ in the anticlinal direction ($RERG_{l(ant)}$). Specification of the matrix depends on determining the scale factors and the components of the vector field $\bar{V}$.

FIELD $\bar{V}$ FOR THE ISOTROPIC SURFACE GROWTH, SPECIFICATION OF THE GROWTH TENSOR (PHYSICAL COMPONENTS)

The feature of isotropic *RERG* in area on the dome surface (we will call it an isotropic surface growth) means that for each point on the surface, $RERG_l$ is the same in any direction in the plane tangent to the surface at this point. It is possible, however, that the values of $RERG_l$ for the points differing in the distance from the vertex, are different. We know that in the plane tangent to the surface, two *PDG* exist, namely periclinal and latitudinal, therefore, $RERG_{l(per)}$ must be equal to $RERG_{l(lat)}$ for $v = v_s$. Denoting the components of $\bar{V}$ on the surface v_s by $\tilde{V}_u$, $\tilde{V}_v$, $\tilde{V}_\varphi$, from (3) the following condition is obtained:

$$\frac{1}{\tilde{h}_u}\left(\frac{\partial \tilde{V}}{\partial u}+\frac{1}{\tilde{h}_v}\,\frac{\partial \tilde{h}_u}{\partial v}\,\tilde{V}_v\right)=\frac{1}{\tilde{h}_\varphi}\left(\frac{\partial \tilde{V}_\varphi}{\partial \varphi}+\frac{1}{\tilde{h}_u}\,\frac{\partial \tilde{h}_\varphi}{\partial u}\,\tilde{V}_u+\frac{1}{\tilde{h}_v}\,\frac{\partial \tilde{h}_\varphi}{\partial v}\,\tilde{V}_v\right), \tag{4}$$

where $\tilde{h}_u$, $\tilde{h}_v$, $\tilde{h}_\varphi$ are the scale factor of the system for $v = v_s$. For domes *A* and *B*, $V_v = V_\varphi = 0$ and V_u does not depend on φ because their growth is steady and without rotation, thus there remains:

$$\frac{\partial \tilde{V}_u}{\partial u}=\frac{1}{\tilde{h}_\varphi}\,\frac{\partial \tilde{h}_\varphi}{\partial u}\,\tilde{V}_u. \tag{5}$$

After the integration (5) with respect to u (for $\varphi = \text{const.}$), $\tilde{V}_u$, i.e., V_u on the surface of the dome, can be obtained. The field V_u for the whole dome, from the relation $V_u(u, v) = \frac{h_u}{\tilde{h}_u}\,\tilde{V}_u(u, v_s)$ (Hejnowicz 1984), one can calculate. By this means, we will determine V_u, and then the growth tensor for both domes *A* and *B*.

Dome A: The variant of isotropic surface growth in a paraboloidal coordinate system was already considered in the previous paper (Hejnowicz et al. 1984b). The following expression for V_u was obtained there:

$$V_u(u, v) = c_1 u \sqrt{\frac{u^2+v^2}{u^2+v_s^2}}, \tag{6}$$

where c_1 is constant. Accordingly, the growth tensor (3) (physical components) for dome A is:

$$\frac{c_1}{\sqrt{u^2+v_s^2}\; u^2+v^2} \begin{Bmatrix} \frac{u^4+2u^2 v_s^2+v^2 v_s^2}{u^2+v_s^2} & -uv & 0 \\ uv & u^2 & 0 \\ 0 & 0 & u^2+v^2 \end{Bmatrix} \tag{7}$$

Dome B**:** For a convergent parabolic system, condition (5) is the following:

$$\frac{\partial \tilde{V}_u}{\partial u} - \frac{4u^3}{v_s^4\, \tilde{m}(\tilde{m}-1)} \tilde{V}_u = 0,$$

where $\tilde{m} = \frac{1}{v_s^2}\sqrt{4u^4+v_s^4}$. Upon integration $\tilde{V}_u = c_2\sqrt{\tilde{m}-1}$, where c_2 is the integration constant. Introducing scaling factor we obtain the displacement velocity for all points in the dome:

$$V_u(u, v) = c_2 \frac{v_s^2 \sqrt{\tilde{m}(\tilde{m}-1)}}{v^2 \sqrt{m(m-1)}} \sqrt{\tilde{m}-1}, \tag{8}$$

where $m = \frac{1}{v^2}\sqrt{4u^4+v^4}$ and $\tilde{m}$ is the same as previously. The specific form of the growth tensor (3) for dome B is thus:

$$\frac{c_2 v_s^2 \sqrt{\tilde{m}}(\tilde{m}-1)}{v^4 m(m-1)} \begin{Bmatrix} H & -\frac{\sqrt{m-1}}{m} & 0 \\ \frac{\sqrt{m-1}}{m} & \frac{m+1}{m} & 0 \\ 0 & 0 & 1 \end{Bmatrix}, \tag{9}$$

where m and $\tilde{m}$ are as previously, and

$$H = \frac{m^2(\tilde{m}-1)-\tilde{m}^2(m-1)}{\tilde{m}^2 m(m+1)} + \frac{m(\tilde{m}+1)}{\tilde{m}(m+1)}.$$

It is worth noting that conditions (4) and (5) say nothing about the values of $RERG_l$ at different points on the surface v_s. In order to have equal values of $RERG_l$ in corresponding points on the surfaces of both domes, it must be assumed that velocity (6) is equal to velocity (8) at corresponding points of both domes, for instance at vertices and on base levels. As can be seen, this is satisfied at vertices because $V_u = 0$ there for $u = 0$ and $v = v_s$. Let us consider the second point. Denoting by u_b^A and u_b^B the coordinates for which the surfaces of domes A and B are crossed by the base level, from (6) and (8) there is:

$$c_1 u_b^A = \frac{c_2}{v_s}\sqrt{\sqrt{4(u_b^B)^4 + v_s^4} - v_s^2}. \tag{10}$$

Let us assume that v_s for both domes is $v_s = 3$ and the coordinates u_b are as follows: $u_b^A = 6$ in the paraboloidal system and $u_b^B \cong 4.69$ in the convergent parabolic system. Thus, for $c_1 = 1$ from (10), there must be $c_2 \cong 3$. For these constants, the velocities V_u on the surfaces of domes A and B are identical in corresponding points, in consequence, T_{uu} and $T_{\varphi\varphi}$ in (7) are equal to T_{uu} and $T_{\varphi\varphi}$ in (9). Thus the fields $\bar{V}$ and the growth tensors in physical components for domes A and B are fully specified.

DISTRIBUTION OF GROWTH RATES

$RERG_l$ in different directions and $RERG_{vol}$ for domes A and B, were calculated from the specified growth tensors. The results are shown in the form of computer-made maps in Figs. 2, 3 and 4. In Fig. 2a, b growth rates in the planes PL (see Fig. 1a), are given. The maps of $RERG_l$ for domes A and B are similar there, except for a small region near the focus in the dome A. On the surfaces of both domes there is an isotropy of the relative elemental rate of growth in area. The plots of $RERG_l$ around the points on the surface are circles, but values of $RERG_l$ decrease with increasing distance from the vertex. In corresponding points on the surfaces of both domes the $RERG_l$'s are equal, as was assumed. Below the surface, within the dome interior, $RERG_l$ in the PL planes becomes anisotropic, $RERG_{l(per)}$ becomes higher than $RERG_{l(lat)}$. Maximum of $RERG_{l(per)}$ is in the distal part of both domes, for dome A particularly at the geometric focus.

In axial plane PA (see Fig. 1a), growth rates for both domes are similar at the base level only (Fig. 3a, b). On the axis of each dome, $RERG_{l(per)}$ is more or less twice as large as $RERG_{l(ant)}$, but on the way

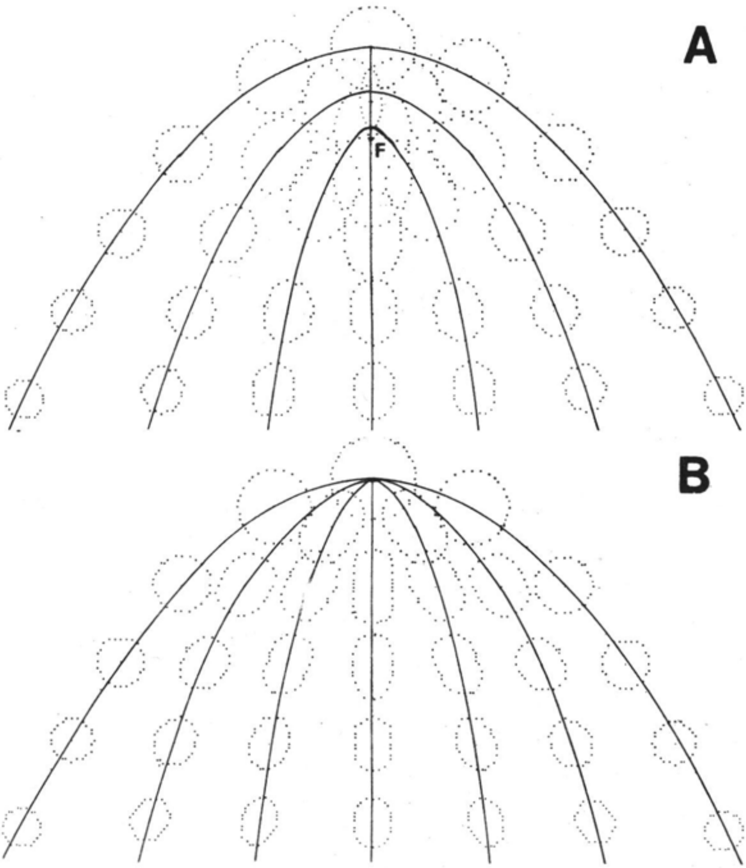

Fig. 2. Two patterns of variations of the linear growth rate, $RERG_l$ in the planes PL for domes A and B (see Fig. 1a). Values $RERG_l$ are displayed in the form of two-dimensional computer--made plots of $RERG_l$ around a number of points lying on the parabolas in the axial plane (for each plot the latitudinal direction is oriented anticlinally as the result of the rotation of PL plane by 90° around pericline). For a given point, the $RERG_l$ in different directions every 10-15°, were evaluated. The positions of points on the surface and on the axis in both domes A and B are the same. For all the points, plots of $RERG_l$ are drawn in the same scale

from the axis to the surface $RERG_{l(ant)}$ decreases in dome A, whereas it increases in dome B. In the latter there is the maximum of $RERG_{l(ant)}$ in the distal part of the dome. This maximum occurs on the surface around the vertex. In dome A in the segment of the dome axis between the focus and the tip, $RERG_{l(ant)}$ disappears, whereas in dome B in the same region there is $RERG_{l(ant)} > 0$.

Figure 4 shows variations in volumetric growth rates: $RERG_{vol}$ are smallest at the base level of domes, then they increase as the distance from the tip decreases. The maximum of $RERG_{vol}$ for dome A is in the distal part at the focus, and for dome B it is on the surface around the vertex.

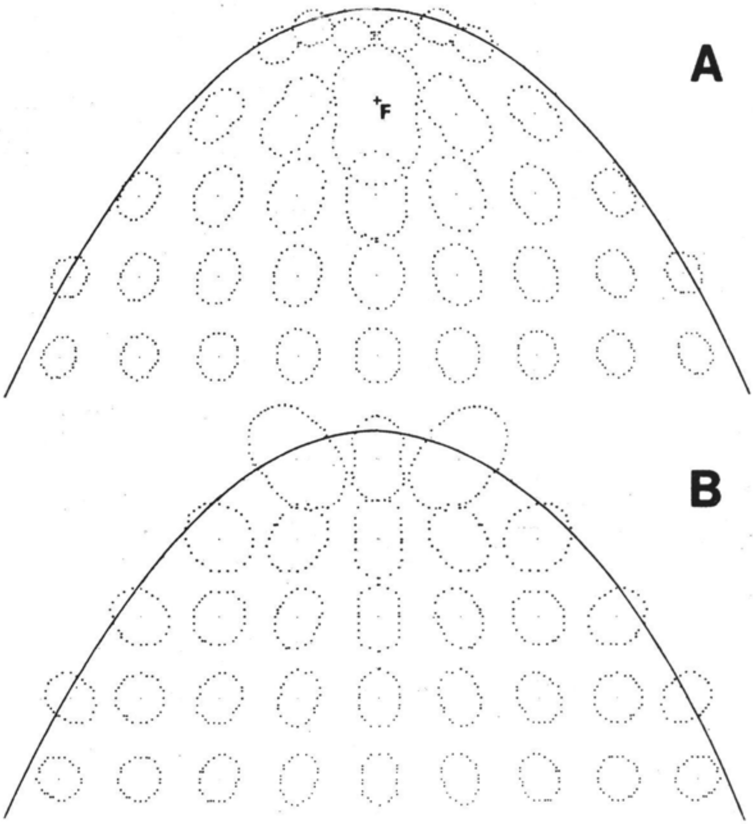

Fig. 3. Two patterns of variations of the linear growth rate, $RERG_l$, in the axial plane PA for domes A and B. Explanation as in Fig. 2, except that the points for which $RERG_l$ were evaluated lie in the nodes of the rectangular net. The positions of all corresponding points in domes A and B are the same

The area of the higher values of $RERG_{vol}$, from ranges 4 and 5 in the legend for Fig. 4, is relatively small when compared to the size of the whole dome. The mean $RERG_{vol}$ calculated for the whole dome is more or less similar for domes A and B.

DISCUSSION

The patterns of distribution of growth rates for domes A and B are different, as was expected, but it appears that the differences are not large. On one hand, PDG (principal directions of growth) are of great importance in connection with the growth variation pattern inside the dome,

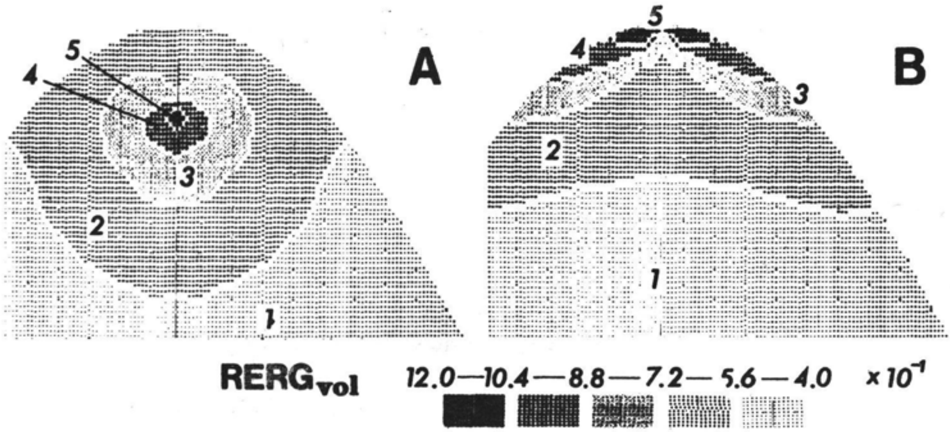

Fig. 4. Computer-made maps of volumetric growth rate, $RERG_{vol}$, for domes *A* and *B*. $RERG_{vol}$ for about 120 points within each dome were taken into interpolation. The full range of values of $RERG_{vol}$ was divided into 5 equal parts numbered from 1 to 5 and marked by different graphical symbols, shown in the legend. The program SYMAP for the Riad 32 computer was used to obtain the regions on the map

on the other hand, even considerable changes in the pattern of *PDG* trajectories do not matter much for the picture of growth of the dome as a whole. The maps presented in this paper indicate that the mean $RERG_{vol}$ calculated for the whole dome is similar in the cases *A* and *B*, moreover, they show that mean $RERG_{vol}$ calculated for the distal part only is also similar, althought in this part, the differences between *A* and *B* dome in the pattern of growth variations are the biggest.

In both domes, maxima of volumetric growth rates are present in their distal parts. Such maxima are characteristic not only for paraboloidal domes, they were also found in elliptic and hyperbolic domes in the case of an isotropic surface growth on the surfaces of domes (Hejnowicz et al. 1984b). All this cases with the local maximum seem to be unrealistic when confronted with known empirical facts. The results that have been obtained indicate that the maxima are related either to the type of coordinate system, or to the mode of the growth specified on the surface of the dome. They appear in a small region of the dome around the origin of the coordinate system. In this region, anticlinal distance between periclinal trajectories increases relatively quickly over a small area and it can give a local maximum.

For the description of growth in an organ in terms of the growth tensor, we use appropriate orthogonal coordinate systems. Appropriate — it means that the coordinate lines resemble a real pattern of *PDG* trajectories. Often the adjustment can be done only roughly, however, knowing how different the system is from a real pattern of trajectories, one can indicate in what direction the calculated rates should be corrected to approach the real rates.

Comparing both paraboloidal and convergent parabolic systems proves that the second one is more complicated mathematically, admittedly, a lot of difficulties may be liminated by computer technique.

From the two patterns of *PDG* used in this paper the first was proposed for a tunical dome and the second for a dome without the tunica. The tunica is defined as a surface layer of cells in the shoot apex without periclinal divisions (Hejnowicz 1980). Hence, there is no anticlinal growth within this layer. Such a feature in relation to the apical dome is well represented in the paraboloidal coordinate system. In this system the assumption: $RERG_{l(ant)} = 0$ for the segment of the dome axis between the focus and the tip, makes it possible that the segment mentioned does not increase during dome growth and, therefore, the tunica layer can be formed. The absence of the tunica can be interpreted as the decrease of the same segment to 0. Hence the proposition that a convariant parabolic system may be the natural system for the dome without a tunica growing steadily, has been made.

There is an interesting case of a potential tunica (Foster 1939) which occurs in conifers. There are some periclinal divisions in the surface layer of cells in the shoot apex, and so, in the apex there is no tunica in a strict sense. What coordinate system, paraboloidal or convergent parabolic, is more natural for this case? This question cannot be answered explicitly because both systems have some strong and some weak points. For the study of growth variations within the apices of spruce seedlings (Nakielski 1987), the convergent parabolic system was chosen.

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Przestrzenna zmienność wzrostu w wierzchołkach z różnymi wzorami głównych kierunków wzrostu

Streszczenie

Badano rozmieszczenie szybkości wzrostu w dwóch paraboloidalnych wierzchołkach *A* i *B*, identycznych z zewnątrz, ale różniących się wzorem trajektorii głównych kierunków wzrostu we wnętrzu. W wierzchołku *A* trajektorie peryklinalne w płaszczyźnie osiowej dane były przez współogniskowe parabole zbiegające się na odcinku osi wierzchołka (jak w wierzchołku z tuniką), zaś w wierzchołku *B* przez parabole zbiegające się w szczycie (co może odpowiadać wierzchołkowi bez tuniki). W obu przypadkach wzrost powierzchniowy na powierzchniach wierzchołków był izotropowy i identyczny w odpowiadających sobie punktach. Szybkości wzrostu określano za pomocą tensora wzrostu w dwóch naturalnych układach współrzędnych: paraboloidalnym (dla *A*) i parabolicznym konwergentnym (dla *B*). Wyniki przedstawiono w formie komputerowych map względnych szybkości wzrostu liniowego i objętościowego. Okazało się, że szybkości wzrostu wewnątrz wierzchołków *A* i *B* są podobne w strefach centralnej i peryferycznej, natomiast różnią się w strefie dystalnej. W tej ostatniej strefie szybkości wzrostu są największe, z tym że w wierzchołku *A* maksimum zlokalizowane jest w geometrycznym ognisku, zaś w wierzchołku *B* przy powierzchni w pobliżu szczytu. Najmniejsze szybkości wzrostu są przy podstawach obu wierzchołków.