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Modeling of spatial variations of growth within apical domes by means of the growth tensor. II. Growth specified on dome surface

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Abstract

Variations of the elemental relative rate of growth are modeled for parabolic, elliptic and hyperbolic domes of shoot apices by using the growth tensor in a suitable curvilinear coordinate system when the mode of area growth on the dome surface is known. Variations of growth rates within the domes are obtained in forms of computer-made maps for the following variants of growth on the dome surface: (1) constant meridional growth rate, (2) isotropic area growth, (3) anisotropy of area growth which becomes more intensive with increasing distance from the vertex. In variants 1 and 2 a maximum of volumetric growth rate appears in the center of the dome. Such a distribution of growth seems to be unrealistic. However, the corresponding growth tensors are interesting because they can be used in combination with other growth tensors to get the expected minimum volumetric growth rate in the dome center.

Key words; apical dome, growth tensor, growth variations

INTRODUCTION

In the previous paper of this series (Hejnowicz et al. 1984) we illustrated use of the growth tensor and of a natural coordinate system in modeling spatial variations of growth within shoot apical domes of different shapes. For such modeling it is necessary to have information about the variation of growth along one displacement line. In the previous paper this information concerned the axis of the done, and was in the form of an assumed pattern of the elemental relative rate of growth in length, $RERG_l$, along the axis.

In this paper we illustrate modeling based on knowledge either of the meridional $RERG_l$ or of the anisotropy of surface growth along one displacement line on the dome surface. The questions we pose are: what is the distribution of growth rates within the dome if the meridional $REGR_l$ is constant on the surface, and what is the distribution if there is isotropy of the surface growth (the meridional $RERG_l$ is the same as the latitudinal $RERG_l$) or a certain type of directionality of growth on the surface?

METHODS OF CALCULATIONS

The methods are the same as in the previous paper (Hejnowicz et al. 1984), except that the displacement velocity vector, V, is given on the dome surface instead of on the dome axis. As in the previous paper, we consider three shapes of apical domes: (A) parabolic, (B) elliptic, and (C) hyperbolic, assuming that the natural coordinate systems for these domes are: paraboloidal (u, v, φ) for A, and prolate spheroidal (ξ, η, φ) for B and C. To have the general forms of the growth tensor for such domes at hand we are repeating the tensors from the previous paper (Fig. 1).

RESULTS

A. PARABOLIC DOME

Variant A$_3$*: $RERG_{l(meridional)}$ is constant on the dome surface on which $v = v_s$.

The condition specifying this variant is $RERG_{l(mer)} = \frac{1}{\sqrt{u^2+v_s^2}} \frac{\partial V_u}{\partial u} =$ $= \text{const} = k$ on the surface $v = v_s$.
By integrating we obtain:

$$V_u = \frac{1}{2} k \left(u \sqrt{u^2+v_s^2} + v_s^2 \ln \left|u + \sqrt{u^2+v_s^2}\right| + c\right)$$

on the surface. Since at the vertex ($u = 0$) V_u must be null, we use this condition to determine the integration constant C, and find that $C = -v_s^2 \ln v_s$. We have thus on the surface:

$$V_{u(v=v_s)} = \frac{k}{2}\left(u \sqrt{u^2+v_s^2} + v_s^2 \ln \left| \frac{u+\sqrt{u^2+v_s^2}}{v_s} \right|\right)$$

*) The numbering of the variants is in continuation with those of the previous paper.

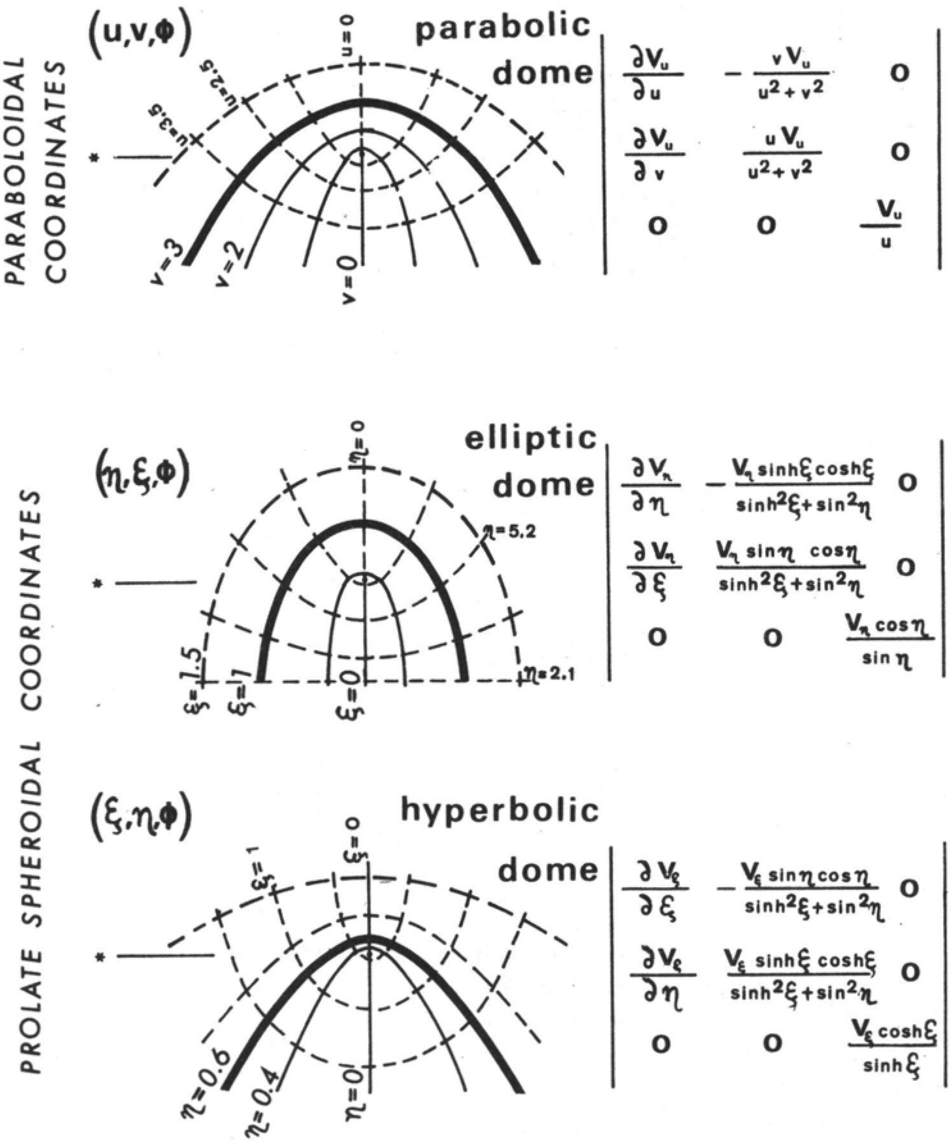

Fig. 1. Orthogonal curvilinear coordinate systems, aplical domes and corresponding growth tensors. The upper left diagonal element of the tensor represents the $RERG_1$ in periclinal direction (meridional on dome surface). In the series of coordinate variables, e.g. u, v, Φ, the one corresponding to the periclinal curves is given first, then follows the variable corresponding to the anticlinal coordinate (curve) and the last corresponds to the latitudinal coordinate. The surface of the dome is indicated by the heavy curve. The geometric focus of a dome (focal point of the parabolas, ellipses or hyperbolas) is on the level indicated by the asterick. The growth tensor should be multiplied by a corresponding scale factor i.e. $\frac{1}{\sqrt{u^2+v^2}}$ for the parabolic dome and $\frac{1}{\sqrt{\sinh^2\xi+\sin^2\eta}}$ for elliptic and hyperbolic domes

and in the whole dome

$$V_u = \frac{k}{2} \frac{\sqrt{u^2+v^2}}{\sqrt{u^2+v_s^2}} \left(u\sqrt{u^2+v_s^2} + v_s^2 \ln \left| \frac{u+\sqrt{u^2+v_s^2}}{v_s} \right| \right).$$

Introducing this into the general form of the growth tensor we obtain the specific growth tensor for the variant being considered:

$$\frac{k}{2(u^2+v^2)\sqrt{u^2+v_s^2}} \left| \begin{matrix} (2u^2+v^2)\sqrt{u^2+v_s^2} + \dfrac{v_s u (v^2-v_s^2) LN}{u^2+v_s^2} + \dfrac{v_s^2 (u^2+v^2)}{\sqrt{u^2+v_s^2}} & -v\left(u\sqrt{u^2+v_s^2}+v_s^2 LN\right) & 0 \\ v\left(u\sqrt{u^2+v_s^2}+v_s^2 LN\right) & u\sqrt{u^2+v_s^2}+v_s^2 LN & 0 \\ 0 & 0 & \dfrac{(u^2+v^2)\left(u\sqrt{u^2+v_s^2}+v_s^2 LN\right)}{u} \end{matrix} \right|$$

$$\text{where } LN = \ln \left| \frac{u+\sqrt{u^2+v_s^2}}{v_s} \right|.$$

From inspection of this growth tensor it follows that: (1) the ratio of $RERG_{l(mer)}$ to $RERG_{l(lat)}$, i.e. the ratio of the 1 st diagonal term of the 3rd diagonal term, is 1 at the vertex ($u \to 0$) as it should be though at first sight such a result is not obvious; and that (2) $RERG_{l(lat)}$ is the same along a v-line. The maps provided by the computer for $RERG_l$ in different directions are not shown here. They indicate that there is a slow decrease of the latitudinal $RERG_l$ with increasing distance from the vertex, and a rather pronounced increase of anticlinal $RERG_l$ with this distance in the peripheral part of the dome. Also an increase of this rate with distance from the surface is indicated, so that the maximal $RERG_l$ in the anticlinal direction is at the geometric focus of the dome.

The distribution of the volumetric growth rate is shown on Fig. 2 (A_3). There is maximum of this growth rate in the central part of the dome (quite far from the focus), however the variation is not especially pronounced because the minimal $RERG_{vol}$, which occurs at the vertex, amounts to 71% of the maximum rate.

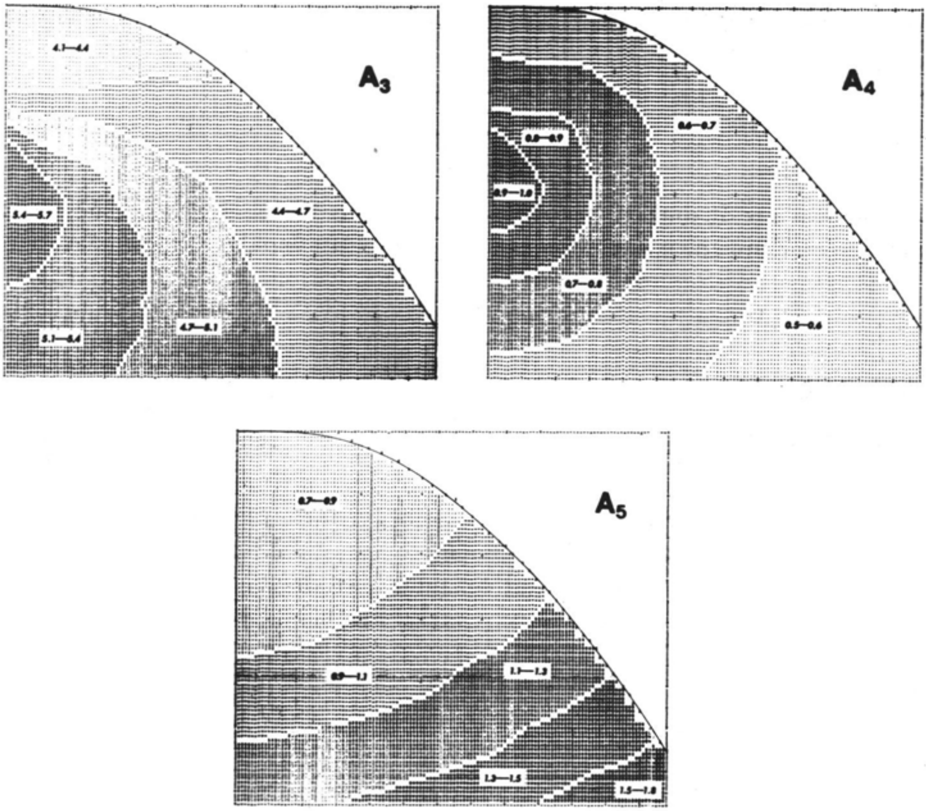

Fig. 2. Computer maps of volumetric growth rate ($RERG_{vol}$) for 3 variants of parabolic dome. Each map represents half of a longitudinal axial section through the dome. The full range of growth rate variation was divided by computer in 5 equal parts and the position of each part is marked by one symbol on the map. The growth rate in each part is indicated by inserted numbers. The constant k (or c) for which the map was computed, is taken as unit. It should be observed that this constant does not affect the proportions between the rates in different parts of the dome, though it affects the absolute values of the rates. The map for the variant A_5 was computed on the assumption that $a = 0.07$. This constant affects the proportions between growth rates

Variant A_4: Growth is isotropic on the surface of the dome i.e. $RERG_{l(mer)} = RERG_{l(lat)}$ when $v = v_s$. Thus we have:

$$\frac{1}{\sqrt{u^2+v_s^2}} \; \frac{\partial V_u}{\partial u} = \frac{V_u}{u\sqrt{u^2+v_s^2}}.$$

Integration gives $V_u = cu$ on the dome surface; c is the integration constant.

By means of scaling factors we obtain the vector point function for the whole dome:

$$V_u = \frac{c\sqrt{u^2+v^2}}{\sqrt{u^2+v_s^2}}\, u.$$

On introducing V_u and its partial derivative into the general form of growth tensor we obtain the specific form of growth tensor for the considered variant:

$$\frac{c}{(u^2+v^2)\sqrt{u^2+v_s^2}} \begin{vmatrix} \frac{u^4+2u^2 v_s^2+v^2 v_s^2}{u^2+v_s^2} & -uv & 0 \\ uv & u^2 & 0 \\ 0 & 0 & u^2+v^2 \end{vmatrix}$$

The maps of the distribution of linear growth rates (not shown here) indicate that the absolute values of $RERG_{l(mer)}$ and $RERG_{l(lat)}$ decrease with increasing distance from the vertex on the dome surface. Beyond the surface, the $RERG_{l(mer)}$ is equal to $RERG_{l(lat)}$ at points lying on the axis above the focus. At any other point within the dome the tangential growth is not isotropic; the meridional rate is higher than that in the latitudinal direction. The highest ratio is 2 when approaching the focus from the bottom. $RERG_l$ in the direction of v-lines increases with distance from the vertex, however, its contribution is relatively small. Accordingly, there is a maximum of volumetric growth rate in the center of the dome but below the focus (Fig. 2, A_4). The rate of volumetric growth at the vertex amounts to 50% of the maximal rate.

Variant A_5: On the dome surface there is increasing anisotropy of area growth with increasing distance from the vertex.

We assumed the following specification of this variant: $RERG_{l(mer)} = RERG_{l(lat)}\,(1+au^2)$, where $a > 0$ and is constant. This specification is for the dome surface i.e. $v = v_s$. From the growth tensor we have thus $\frac{\partial V_u}{\partial u} = \frac{1}{u}(1+au^2)\, V_u$. Integration gives the displacement velocity on the surface:

$$V_u = cue^{\frac{1}{2}au^2},$$

where c is integration constant. For every point in the dome we have:

$$V_u = \frac{c\sqrt{u^2+v^2}}{\sqrt{u^2+v_s^2}}\, ue^{\frac{1}{2}au^2}$$

and therefore the specific form of growth tensor for this variant is:

$$ce^{\frac{1}{2}au^2}\begin{vmatrix} 1+au^2-\dfrac{u^2(v^2-v_s^2)}{(u^2+v^2)(u^2+v_s^2)} & -\dfrac{uv}{u^2+v^2} & 0 \\ \dfrac{uv}{u^2+v^2} & \dfrac{u^2}{u^2+v^2} & 0 \\ 0 & 0 & 1 \end{vmatrix}$$

Computer data show that this variant gives minima of all growth rates in the distal region of the dome. Data for the volumetric growth rate is shown in Fig. 2, A_5. The fastest linear growth rate is in the direction of u-lines everywhere.

B. ELLIPTIC DOME

Variant B_3: $RERG_{l(mer)}$ is constant on the dome surface.

We have thus:

$$\frac{1}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \frac{\partial V_\eta}{\partial \eta} = k$$

on the dome surface, where $\xi = \xi_s$. Integration of this equation leads to elliptic integral, thus the components of the growth tensor cannot be expressed by means of elementary functions. For this reason we will not further consider this variant. However, we will modify condition specifying the $RERG_{l(mer)}$ on the surface in the following way:

$$\frac{1}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \frac{\partial V_\eta}{\partial \eta} = \frac{k}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}},$$

which means that the $RERG_{l(mer)}$ on dome surface is not constant but decreases slightly with distance from the vertex. This decrease is from $k/1.18$ at the vertex to $k/1.54$ at the dome basis (for $\eta = 1.48$) when the dome surface is specified by $\xi_s = 1$, or in an even narrower range when is higher than 1. This variant is numbered as B_{3a}.

In the variant B_{3a} we have $\dfrac{\partial V_\eta}{\partial \eta} = k$. Integration gives $V_\eta = k\eta + c$ on the surface. For $\eta = 0$ V_η must be null thus $C = 0$. Upon introducing the scalling factor, we obtain a general expression for V_η for all points in the dome:

$$V_\eta = k \frac{\sqrt{\sinh^2 \xi + \sin^2 \eta}}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \eta.$$

The specific form of the growth tensor for this variant is thus:

$$\frac{k}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \times$$

$$\begin{vmatrix} 1 + \frac{\eta \sin \eta \cos \eta (\sinh^2 \xi_s - \sinh^2 \xi)}{(\sinh^2 \xi + \sin^2 \eta)(\sinh^2 \xi_s + \sin^2 \eta)} & -\frac{\eta \cosh \xi \sinh \xi}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ \frac{\eta \cosh \xi \sinh \xi}{\sinh^2 \xi + \sin^2 \eta} & \frac{\eta \sin \eta \cos \eta}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ 0 & 0 & \eta \operatorname{ctg} \eta \end{vmatrix}$$

Computer data show that linear growth rates in all directions decrease with increasing η and ξ. The least variable is the $RERG_{l(mer)}$ on the dome surface, the highest rates are at the focus. Correspondingly the volumetric growth rate has a very sharp maximum at the focus, (Fig. 3, B_{3a}). It should be noted that the computer, when preparing the map B_{3a}, divided the range of $RERG_{vol}$ variation into 5 equal parts, thus in the case of a sharp maximum the largest region of the dome is within the part characterized by the lowest rate. Within this region there is quite a high variation of the rate; the highest (1.8) is in the distal zone of the dome, the lowest (0.65) is at its basis.

Variant B_4: Area growth is isotropic on the surface of the dome.

The condition specifying this variant is:

$$\frac{1}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \frac{\partial V_\eta}{\partial \eta} = \frac{\operatorname{ctg} \eta V_\eta}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}}$$

on dome surface, where $\xi = \xi_s$. Integration gives $\dot{V}_\eta = c \sin \eta$ on the surface. Thus the displacement velocity for the whole dome is:

$$V_\eta = \frac{c\sqrt{\sinh^2 \xi + \sin^2 \eta}}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \sin \eta.$$

The specific form of the growth tensor for this variant is:

$$\frac{c \cos \eta}{\sqrt{\sinh^2 \xi_s + \sin^2 \eta}} \times$$

$$\begin{vmatrix} 1 + \frac{\sin^2 \eta (\sinh^2 \xi_s - \sinh^2 \xi)}{(\sinh^2 \xi + \sin^2 \eta)(\sinh^2 \xi_s + \sin^2 \eta)} & -\frac{\sinh \xi \cosh \xi \operatorname{tg} \eta}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ \frac{\sinh \xi \cosh \xi \operatorname{tg} \eta}{\sinh^2 \xi + \sin^2 \eta} & \frac{\sin^2 \eta}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ 0 & 0 & 1 \end{vmatrix}$$

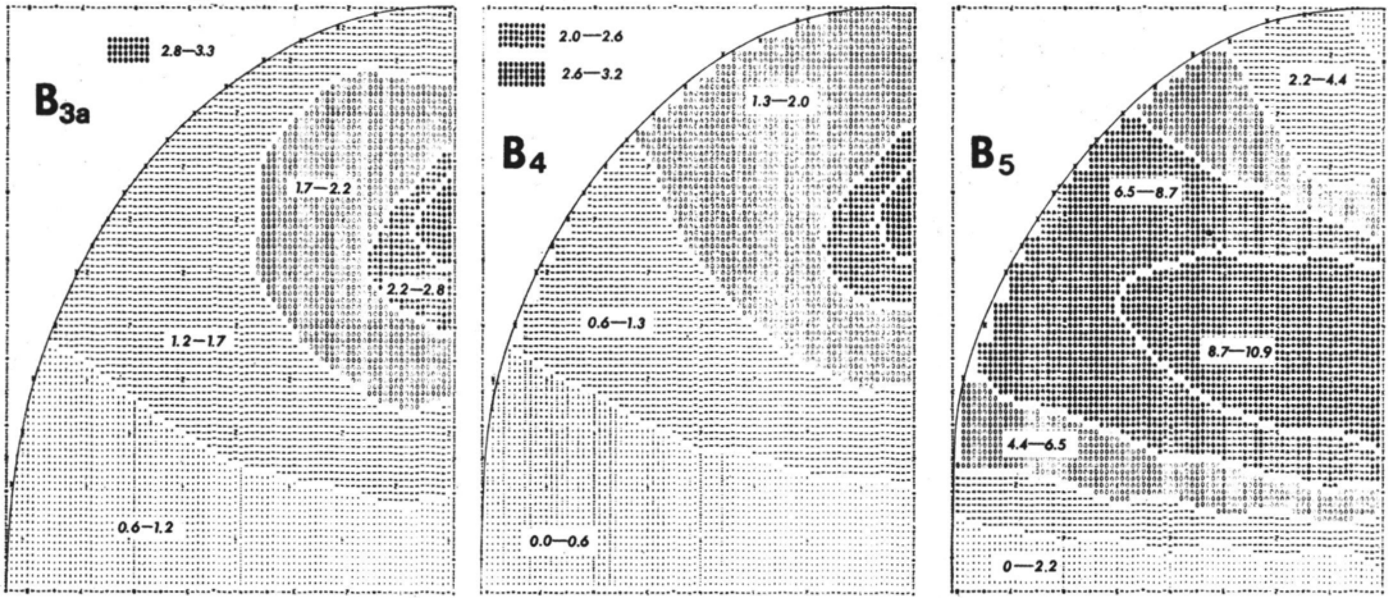

Fig. 3. As Fig. 2 but for elliptic dome, except that the map B_5 is for the constant $a = 1.99$

Computer data show that the variation of growth rates in the B_4 are similar to that for the previous variant, however, the maxima of growth rates in the dome center (at the focus) are not as pronounced as previously. Fig. 3, B_4 illustrates the distribution of $RERG_{vol}$.

Variant B_5: Anisotropy of growth in area on dome surface increases with distance from the vertex.

We assumed the following condition specifying this variant: $RERG_{l(mer)} = RERG_{l(lat)}(1+a\sin\eta)$, where $a>0$. Introducing the $RERG_l$ from the general form of growth tensor we obtain:

$$\frac{1}{\sqrt{\sinh^2\xi_s+\sin^2\eta}}\,\frac{\partial V_\eta}{\partial\eta}=\frac{\operatorname{ctg}\eta}{\sqrt{\sinh^2\xi_s+\sin^2\eta}}(1+a\sin\eta)\,V_\eta.$$

Upon integration $V_\eta = c\sin\eta e^{a\sin\eta}$, where c is integration constant. The last equation is valid for the dome surface where $\xi=\xi_s$. Introducing scaling factor we obtain the displacement velocity for every point in the dome:

$$V_\eta=\frac{c\sqrt{\sinh^2\xi+\sin^2\eta}}{\sqrt{\sinh^2\xi_s+\sin^2\eta}}\sin\eta e^{a\sin\eta}.$$

The specific form of the growth tensor is thus:

$$\frac{c\cos\eta e^{a\sin\eta}}{\sqrt{\sinh^2\xi_s+\sin^2\eta}}\times$$

$$\times\begin{vmatrix} 1+a\sin\eta+\dfrac{\sin^2\eta(\sinh^2\xi_s-\sinh^2\xi)}{(\sinh^2\xi+\sin^2\eta)(\sinh^2\xi_s+\sin^2\eta)} & -\dfrac{\sinh\xi\cosh\xi\operatorname{tg}\eta}{\sinh^2\xi+\sin^2\eta} & 0\\ \dfrac{\sinh\xi\cosh\xi\operatorname{tg}\eta}{\sinh^2\xi+\sin^2\eta} & \dfrac{\sin^2\eta}{\sinh^2\xi+\sin^2\eta} & 0\\ 0 & 0 & 1\end{vmatrix}$$

The maps showing $RERG_l$ in different directions indicate a very interesting distribution of growth rates. The growth rate in every direction at points along η-line increases first with distance from the vertex (increasing η), attains a maximum and further decreasses. The maximum of the $RERG_l$ tangent to η-line is more pronounced in the axial region of the dome (i.e. for lower ξ-values) and is located clearly below the focus. Similarly maxima of other principal growth rates in the axial region of the dome are located below the focus. Correspondingly, there is a maximum of volumetric growth rate in the central part of the dome below the focus (Fig. 3, B_5). This is a wide maximum, and relatively very high in comparison to growth rates at the vertex and at dome base.

C. HYPERBOLIC DOME

Variant C_3: $RERG_{l(mer)}$ is constant on the dome surface where $\eta = \eta_s$. The equation specifying this variant is:

$$\frac{1}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \frac{\partial V_\xi}{\partial \xi} = k.$$

As in the case of elliptic dome, integration of this equation does not lead to V_ξ as an elementary function. Instead of this variant we thus consider the modified variant C_{3a} defined in the following way:

$$RERG_{l(mer)} = \frac{k}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}}$$

on the surface $\eta = \eta_s$. We obtain:

$$\frac{1}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \frac{\partial V_\xi}{\partial \xi} = \frac{k}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}}.$$

Upon integration $V_\xi = k\xi + c$. For $\xi = 0$ V_ξ must be null, thus $c = 0$. Hence:

$$V_\xi = \frac{k\sqrt{\sinh^2 \xi + \sin^2 \eta}}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \xi$$

for every point in the dome.

The specific form of the growth tensor for this variant is:

$$\frac{k}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \times$$

$$\times \begin{vmatrix} 1 + \xi \sinh \xi \cosh \xi \left(\dfrac{\sin^2 \eta_s - \sin^2 \eta}{\sinh^2 \xi + \sin^2 \eta} \right) & -\dfrac{\xi \sin \eta \cos \eta}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ \dfrac{\xi \sin \eta \cos \eta}{\sinh^2 \xi + \sin^2 \eta} & \dfrac{\xi \cosh \xi \sinh \xi}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ 0 & 0 & \xi \operatorname{ctgh} \xi \end{vmatrix}$$

The computer prepared maps of $RERG_l$ in different directions indicate that in this variant each principal growth rate has a low maximum at the focus. Correspondingly, the distribution of the volumetric growth rate is such as illustrated by the Fig. 4, C_{3a}.

Variant C_4: Area growth is isotropic on the dome surface, i.e. $RERG_{l(mer)} = RERG_{l(lat)}$.

The equation specifying this variant is for $\eta = \eta_s$:

$$\frac{1}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \frac{\partial V_\xi}{\partial \xi} = \frac{V_\xi \operatorname{ctg} \xi}{\sqrt{\sinh^2 \xi + \sin^2 \eta}}.$$

Upon integration $V_\xi = c \sinh \xi$ on the dome surface and

$$V_\xi = \frac{c \sqrt{\sinh^2 \xi + \sin^2 \eta}}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \sinh \xi$$

in every point of the dome.

The specific form of the growth tensor is:

$$\frac{c \cosh \xi}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \begin{vmatrix} 1 + \sinh^2 \xi \left(\frac{\sin^2 \eta_s - \sin^2 \eta}{\sinh^2 \xi + \sin^2 \eta} \right) & -\frac{\sin \eta \cos \eta \operatorname{tgh} \xi}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ \frac{\sin \eta \cos \eta \operatorname{tgh} \xi}{\sinh^2 \xi + \sin^2 \eta} & \frac{\sinh^2 \xi}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ 0 & 0 & 1 \end{vmatrix}$$

The computer data show that there is only little variation of $RERG_l$ in different directions in the dome. The distribution of volumetric growth rate is shown in Fig. 4, C_4.

Variant C_5: Anisotropy of area growth on the dome surface increases with increasing distance from the vertex.

We assumed the following specification of this variant: $RERG_{(mer)} = RERG_{(lat)} (1 + a \sinh \xi)$ i.e.:

$$\frac{1}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \frac{\partial V_\xi}{\partial \xi} = \frac{(1 + a \sinh \xi) V_\xi}{\sqrt{\sinh^2 \xi + \sin^2 \eta}}.$$

Upon integration $V_\xi = c e^{a \sinh \xi} \sinh \xi$ on the dome surface $\eta = \eta_s$. Introducing the scaling factor we obtain:

$$V_\xi = \frac{c \sqrt{\sinh^2 \xi + \sin^2 \eta}}{\sqrt{\sinh^2 \xi + \sin^2 \eta_s}} \sinh \xi e^{a \sinh \xi}$$

for the whole dome. The specific form of the growth tensor is:

$$\frac{c \cosh \xi e^{a \sinh \xi}}{\sqrt{\sinh^2 \xi + \sin^2 \eta}} \begin{vmatrix} 1 + \sinh^2 \xi \left(a + \frac{\sin^2 \eta_s - \sin^2 \eta}{\sinh^2 \xi + \sin^2 \eta} \right) & -\frac{\sin \eta \cos \eta \operatorname{tgh} \xi}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ \frac{\sin \eta \cos \eta \operatorname{tgh} \xi}{\sinh^2 \xi + \sin^2 \eta} & \frac{\sinh^2 \xi}{\sinh^2 \xi + \sin^2 \eta} & 0 \\ 0 & 0 & 1 \end{vmatrix}$$

Computer data show that each principal growth rate increases with ξ. The $RERG_l$ tangent to the ξ-line increases the fastest. The map for the

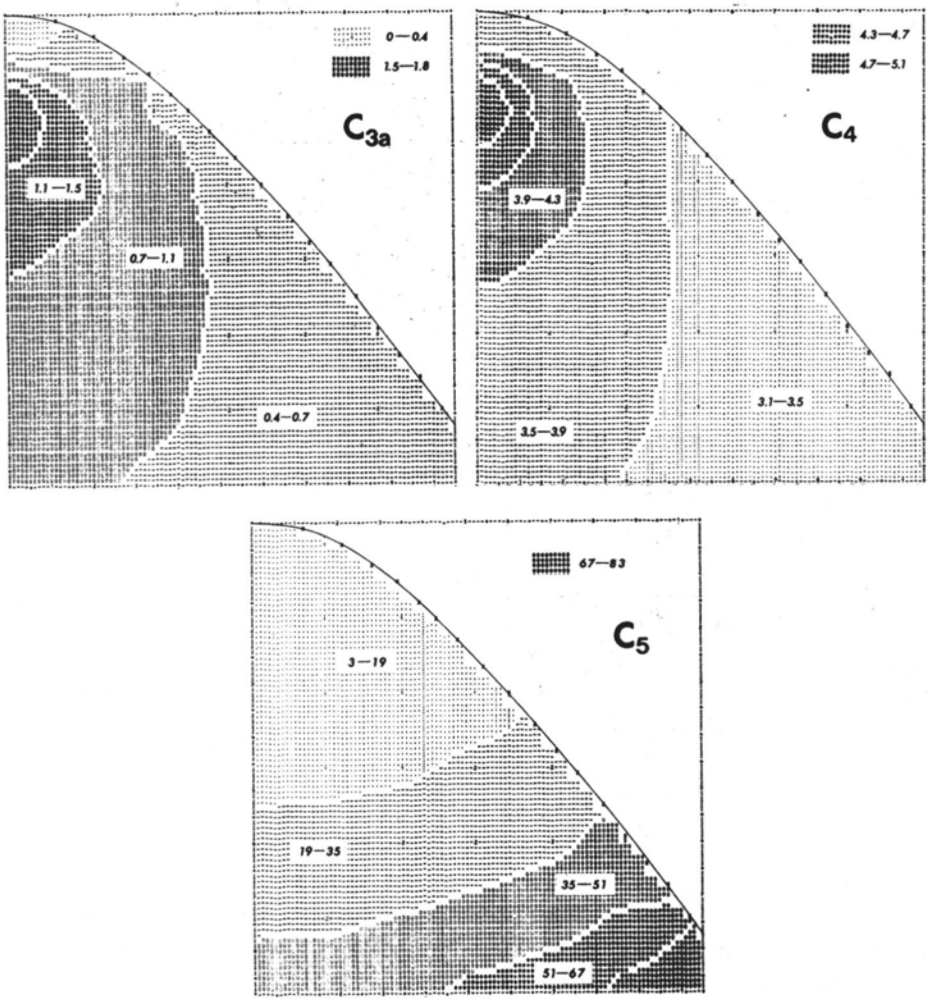

Fig. 4. As Fig. 2 but for hyperbolic dome, except that the map C_5 is for the constant $a=0.07$

volumetric growth rate is shown in Fig. 4, C_5. It can be seen that the variant under consideration gives similar variation of the volumetric growth rate as the corresponding variant A_5 for a parabolic dome.

DISCUSSION

Some patterns of growth rate distribution considered in this paper show a very interesting feature: the appearance of a maximum of volumetric growth rate in the central part of the dome. Is such a central maximum of the growth rate realistic? Certainly not. Volumetric growth rate in case of constant cell size is reflected in the proportional relative rate of cell division, which in turn is reflected in the mitotic index. A maximum of the mitotic rate in the central part of apical dome has not been hitherto described for a vegetative phase of shoot development, though it might be possible in the dome during transformation to the generative phase (Lyndon 1976). A possibility exists that the central maximum of volumetric growth rate occurs but does not cause a maximum of mitoses in this part, because the higher volumetric growth rate is compensated for by the increasing cell volume as they move through the central region of the dome during its growth. Indeed, in vegetative apices the cells are often larger in the central part of the dome (central mother cells). To determine whether such a possibility is realistic, we need calculations based on the relationship between growth rates, cell division rates, and cell pattern. Such calculation is now possible (Hejnowicz and Romberger 1984) and preliminary analysis leads to the conclusion that a deep minimum of mitotic frequency cannot be explained by the occurrence of slightly larger cells in the central part of a dome if the volumetric growth rate in the dome is as uniform as possible. Thus it is even more unrealistic for a maximum of the growth rate in the center of the dome. It appears that variants of growth specifying central maximum of volumetric growth rate are not realistic; on the contrary variants with a central minimum of the rate would be realistic. We have not yet found such a variant.

The variants considered in previous papers (Hejnowicz and Nakielski 1979, Hejnowicz et al. 1984), as well as the variants A_5 and C_5 in this paper, have a minimum of volumetric growth rate in the distal part of the dome but not in its center. However, the variants considered previously and those now under consideration cover such a wide range of growth variations that they offer possibilities of getting a minimum in the dome center by a suitable combinations of them. Observe first that the growth tensor is an additive quantity. We may, therefore, add simple growth tensors to get a more complex one. Additivity of tensors is a mathematical statement, additivity of growth tensors can be easily illustrated. Assume that we have different specifications of $RERG_{l(mer)}$ on the surface of a parabolic dome, $RERG_{l(mer)} = f(u, v_s)$ where v_s represents the dome surface, and the specifications are in form of different functions $f_1(u, v_s)$, $f_2(u, v_s) \ldots f_n(u, v_s)$. We have:

$$\frac{1}{\sqrt{u^2+v^2}} \frac{\partial V_u}{\partial u} = f(u, v_s)$$

thus $V_u = \int \sqrt{u^2+v^2}\, f(u, v_s)\, du$ on the surface. If we denote the integral on the right side by $F(u, v_s)$ the displacement velocity in the whole dome is:

$$V_u = \frac{\sqrt{u^2+v^2}}{\sqrt{u^2+v_s^2}}\, F(u, v_s) \equiv G(u, v)$$

we have thus $(V_u)_i = G_i$. G_i, of course, is a function of u and v, v_s enters it only as a constant parameter, the same for different i.

The growth tensors for different variants are of the form:

$$\frac{1}{\sqrt{u^2+v^2}}\begin{vmatrix} \frac{\partial G_i}{\partial u} & -\frac{vG_i}{u^2+v^2} & 0 \\ \frac{\partial G_i}{\partial v} & \frac{uG_i}{u^2+v^2} & 0 \\ 0 & 0 & \frac{G_i}{u} \end{vmatrix}$$

Let us now assume that we can specify the meridional growth rate by a linear combination of the functions f_i, i.e. $RERG_{l(mer)} = k_1 f_1(u, v_s) + k_2 f_2(u, v_s) + \ldots k_n f_n(u, v_s)$ where k_n represents coefficients of the combination. Some of the coefficients may be negative. We have:

$$V_u = \int \sqrt{u^2+v^2} \sum_i k_i f_i(u, v_s)\, du = k_1 F_1(u, v_s) + k_2 F_2(u, v_s) + \ldots k_n F_n(u, v_s)$$

on the surface and

$$V_u = \frac{\sqrt{u^2+v^2}}{\sqrt{u^2+v_s^2}} \sum_i k_i F_i = k_1 G_1 + k_2 G_2 + \ldots k_n G_n$$

in the whole dome.

The growth tensor then has the form:

$$\frac{1}{\sqrt{u^2+v^2}}\begin{vmatrix} k_1\frac{\partial G_1}{\partial u}+\ldots+k_n\frac{\partial G_n}{\partial u} & -\frac{v(k_1 G_1+\ldots+k_n G_n)}{u^2+v^2} & 0 \\ k_1\frac{\partial G_1}{\partial v}+\ldots+k_n\frac{\partial G_n}{\partial v} & \frac{u(k_1 G_1+\ldots+k_n G_n)}{u^2+v^2} & 0 \\ 0 & 0 & \frac{k_1 G_1+\ldots+k_n G_n}{u} \end{vmatrix}$$

which means that it is the sum of the growth tensors corresponding to separate functions $f_i(u, v_s)$ taken in proportion to their coefficients. As mentioned the coefficients may be negative, however the limitation is now obvious: the resulting tensor must have all diagonal components which are either null or positive everywhere in the apex (for all possible u and v), because we assume that the cells of the dome can either grow or not grow but cannot shrink.

How to use the different variants hitherto described, among them the unrealistic ones with maximum of $RERG_{vol}$ in the dome center, in order to obtain a new variant with a minimum of the volumetric growth rate at the center? Let us assume that we have two functions $V_u^1 = f_1(u, v_s)$ and

$V_u^2 = f_2(u, v_s)$ of which the first, f_1, gives nearly uniform volumetric growth rate and the second, f_2, gives a maximum of the rate in the dome center. We can obtain a new function, $V_u = f(u, v_s)$ which is the difference between the two functions, i.e. $V_u = f(u, v_s) = k_1 f_1(u, v_s) - k_2 f_2(u, v_s)$, where k_1 and k_2 are coefficients. Obviously, by proper adjustment of the coefficients the growth rate distribution obtained from V_u will have a minimum of volumetric growth rate in the center and the requirement of no shrinkage will be fullfilled. Modeling based on combinations of the variants of growth will be illustrated in the next paper.

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Modelowanie przestrzennej zmienności wzrostu w apikalnych częściach wierzchołków pędu za pomocą tensora wzrostu. II. Gdy znany jest sposób wzrostu na powierzchni wierzchołka

Streszczenie

W pracy pokazano jak można przy pomocy tensora wzrostu i układu współrzędnych naturalnych wyznaczać względne elementarne szybkości wzrostu wewnątrz wierzchołka pędu gdy znany jest sposób wzrostu na powierzchni wierzchołka. Wyznaczono rozmieszczenie szybkości wzrostu w trzech typach wierzchołków — parabolicznym, eliptycznym i hiperbolicznym — przyjmując dla każdego z nich następujące warianty wzrostu na powierzchni wierzchołka: (1) stałość względnej elementarnej szybkości wzrostu południkowego, (1) izotropia wzrostu powierzchniowego tzn. równość szybkości wzrostu południkowego i równoleżnikowego w każdym punkcie powierzchni, (3) anizotropia wzrostu powierzchniowego nasilająca się z odległością od szczytu. Komputerowe mapy wykazują maksimum szybkości wzrostu objętościowego w centrum wierzchołka dla dwóch pierwszych wariantów, oraz minimum szybkości wzrostu objętościowego w części dystalnej dla trzeciego wariantu. Warianty z centralnym maksimum szybkości wzrostu wydają się być nierealistyczne, bowiem ekstremum szybkości wzrostu, jeżeli takowe występuje w centrum realnego wierzchołka, jest typu minimum a nie maksimum. Są one jednak użyteczne, bowiem odpowiadające im tensory wzrostu w liniowej kombinacji z innymi tensorami wzrostu umożliwiają otrzymanie minimum szybkości wzrostu w centralnej części wierzchołka.