

Geometry of shoot apical dome and distribution of growth rates

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Abstract

The distribution of the relative elementary rate of growth (RERG) in apical domes of various shapes and patterns of displacement lines can be analytically examined. The geometry of these domes may be described by parabolas of n -th order, the variant of the distribution of linear growth rate should be established along any displacement line (e.g. along the axis) and then the RERG can be studied as the function depending on the position coordinates and the parameter n . Such investigations of several apical domes of various shapes have been performed. The results confirm the occurrence of the minimum of relative, elementary growth rate (in volume) in the subapical region of the dome independently of the type of geometry (n parabola order).

INTRODUCTION

In earlier papers (Hejnowicz and Nakielski 1979, Hejnowicz 1982) a model of a growing shoot apical dome has been suggested in which the field of displacement velocity of the elements of the wall network is described by the formula:

$$\underline{V}(r, z) = \frac{1}{\mu(r, z)} \underline{\text{grad}} G(r, z), \quad (1)$$

where $\mu(r, z)$ and $G(r, z)$ are scalar position functions. The field $\mu(r, z)$ depends on the dome geometry, consists of: the shape of the apical dome, the pattern of the displacement lines and of the increment lines, the outer displacement line constituting the surface of the apical dome. The $G(r, z)$ field depends on the geometry and distribution of the rate of linear growth along one arbitrarily chosen displacement line. To the given distribution of

the rate of linear growth along this displacement line corresponds the variant of growth of the whole apical dome, determined by this distribution and dependent only on the geometry. Distribution of the rate of linear growth along one displacement line generates thus, the growth organisation of the whole organ. This distribution will be further referred to as „promoter” of growth. The field $V(r, z)$ is shaped, therefore, by two independent factors — geometry of the organ and growth promoter.

The apical dome was so far the object of studies (Hejnowicz and Nakielski 1979). Its geometry (shape and displacement lines pattern) were determined by a family of parabolas, whereas the growth promoter was deduced from the knowledge of the rate of growth in different regions of the apical dome. It was found that an interesting depression of the relative elementary growth rate in volume ($RERG_{vol}$) occurs at the apex in the core of the subapical region. Such a picture of growth corresponds to the situations observed in the apices of seed plants. The question arises whether a similar depression is present in apices with a different geometry. This will be dealt with in the present paper. Its chief aim, however, is to introduce a variety of geometries.

It seems that a wide class of geometry types may be obtained by using power functions $z = a_i r^n$, where a_i and n are constant positive parameters. For $r \geq 0$, with established n and changing a_i they describe a family of curves starting from the origin of the coordinates system. It is assumed that this point is the tip of the dome and the curves are the pathways along which the points of the dome are displaced during growth. With their mirror image in relation to the z axis they represent the displacement line pattern in the medial plane of the longitudinal section through the shoot apex. According to the conclusions from earlier papers (Hejnowicz and Nakielski 1979, Hejnowicz 1982) it is assumed that the pattern of increment lines in the same plane forms trajectories orthogonal to the displacement lines. The equations of the increment lines are thus: $\frac{1}{2}r^2 + \frac{1}{2}nz^2 = \text{const}$. This results from the condition $f' = -\frac{1}{g'}$, which must be fulfilled by the derivatives of the two arbitrary functions f and g the graphs of which intersect at a right angle.

The apical dome is a figure of revolution open at the level at which leaf primordia emerge, formed by the revolution of the outermost displacement line around axis z . A cylindrical coordinate system r, φ, z is used in which, according to the premisses adopted, the displacement lines do not depend on φ .

Domes with various geometries may be obtained by taking families of curves characterised by different parameters n . Within one family the displacement lines depend on a_i . To various families correspond various displacement line patterns, patterns of increment lines and shapes of the apical domes. The latter for the examined domes are shown in Fig. 1.

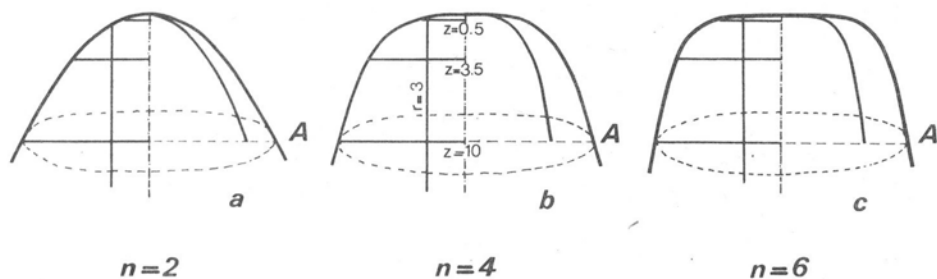


Fig. 1. Shapes of three apical domes described in the paper. The geometry of the domes is represented by families of parabolas of the order: $a-n=2$, $b-n=4$, $c-n=6$. In the right part of each dome two displacement lines from each family are shown. The outer line constitutes the surface of the dome. In the left part the straight lines: $z=0.5$, $z=3.5$, $z=10$, $r=3$ are marked. For these lines and the line corresponding to the surfaces of the domes $RERG_{vol}$ graphs are presented in Fig. 4. The domes are truncated at the same level by the plane passing through point A (10, 10)

At any point of the dome vector \underline{V} is described by formula (1). The direction of this vector is the same as that of gradient G and coincides with the tangent to the displacement line passing through this point. The absolute value of \underline{V} depends on the values of the partial G derivatives and on the μ function. The field $G(r, z)$ is of potential type. The lines of the field coincide with the displacement lines, whereas the equipotential lines with the increment lines. On each increment line the G value is different according to the dependence introduced by the growth promoter. The field $\mu(r, z)$ is described as follows:

$$\mu(r, z) = \frac{(\Delta m)^2}{(\Delta z_0)^2}, \quad (2)$$

where Δm , Δz_0 are the distances between neighbouring increment lines (Fig. 2).

On the dome axis $\mu = 1$, whereas $\underline{\text{grad}} G$ has only the component $\frac{\partial G}{\partial z}$. This component is, according to eq. (1), the rate of linear growth along the axis. If we know this rate and are able to express it in the form of a function — the promoter — it will be easy to obtain $G(0, z_0)$ by integration of the promoter. Hence, on the basis of the geometry of equipotential lines we find the scalar field $G(r, z)$ and further the vector field $\underline{V}(r, z)$. Differentiation of field $\underline{V}(r, z)$ supplies information on linear, in area and in volume relative elementary growth rates in the whole organ (Erickson 1976, Hejnowicz and Nakielski 1979, Hejnowicz 1982).

Mathematical description of the dome geometry by means of power functions has two advantages: 1) it allows to include in the investigations a relatively wide scope of shapes found in real shoot apices; 2) it makes the geometry dependent on parameter n only, this giving the possibility

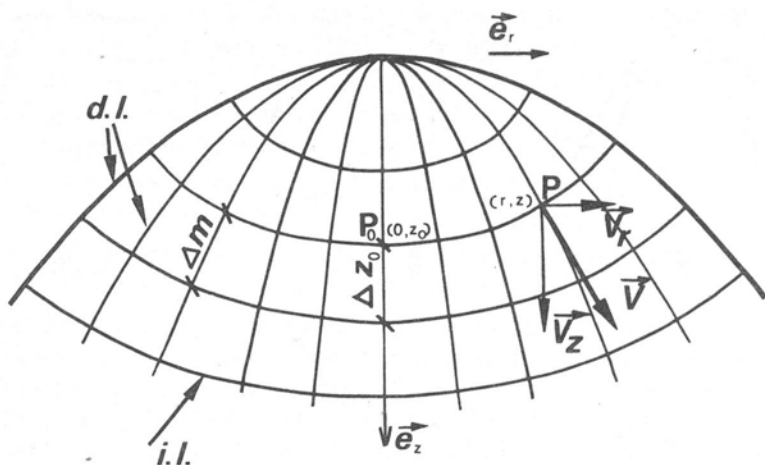


Fig. 2. Apical dome with pattern of displacement lines and pattern of increment lines. Displacement lines (d.l.) are 2nd order parabolas, the increment lines (i.l.) are trajectories orthogonal to the displacement lines. Points P and P_0 lie on one increment line and will remain in the growing apex on the same line at any moment. Segments Δm and Δz_0 denote the distances between the neighbouring increment lines, measured along the line denoted by m and along the axis

of analytically studying the RERG distribution as the function of the position and the latter parameter. Such studies for n in the interval $1 < n \leq 6$ were performed in the present work. Two variants of growth promoter were applied:

- I. The relative elementary linear growth rate is constant along the axis.
- II. The relative elementary rate of linear growth along the axis is proportional to the distance from the tip.

The results are graphically presented in the form of RERG_{vol} graphs for the domes shown in Fig. 1. They illustrate the distribution of the relative elementary rate of growth in volume along the longitudinal line $r = 3$, along the transverse lines $z = 0.5$, $z = 3.5$, $z = 10$ and along the surface contour of the domes. A general analytical expression is given for the relative elementary rate of linear growth (RERG_l) in any direction.

SCALAR FUNCTIONS $\mu(r, z)$ AND $G(r, z)$ IN THE PARABOLIC APICAL DOME

We shall now deal with the shoot apical domes in which the patterns of displacement lines are given in families of power functions of n -th order where n is an integer number greater than unity. They will be further referred to as parabolic domes of n -th order.

Let the rate of displacement of the points lying on the dome axis be any function of their distance from the tip: $|V(0, z_0)| = \frac{\partial G}{\partial z} = f(z_0)$.

Then $G(0, z_0)$ is: $G(0, z_0) = F(z_0) = \int f(z_0) dz_0$. We have the same G value in all points lying on the increment line passing through $(0, z_0)$ (see Fig. 2). Thus, $G(r, z)$ is:

$$G(r, z) = F\left(\sqrt{\frac{1}{n} r^2 + z^2}\right). \quad (3)$$

This is a general expression for the field $G(r, z)$ on the parabolic domes. Let us give it more specificity by adopting variants I and II of distribution of the relative elementary linear growth rate $\text{RERG}_{l(z_0)}$ on the axis.

Variant I. $\text{RERG}_{l(z_0)} = c$. This $\text{RERG}_{l(z_0)}$ is obtained when on the axis $\frac{\partial G}{\partial z} = cz_0$. Let us assume $c = 1$; by integration we get $G(0, z_0) = \frac{1}{2} z_0^2$ and finally:

$$G(r, z) = \frac{1}{2} \left(\frac{1}{n} r^2 + z^2 \right). \quad (4)$$

Variant II. $\text{RERG}_{l(z_0)} = cz_0$. We get it for $\frac{\partial G}{\partial z} = \frac{1}{2} cz_0^2$, hence, by the same procedure as before we get: $G(0, z_0) = \frac{1}{6} z_0^3$ and

$$G(r, z) = \frac{1}{6} \left(\frac{1}{n} r^2 + z^2 \right)^{\frac{3}{2}}. \quad (5)$$

The derivatives $\frac{\partial G}{\partial r}$ and $\frac{\partial G}{\partial z}$ fulfill in both variants the relation:

$$\frac{1}{r} \frac{\partial G}{\partial r} = \frac{1}{nz} \frac{\partial G}{\partial z}. \quad (6)$$

This relation can be utilised for calculation of the field $\mu(r, z)$. As known, μ changes according to eq. (2) with the distance between the neighbouring increment lines. But it is also known that the increment lines are equipotential lines of the field $G(r, z)$. Hence eq. (2) is equivalent to the following one:

$$\mu(r, z) = \frac{|\text{grad } G_{(r,z)}|^2}{|\text{grad } G_{(0,z_0)}|^2}, \quad (7)$$

where, like before, we take gradients G at points (r, z) and $(0, z_0)$ lying on the same increment line. Let us calculate gradients G from formula (3) and, taking into account eq. (6) let us introduce it into eq. (7). We then get:

$$\mu(r, z) = \frac{r^2 + n^2 z^2}{nr^2 + n^2 z^2}. \quad (8)$$

This equation does not contain $G(r, z)$, it is the same for any variant of promoter growth. This is in agreement with the statement at the beginning that the field $\mu(r, z)$ depends exclusively on the dome geometry. For fixed r, z the μ values are however, different in dependence on the n -th order of parabola passing through point $P(r, z)$. Thus, different parabolic domes have different $\mu(r, z)$ fields.

The parameter n is also present in eqs. (3, 4, 5) defining the field $G(r, z)$. This results from the fact that in function G a certain dependence on geometry is inherently associated with the course of the equiscalar line on the $[r, z]$ plane.

GROWTH RATES

The general expressions for linear, in area and in volume growth rates may be found in the papers of: Richards and Kavanaugh (1943), Erickson (1976), Hejnowicz and Nakielski (1979). We shall now deal with relative elementary growth rate in volume RERG_{vol} . In each point of the growing organ $\text{RERG}_{\text{vol}} = \text{div } \underline{V}$. The divergence of vector \underline{V} in the cylindrical coordinate system is calculated by the formula:

$$\text{div } \underline{V} = \frac{\partial V_z}{\partial z} + \frac{1}{r} \frac{\partial}{\partial z} (r \cdot V_r) + \frac{1}{r} \frac{\partial V_\varphi}{\partial \varphi}, \quad (9)$$

where V_r, V_φ, V_z are components of \underline{V} in the coordinate directions. Let us transform eq. (9) by expressing the component rates by μ and G functions according to eq. (1) at $\frac{\partial V_\varphi}{\partial \varphi} = 0$ (this resulting from the model construction). Taking into account eqs. (6) and (8) we get:

$$\begin{aligned} \text{RERG}_{\text{vol}} = \frac{r^2 + n^2 z^2}{r^2 + n^2 z^2} \left[n \frac{\partial^2 G}{\partial z^2} + \frac{2}{z} \frac{\partial G}{\partial z} + \frac{r}{z} \frac{\partial^2 G}{\partial r \partial z} \right] - \\ - \frac{2nr^2 z (n-1)^2}{(r^2 + n^2 z^2)^2} \frac{\partial G}{\partial z}, \end{aligned} \quad (10)$$

G being any function fulfilling eq. (3). Particularly for G given by eqs. (4) and (5) in cases I and II of the growth promoter variant we have, respectively:

$$\text{RERG}_{\text{vol}} \text{ (I)} = \frac{(2+n)r^4 + (7-n)n^2 r^2 z^2 + (2+n)n^3 z^4}{(r^2 + n^2 z^2)^2}, \quad (11)$$

$$\text{RERG}_{\text{vol}} \text{ (II)} = \frac{\left(\frac{1}{n}r^2 + z^2\right)^{\frac{1}{2}}}{(r^2 + n^2 z^2)^2} \left[\frac{(3+n)}{2}r^4 + \frac{(9-n)n^2}{2}r^2 z^2 + n^3(1+n)z^4 \right]. \quad (12)$$

In both these expressions RERG_{vol} depends on the coordinates and the n -th order of the parabolas forming the displacement line pattern.

When studying the function at various n one may conclude as to the distribution of the growth rate on domes of various shape.

In the same way the relative elementary rate of linear growth (RERG_l) may be expressed. For any direction \underline{e} $\text{RERG}_{l(\underline{e})}$ is given by the following expression:

$$\begin{aligned} \text{RERG}_{l(\underline{e})} = & \left[\frac{2n^2 r z^2 (n-1)}{(r^2 + n^2 z^2)^2} \frac{\partial G}{\partial r} + \frac{n r^2 + n^2 z^2}{r^2 + n^2 z^2} \frac{\partial^2 G}{\partial r^2} \right] \cos^2 \alpha + \\ & + \left[\frac{-2n^2 r^2 z (n-1)}{(r^2 + n^2 z^2)^2} \frac{\partial G}{\partial z} + \frac{n r^2 + n^2 z^2}{r^2 + n^2 z^2} \frac{\partial^2 G}{\partial z^2} \right] \cos^2 \beta + \\ & + \left[\frac{2n^2 r z^2 (n-1)}{(r^2 + n^2 z^2)^2} \frac{\partial G}{\partial z} - \frac{2n^2 r^2 z (n-1)}{(r^2 + n^2 z^2)^2} \frac{\partial G}{\partial r} + \right. \\ & \left. + \frac{2n(r^2 + n z^2)}{r^2 + n^2 z^2} \frac{\partial^2 G}{\partial r \partial z} \right] \cos \alpha \cdot \cos \beta + \left[\frac{n}{r} \frac{r^2 + n z^2}{r^2 + n^2 z^2} \frac{\partial G}{\partial r} \right] \cos^2 \gamma, \quad (13) \end{aligned}$$

where $\cos \alpha$, $\cos \beta$, $\cos \gamma$ are direction cosines of \underline{e} to the base unit vectors of the cylindrical coordinate system. The partial derivatives of G may be calculated from eqs. (4) and (5), respectively, for variants I and II of distribution of linear growth rate on the axis.

RESULTS

In the first part the results of study of the functions RERG_{vol} (I) and RERG_{vol} (II) will be presented in reference to r , z and parameter n assuming values from the $1 < n \leq 6$ interval. RERG_{vol} is the function of two variables defined in the plane of positive r , z . One variable remains fixed and the respective chance of variability of the other is studied. Hence the RERG_{vol} graphs characterise the distribution of the relative elementary rate of growth in volume either along straight lines $z = \text{const}$ (r variable) or along straight lines $r = \text{const}$ (z variable). These lines correspond in the three-dimensional dome to the surface of cylinders with radius r (where z is the symmetry axis) and to cross sections at distance z from the tip.

In the second part, based on the results of investigation of the functions,

the distribution of $RERG_{vol}$ is presented for three different domes. These will be parabolic domes of $n = 2, 4, 6$ (Fig. 1).

MATHEMATICAL ASPECTS OF FUNCTIONS $RERG_{vol}(r, z)$

Variant I. $RERG_{vol}$ (I) given by eq. (11) runs as follows:

1. For z constant (Fig. 3a) in the interval $1 < n \leq 4$ it is the increasing function of r . Its minimum lies on the axis ($r = 0$), then it increases changing the sign of the derivative at the point of inflection. The points of inflection for $z = 2$, at $n = 2$ and $n = 4$ are marked with arrows in Fig. 3a. They are determined by the positive roots of the equation: $-9r^4 + 2z^2 n (7n - 10) r^2 - z^2 n^3 (n - 4) = 0$. For various z the points are situated on straight lines $r = 1.58z$ and $r = 4z$, respectively. In the interval $n > 4$ $RERG_{vol}$ (I) shows a slight maximum on the axis (when $r = 0$) and a minimum

for $r = \sqrt{\frac{n(n-4)}{3}} z$. It passes twice through the inflection points. For various z in the case $n = 6$ (Fig. 3a) they lie on the straight lines $r = 1.07z$ and $r = 6.44z$.

2. For $r = \text{const}$ (Fig. 3b) in the interval $1 < n \leq 4$ $RERG_{vol}$ (I) is a decreasing function of z . It has a maximum for $z = 0$ (equal to $n + 2$), it then decreases with the increase of z . The inflection point is determined by the equation: $-n^3 (n - 4) z^4 + 2n (3n - 2) r^2 z^2 - r^4 = 0$. In the interval $n > 4$ $RERG_{vol}$ (I) has

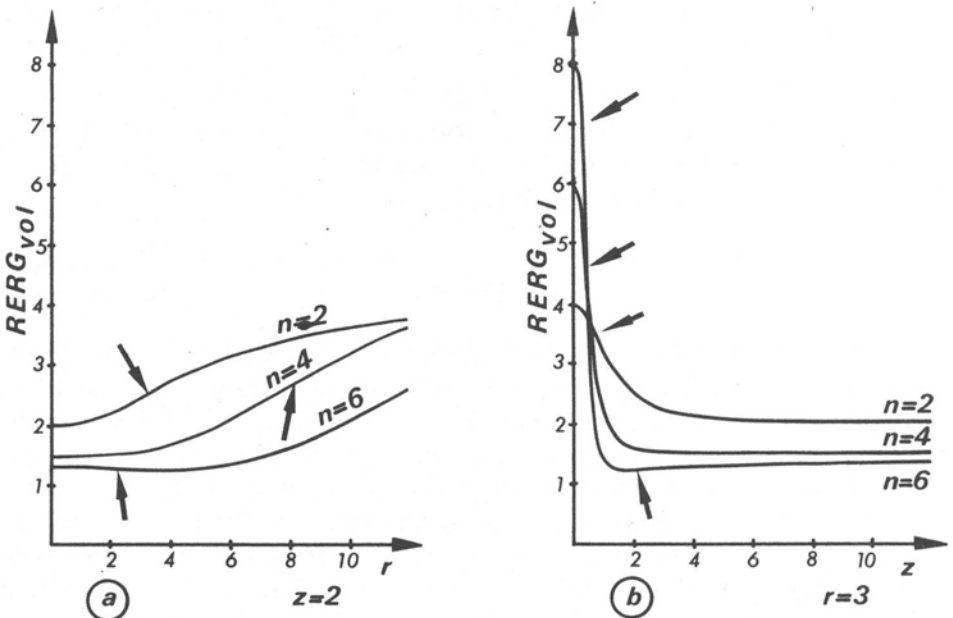


Fig. 3. Graphs of $RERG_{vol}$ (I): a—in dependence on r for $z=2$, b—in dependence on z for $r=3$, for the parameters $n=2, 4, 6$, respectively. Description of function in text. Arrows show points of inflection

a maximum at $z = 0$ and a minimum at $z = \sqrt{\frac{3}{n(n-4)}} r$. It passes twice through the inflection points for the line $r = 3$ shown in Fig. 3b, which at $n = 6$ are $z = 0.19$ and $z = 1.99$.

Variant II. From the analysis of function $RERG_{vol}$ (II), eq. (12) we get:

1. For $z = \text{const}$ $RERG_{vol}$ (II) is an increasing function of r for all n parameters. It has a minimum on the axis ($r = 0$) and increases in the direction r . The slope of the function plot depends on the value of constant z . For three values of $z = \text{const}$ ($z = 0.5$, $z = 3.5$, $z = 10$) and parameters $n = 2, 4, 6$ the $RERG_{vol}$ (II) graphs are shown in Figs. 4b, d, f.
2. In the same figure the graphs of $RERG_{vol}$ (II) are visible for $r = 3$. The function $RERG_{vol}$ (II) at first decreases and then increases in the direction of z . It reaches minimum at the points which constitute positive roots of the equation: $2n^5 z^6 (n+1) + n^3 (n^2 + n + 10) r^2 z^4 + 2n^2 (n^2 - 8n + 13) r^4 z^2 + r^6 (-6n^2 + 7n + 3) = 0$. In plane $[r, z]$ for $n = 2, 4, 6$ the minima are determined by the straight lines $z = 0.43r$, $z = 0.39r$, $z = 0.30r$, respectively.

$RERG_{vol}$ DISTRIBUTION ON SHOOT APICAL DOMES

Let us consider the parabolic domes of the shoot of n -th order ($n = 2, 4, 6$). The distributions of the rate of growth on these domes along the longitudinal line $r = 3$, along transverse lines $z = 0.5$, $z = 3.5$, $z = 10$ and along the contour of the dome surface in the axial plane are shown in Fig. 4. Although the graphs were prepared for only several lines, a quite good picture of growth in the whole organ is obtained. In the description of the distribution of growth rate three zones are distinguished: the subapical one, the pith-rib meristem and the peripheral zone.

Variant I. The constant relative elementary rate of linear growth along the axis, the same for all domes, implies a constant, but different for various domes, relative elementary rate of growth in volume along this line. The surface of $RERG_{vol}$ (I) resembles a trough the bottom of which is situated at a constant depth, whereas the walls are more and more steep as we advance along the bottom towards the tip. For increasing z 's the walls slope milder and milder and at the level $z = 10$ the trough is almost unnoticeable. For $n = 6$ (Fig. 4e) in the subapical part the trough separates two small maxima lying along the axis. The increase of the relative elementary rates of growth in volume with the distance from the axis in the direction of the dome surface in the subapical part is characteristic. At the height of $z = 0.5$ at the surface of dome $RERG_{vol}$ (I) for $n = 2$ the rate is two times higher than close to the axis. For $n = 4$ and $n = 6$ these proportions are still larger (four to six times).

Variant II. For this variant of promoter the $RERG_{vol}$ graphs along the dome axis are straight lines ascending with the z values. Their slope

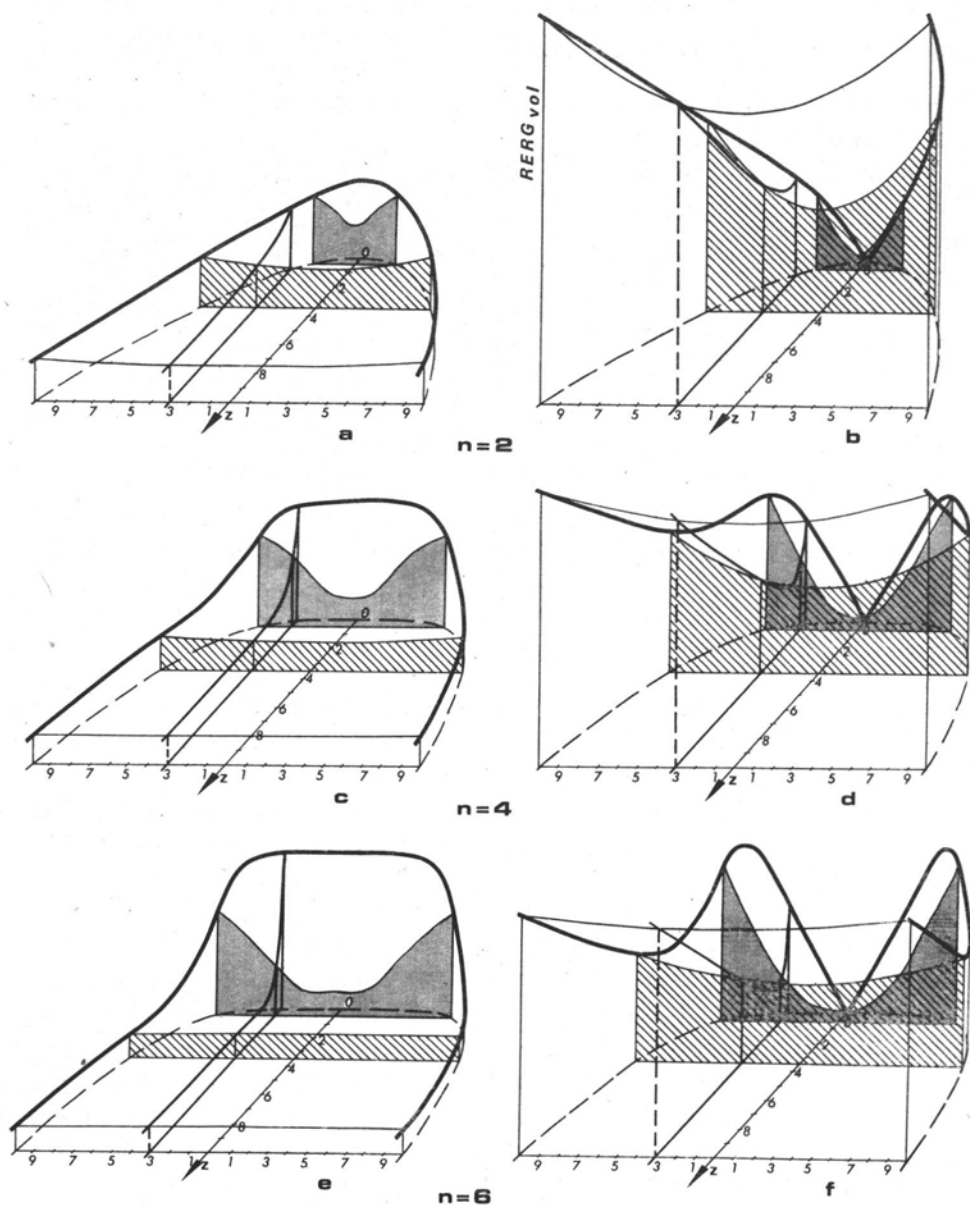


Fig. 4. Distribution of $RERG_{vol}$ on parabolic domes of $n=2, 4, 6$ th order for two variants of linear growth rate along the axis: 1— $RERG_{l(z_0)=1}$ (Figs. a, c, e). 2— $RERG_{l(z_0)=z}$ (Figs. b, d, f). In the base of each graph (i.e. in plane $[r, z]$) the central longitudinal section is inserted (Fig. 1.) seen laterally. $RERG_{vol}$ is laid off on the axis perpendicular to the plane of the base. The $RERG_{vol}$ graphs are denoted as follows: for line $z=0.5$ by the upper edge of the shaded surface, for line $z=3.5$ by the upper edge of the hatched surface, for line $z=10$ by the upper edge of the clear transverse surface visible at the front, for line $r=3$ by the upper edge of the longitudinal surface on the left side of the axis, for the contour of the surface of the domes by heavy continuous line. All graphs are in the same scale, but the $RERG_{vol}$ unit is one half that in Fig. 3

diminishes with the increase of n . $RERG_{l(z_0)}$ the same for all domes, gives different, but proportional to the distance from the tip, values of relative elementary growth rate in volume. The $RERG_{vol}$ (II) surface resembles a trough more distinct than in the former case tapering and strongly sloping towards the tip. It is limited by two straight lines symmetric to axis z and meeting in the dome tip where the function has a zero value. The trough is narrower and shallower for $n = 2$, wider and deeper for larger n 's. On the dome surface (heavy continuous line in Figs. 4b, d, f) $RERG_{vol}$ (II) at first rises markedly, then falls forming a characteristic hump and then rises once more. At the $z = 0.5$ level at the surface of the dome the growth rate is 8 (for $n = 2$) to about 25 (for $n = 6$) times higher than on the axis.

DISCUSSION

The results of investigations on the growth rate distribution on various parabolic domes confirm the occurrence of $RERG_{vol}$ depression close to the axis in the subapical part, independently of the geometry type of the dome. The depth of the depression varies. It depends on the order n of the parabolic curves representing the displacement lines and on the variant of the growth promoter. The latter dependence is particularly pronounced. The $RERG_{vol}$ depression in variant II (Figs. 4b, d, f) is greater than in variant I (Figs. 4a, c, e). For the same growth promoter function there are deviations from the n -type dome geometry. This deviation, however, is less important as compared with the basic differences resulting from the adoption of other variant of distribution of the rate of linear growth along the axis.

In the real shoot domes the relative elementary rate of linear growth along the axis is neither constant as in variant I nor proportional to the distance from the tip as in variant II. It would seem that in general it constitutes a certain combination of these two variants. If we assume that it is constant in the subapical part, later increases with the distance from the tip and again becomes constant (the value of the constant will now be different) at the base of the dome, then the $RERG_{vol}$ depression will be still deeper. Such a situation could be visualized by the combination of graphs $RERG_{vol}$ (I) and $RERG_{vol}$ (II) (Fig. 4) within the same n . It has already been discussed for $n = 2$ by Hejnowicz and Nakielski (1979).

Analytical study of the distribution of the growth rate in dependence on the position coordinates and the parameter n (parabolic type of geometry) is not difficult. In the present paper $RERG_{vol}$ was studied. The relative elementary rate of linear growth may be studied similarly in any direction (eq. (13)). Other variants of $RERG_{l(z_0)}$ distribution (the promoter) can also be assumed. Particularly the promoter resembling the linear growth rate distribution

in the real domes may be introduced in the form of a graph (the graphic approach—Hejnowicz and Nakielski 1979).

Extension of the class of parabolas makes it possible to study any domes, even those differing widely in shape. The n may represent temporal change of apical dome shape. The problem will be the subject of a forthcoming paper.

It is known that the internal geometry of the shoot dome (particularly the pattern of the displacement lines) is "read" from the directions of the cell wall elements network on longitudinal sections (Schüepp 1966). The elements of the wall network are arranged in peri- and anticlines distinctly visible in the peripheral parts. If we disregard the subapical zone, it seems that in many seed plants the periclinal lines correspond to the displacement lines and can be described for instance by parabolic curves. Very close to the tip, however, it cannot be established what kind of curve is the displacement line, certainly it is not the pericline there; the pericline in this part runs almost parallelly to the dome surface. Neither could it be a curve of parabola type, rather a straight line segment running from the tip. If it is assumed that the displacement line at the tip it is also the n -th order parabola, an apparent paradox results consisting in a more and more advanced differentiation of $RERG_i$ in various directions when we approach the tip. This differentiation is the greater the greater is the n -th order of the parabolas and it disappears when the parabola passes into a straight line (for the extreme value $n = 1$). Such assumption is unavoidable in the case of analytical studies, where it is required that the displacement line be represented by continuous functions characterised by the same parameter n in the whole region $[r, z]$. Hence this paradox occurred as well in the preceding study (Hejnowicz and Nakielski 1979). In order to avoid it, the displacement lines at the tip should be straight, thus they would differ essentially from the parabolas considered. Since the $RERG_{vol}$ is the sum of $RERG_i$ in mutually orthogonal directions, then in the case when $RERG_i$ reaches higher values in the anticlinal than in the periclinal and latitudinal direction (and such results are actually obtained) the $RERG_{vol}$ values obtained in this region are exaggerated.

In order to describe the growth distribution in any organ it is necessary to know the field $V(r, z)$. In the here presented model of the dome we obtained it by means of the scalar functions G and μ . The knowledge of field V is indispensable not only for calculation of $RERG$, but for investigation of the variability of any quality characterising cells in the growing organ, such as protein concentration, hormonal activity etc. (Silk and Erickson 1979). The material derivative defining the change of this quality (let us denote it $\Phi(x, t)$) is, namely

$$\frac{D\Phi}{Dt} = \frac{\partial\Phi}{\partial t} + \underline{V} \cdot \nabla\Phi.$$

Thus, it is inherently dependent on $V(x, t)$. The model used in this study suggests a method for finding the field V on shoot domes of various shapes.

Many aspects concerning the problems of organ growth can be recognised from their geometry. The great importance of such investigations is stressed by Silk and Erickson (1979) and Nicklas and Mauseth (1980). The latter authors point to the relation between the geometry of the shoot apex and the zonation pattern (zonate pattern within shoot apical meristems). They reach the conclusion that "the zonation pattern" may result from the geometrically conditioned differences in the cell dimensions. The position of the cell in the growing shoot apex influences its dimensions if they can be changed. If the cell volume is assumed constant the influence of geometry becomes visible in a different number of divisions in the particular zones. From the present it follows that the geometry influences the zonation in respect to RER_{vol} . It may be also concluded that the geometry influences the zonation in respect to cell division frequency.

The presented model describing the displacement lines of parabolas of n -th order may be useful, particularly in model studies with the use of computers.

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Wpływ geometrii wierzchołka pędu na rozmieszczenie szybkości wzrostu

Streszczenie

W rosnącym wierzchołku istnieje pole prędkości przesunięć elementów siatki ścian komórkowych w czasie. Można opisać je skalarnymi funkcjami współrzędnych i za pomocą metod

matematycznych, wziętych z analizy pola, obliczać względne elementarne szybkości wzrostu (RERG) w różnych częściach organu. Rozmieszczenie RERG wewnątrz i na powierzchni wierzchołka zależy wtedy od dwóch czynników: geometrii organu i rozmieszczenia względnej elementarnej szybkości wzrostu liniowego ($RERG_1$) wzdłuż jednej, dowolnie wybranej linii przesunięć (n.p. wzdłuż osi). W niniejszej pracy zbadano wpływ obu czynników wprowadzając różnorodność geometrii za pomocą rodzin parabol różnego stopnia n . Względną elementarną szybkość wzrostu objętościowego ($RERG_{vol}$) dla dwóch wariantów $RERG_1$ ($1 - RERG_1$ na osi jest stałe, $2 - RERG_1$ na osi jest proporcjonalne do odległości od szczytu) wyrażono w postaci funkcji, uzależnionej od współrzędnych i parametru n . W oparciu o przebieg zmienności funkcji przedstawiono wykresy $RERG_{vol}$ dla trzech wierzchołków parabolicznych o różnych kształtach. Z rozmieszczenia $RERG_{vol}$ na tych wierzchołkach wynika, że charakterystyczna depresja szybkości wzrostu objętościowego w części przyszczytowej może być cechą wszystkich wierzchołków parabolicznych, niezależnie od stopnia parabol. Zwrócono uwagę na szerokie możliwości, jakie w badaniach wzrostu merystemów wierzchołkowych daje zastosowanie parabol różnego stopnia do opisu geometrii.