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Distribution of linear growth rates in different directions in root apical meristems

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Abstract

Growth of apical meristems in plants may be well described by the growth tensor method. Hejnowicz (Envir. Exp. Bot. 1989, 29) determined growth tensors for roots: one with a minimum and the other with a maximum of the relative elemental growth rate in volume and used them for the description of two types of apices: one with an apical cell and merophytes (I), and the other with files of cells converging towards a quiescent centre, CQ (II). In the present paper the same cases are considered from the point of view of a spatial and directional variation of the relative elemental rate of growth in length, $RERG_1$. Maps of the $RERG_1$ in two planes: axial and tangential, the latter determined by periclinal-longitudinal (PL) and periclinal-tangential (PT) principal growth directions, are shown. In an apical part of apex I where there is maximum volumetric growth, there also occurs a maximum of $RERG_1$ for all directions. In regions other than this $RERG_1$ decreases although $RERG_1$ in the PL direction predominates everywhere. In apex II $RERG_1$ for all directions has a minimum in CQ and becomes increasingly larger with increasing distance from it – the maximum is in the PL direction in the cylindrical part of the apex. In peripheral parts of both apices, in the place of the root/cap junction, $RERG_1$ in the anticlinal direction is significantly small.

Key words: growth tensor, growth modeling, root meristems

INTRODUCTION

Growth is a tensorial attribute, in plant organs growing symplastically (Silk and Erickson 1979, Hejnowicz and Romberger 1984). It may be described by a continuous field of the growth tensor. One of the properties of

the tensor (indicated by eigenvectors of its symmetric part) is that three mutually orthogonal directions are distinguished in each point of the field — they are called the principal directions of growth, PDG (Hejnowicz and Romberger 1984, Hejnowicz 1984). Relative elemental growth rates in length, $RERG_1$, which can be specified for every direction, attain extreme values, either maximal or minimal, only in PDGs.

The consequence of symplasticity is that PDGs change in a continuous way giving a PDG pattern. This pattern consists of three types of mutually orthogonal lines, namely: periclinal-longitudinal (PL), periclinal-trangential (PT) and anticlinal (AN) (the lines were also called the trajectories of PDG, Hejnowicz 1984). It is recognizable in the cell arrangement in the meristem unless growth is isotropic. Since periclinal and anticlinal lines can be drawn based on a network of cell walls, and they preserve orthogonality during growth, the conclusion is that periclinal and anticlinal lines represent the pattern of PDGs (Hejnowicz 1984, 1989).

The fact that periclinal and anticlinal lines in the cellular pattern well-known from anatomical study, fit the pattern of PDG obtained from theory by tensorial analysis is an important correlation. This makes it possible to formulate the growth tensor for a given organ under two conditions (Hejnowicz 1989): 1) PDG lines should be adjusted to the pattern of periclinal and anticlinal cell walls, 2) the grid formed by material points aligned along PDG should change during growth preserving this alignment — the points should remain on PDGs.

A new way of the formulating the growth tensor was introduced by Hejnowicz using the example of roots (1989). In the cited paper Hejnowicz determined two growth tensors — one giving a maximum and the other giving a minimum of the volumetric relative elemental growth rate, $RERG_{vol}$. These tensors were used for the description of two types of root apices: one with an apical cell and merophytes (I) and one with files of cells converging towards a quiescent centre (II). In both cases the detailed specification for calculations of growth tensors was a field of displacement velocity \vec{V} in tensorial components (growth tensor is a covariant derivative of \vec{V}) defined by different relations in each of four parts of the apex (these parts are shown on schemes in the middles of Figs. 2, 3). The relations in paraboloidal coordinates (u, v, φ) were as follows, Hejnowicz (1989):

$$\begin{aligned}
 \frac{du}{dt} &= Au_0 + C(u - u_0) & \frac{dv}{dt} &= 0 & \text{for } u > u_0, v \leq v_0 \\
 \frac{du}{dt} &= Au & \frac{dv}{dt} &= 0 & \text{for } u \leq u_0, v \leq v_0 \\
 \frac{du}{dt} &= Au & \frac{dv}{dt} &= K(u_0 - \frac{u^2}{u_0})(v - v_0) & \text{for } u \leq u_0, v > v_0 \\
 \frac{du}{dt} &= Au_0 + C(u - u_0) & \frac{dv}{dt} &= B(u - u_0)(v_0 - v) & \text{for } u > u_0, v > v_0,
 \end{aligned} \tag{1}$$

where A, B, C, K, u_0, v_0 are constants (the field has a rotational symmetry, hence $d\phi/dt = 0$).

Field (1) with constants: $A = 0.1, B = 0.02, C = 0.05, K = 0.03, u_0 = 1.5, v_0 = 0$ determines the growth tensor for apex I, whereas the field with constants: $A = 0, B = 0.065, C = 0.2, K = 0.07, u_0 = 1.5, v_0 = 1.5$ determined the growth tensor for apex II. The patterns of PDG for both apices were clearly different. Hejnowicz carried out simulations for temporal deformations, at first on a grid of particles initially aligned along PDGs, then of a fragment of the cellular pattern. As could be seen, the patterns of PDGs were relatively steady in sequentially changing time. Moreover, cell arrangements obtained by temporal simulation were typical for real apices — one for pteridophytes the other for angiosperms. Hejnowicz calculated REG_{vol} for both apices, however, he did not consider the distribution of the relative elemental rate of growth in length, REG_1 .

The present paper deals with Hejnowicz's models for roots from the point of view of spatial and directional variations of REG_1 . REG_1 maps are shown in different directions in different parts of the apex, and I compare and discuss proportions between directional growth in different regions of both apices.

METHODS FOR CALCULATION

In a growing organ, material points of the cell wall network are displaced into new positions. At the same time linear, area and volumetric elements of the network increase in length, in area and in volume, respectively. REG (relative elemental rate of growth) is a measure of the rate of this increase per time unit at a given point. REG subindexed by ¹, REG_1 , is a relative elemental rate of growth in length. It gives the most basic information about growth in the sense that other REG s can be calculated from combinations of REG_1 s, for example, REG_{area} and REG_{vol} are equal to the sum of REG_1 s in two and three mutually orthogonal directions, respectively (Hejnowicz and Romberger 1984).

For a given point of a growing organ the field \bar{V} of the displacement velocity can be determined. REG_1 in the direction \bar{e}_s is a gradient of \bar{V} in this direction which can be written as (Hejnowicz and Romberger 1984):

$$REG_{1(s)} = \lim_{\Delta s, \Delta t \rightarrow 0} \frac{\Delta(\Delta s)}{\Delta s \Delta t} = \frac{d(\bar{V} \cdot \bar{e}_s)}{ds} = (\Delta \bar{V}) \bar{e}_s \bar{e}_s, \quad (2)$$

where Δ denotes gradient.

How can REG_1 in a chosen direction be calculated? (ΔV) is a so-called dyadic which consists of nine components. The components of a dyadic are

equal to elements of the matrix of the growth tensor in physical components, T_{ij} where i, j belong to the set of indexes numbering unit vectors of a coordinate system (Hejnowicz and Romberger 1984). They were calculated in the previous paper for curvilinear coordinates with rotational symmetry (Nakielski 1987a). Let us denote unit base vectors of paraboloidal coordinates by $\bar{e}_u, \bar{e}_v, \bar{e}_\varphi$ and direction cosines of \bar{e}_s by k, l, m , namely $k = \cos(\bar{e}_s, \bar{e}_u)$, $l = \cos(\bar{e}_s, \bar{e}_v)$, $m = \cos(\bar{e}_s, \bar{e}_\varphi)$. Thus, $\bar{e}_s = k\bar{e}_u + l\bar{e}_v + m\bar{e}_\varphi$, and dyadic $(\bar{e}V)$ double multiplied by \bar{e}_s gives:

$$\text{RERG}_{1(s)} = T_{uu}k^2 + T_{vv}l^2 + T_{\varphi\varphi}m^2 + (T_{uv} + T_{vu})kl + (T_{u\varphi} + T_{\varphi u})km + (T_{v\varphi} + T_{\varphi v})lm \quad (3)$$

Field (1) refers to a case of growth without rotation thus the four later components in (3) are equal to 0. I do not explicitly mention $T_{uu}, T_{vv}, T_{\varphi\varphi}, T_{uv}, T_{uv}$ here because expressions for them are lengthy and, moreover, different in each of the regions in the plane $[u, v]$ (u_0 and v_0 divide $[u, v]$ plane into 4 regions according to (1), see diagram in the center in Figs. 2, 3). By way of example I shall show, how to obtain T_{uu} for one of the regions, for instance $u \leq u_0, v > v_0$. T_{uu} in physical components, in coordinates with rotational symmetry is (Nakielski 1987a):

$$T_{uu} = \frac{1}{h_u} = \left(\frac{\partial V_u}{\partial u} + \frac{1}{h_v} \frac{\partial h_u}{\partial v} V_v \right),$$

where h_u, h_v are scale factors of the coordinate system, V_u, V_v are physical

components of V , i.e. $V_u = \frac{1}{h_u} \frac{du}{dt}$, $V_v = \frac{1}{h_v} \frac{dv}{dt}$. For paraboloidal coordinates

$h_u = h_v = \frac{1}{2}(u^2 + v^2)$, whereas $\frac{du}{dt}$ and $\frac{dv}{dt}$ are given by (1). Hence,

$$T_{uu} = A + \frac{Au^2}{u^2 + v^2} + \frac{Kv}{u^2 + v^2} \left(u_0 - \frac{u^2}{u_0} \right) (v - v_0).$$

RERG_1 is a tensorial quantity and can be specified in different directions. Its graphical image at a given point is a 3-dimensional closed surface around the point — RERG_1 in \bar{e}_s is equal to the length of a segment from the point to the surface along \bar{e}_s . The surface can be termed an indicatrix of RERG_1 . Such indicatrices can be drawn for many points inside and at the surface of the organ. In the present paper they are shown for a number of points lying in the axial plane of the apex in the form of 2-dimensional plots that are the sections

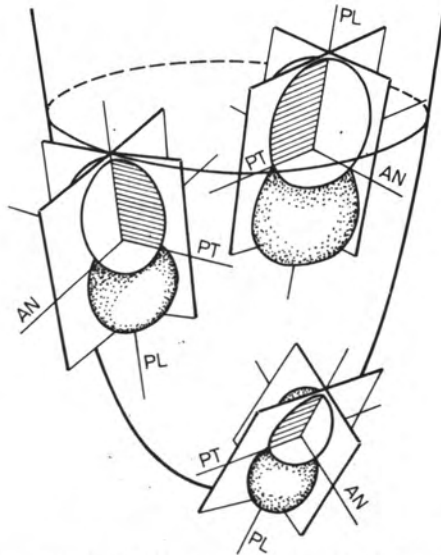


Fig. 1. A diagram of indicatrices of $RERG_1$ crossed by axial and tangential planes for some points of the root apex. For axial and tangential planes $RERG_1$ values are computed and displayed in the following figures. For each point principal directions of growth: periclinal-longitudinal (PL), periclinal-tangential (latitudinal, PT) and anticlinal (AN) are denoted. Axial planes are given by PL and AN directions and tangential ones by PL and PT. An eighth of "pea-nut-shaped" volume has been cut out to aid visualization of the orientation of the planes

of indicatrices by two types of planes: axial and tangential (Fig. 1). Equation (3) specifies the following, depending upon the type of planes for which the plots were made:

$$RERG_{1(s)} = T_{uu}\cos^2\alpha + T_{vv}\sin^2\alpha + (T_{uv} + T_{vu})\cos\alpha\sin\alpha,$$

for \bar{e}_s in the axial plane, where α is an angle between \bar{e}_s and horizontal line, and

$$RERG_{1(s)} = (T_{uu}\cos^2\beta + T_{vv}\sin^2\beta + (T_{uv} + T_{vu})\sin\beta\cos\beta)\cos^2\alpha + T_{\phi\phi}\sin^2\alpha,$$

for \bar{e}_s in tangential plane, where α is as above, whereas β is an angle between \bar{e}_u and the direction for which $RERG_1$ has a maximum ($\beta = 0$ when PDG coincides with coordinate lines of the paraboloidal system).

RESULTS

Spatial and directional variations of $RERG_1$ in root apices with an apical cell and with a quiescent centre are shown in Figs. 2, 3. In the calculations the constants A, B, C, K, u_0 , v_0 were adjusted to Hejnowicz's (1989) specification; their values were given in a previous sections.

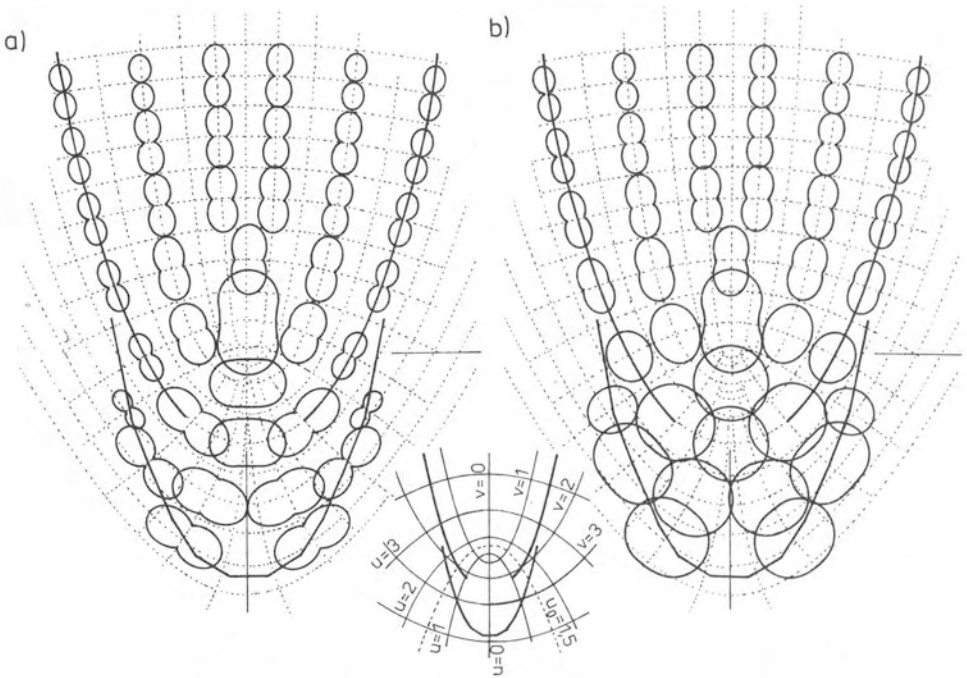


Fig. 2. Spatial and directional variations of the relative elemental rates of growth in length, $RERG_1$, in axial planes (a) and in tangential planes (b) for the apex with an apical cell. Values of $RERG_1$ are displayed in the form of two-dimensional plots around a number of points lying in one of the axial planes. In the figure plane each plot of $RERG_1$ in Fig. 2b has changed orientation as a result of the rotation of the tangential plane by 90° around the PL direction (see Fig. 1). For a given point, the $RERG_1$ in different directions were evaluated every 10° . The pattern of principal directions of growth (dotted lines in the background) and an outline of the apex are drawn. The lower scheme in the center shows the same outline in the background of paraboloidal coordinates (u, v, φ) in the plane $\varphi = \text{const}$. The line $u_0 = 1.5$ is distinguished. Computer drawings

Fig. 2 refers to the apex with an apical cell. $RERG_1$ s within the apex are different in particular parts of the organ. Maximum of $RERG_1$ is in the apical region of the proper root in a place called the growth center (Hejnowicz 1989). This place coincides with the origin of paraboloidal coordinates and at the same time determines a construction center. Relatively large $RERG_1$ s are in the root cap while minimal ones occur at the base of the meristem. Anisotropy of the $RERG_1$ becomes visible in both types of planes: axial (Fig. 2a) and tangential (Fig. 2b). In Fig. 2a the values of $RERG_1$ along the root axis are more or less 2-3 times higher than the ones across the axis. This predominance increases on the way from the axis to the surface of the apex. On the surface, mainly in the semi-cylindrical part, $RERG_1$ in the anticlinal direction decreases practically to zero. In Fig. 2b a small region of the $RERG_1$ isotropy occurs in an apical part in the region of the root/cap junction. Apart from this, linear growth rates are clearly smaller and differentiated, the

$RERG_1$ s along the PL lines become larger than $RERG_1$ s in the PT ones. The comparison of Fig. 2a and Fig. 2b indicates that in the axial part of the proper root, $RERG_1$ s along both PL and AN are equal, but with increased radial distance from the axis, the ones along the PT become higher.

The maps of $RERG_1$ for the apex with a quiescent centre are shown in Fig. 3. In the zone CQ, linear growth rates decrease to zero because, according to our specification, the parameter $A = 0$. Apart from CQ, the $RERG_1$ s become increasingly larger with increasing distance from this zone. In the axial plane (Fig. 3a) the linear growth is anisotropic, $RERG_1$ s along the axis are many times greater than the ones in the radial direction. A maximum of $RERG_1$ occurs in the cylinder-like part at the base of the meristem. In the peripheral parts of the cap in the place of its junction with the proper root, $RERG_1$ s along AT decrease practically to 0. In Fig. 2b a local isotropy of the $RERG_1$ is seen in the cap. In contrast to this anisotropy occurs in the proper root, excepting the CQ zone, $RERG_1$ s along PL are greater than the ones in PT. Comparing Fig. 3a and Fig. 3b one can see that $RERG_1$ s along PT and AN directions are more and less equal near the axis and differ only slightly in other parts of the root.

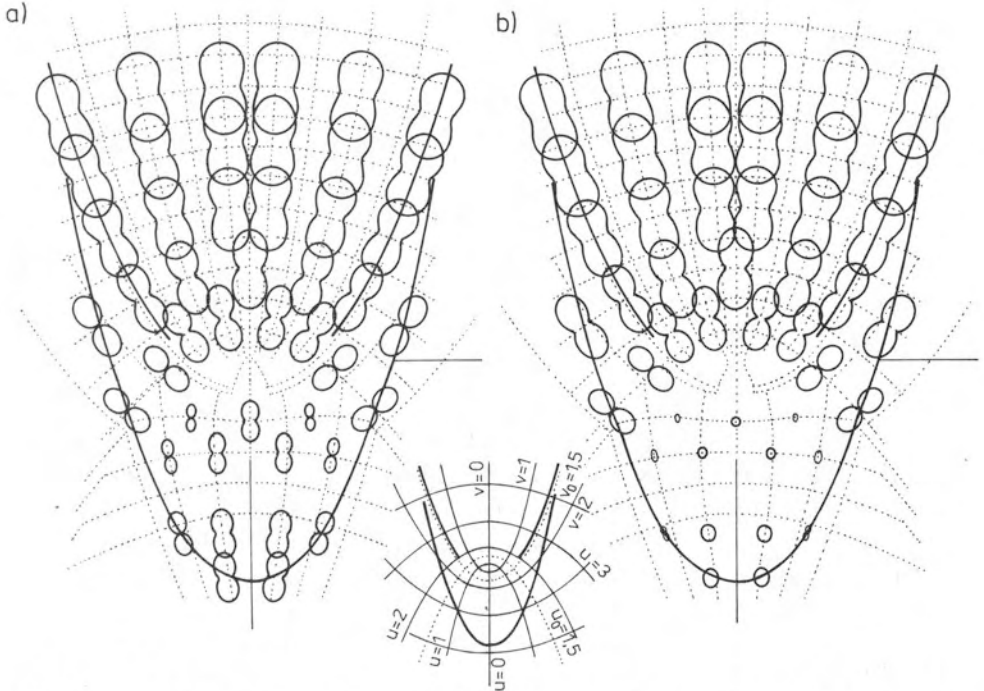


Fig. 3. Spatial and directional variations of $RERG_1$ in axial planes (a) and in tangential planes (b) for the root apex with a quiescent centre. Explanations as in Fig. 1 except that in the scheme in the center two coordinates are denoted, namely $u_0 = 1.5$ and $v_0 = 1.5$

DISCUSSION

The growth tensor method is the only one which gives an overall and exact description of the growth in meristematic plant organs. During the last few years numerous cases, mainly ones of shoot apices, have been analysed by means of it. The considered models refer to domes with different shapes (Hejnowicz et al. 1984a, b) and with different PDG patterns inside (Nakielski 1987a), as well as to domes with different growth specifications (Hejnowicz et al. 1984a, b). Real domes have also been described, namely those of spruce (Nakielski 1987b) and barley (Hejnowicz et al. 1988) shoot apices. Data concerning cell complexes on the surface layer of cells were used in the modeling of both cases.

The apical meristem of the root consists of the proper root and the cap. This was an important difficulty in modeling for two reasons namely: 1) there was no simple curvilinear coordinate system in which coordinate lines could adjust to periclinal and anticlinal lines in both the proper root and the cap; 2) it was difficult to determine $V(u,v)$ which described well the proportions between V_u and V_v in parts of the organ growing so differently as the proper root and the cap. The method proposed by Hejnowicz (1989) appeared to be appropriate here, moreover, it may be convenient also in the description of more complex cases of growth, for instance unsteady-state ones.

The obtained results relate to a great extent to what we already know about the distribution of growth from anatomical studies. A maximum of the number of divisions in the root apices of water ferns is just in the apical cell. Apart from this region, the longitudinal growth at the same distance from the vertex is more or less equal whereas radial growth seems to be maximal mainly in an axial part of the meristem (Gunning 1981, Nitayangkura et al. 1980). Maps in Fig. 2 show a similar image of the growth in the first approximation, but in my opinion growth rates in the basal part of the meristem should be greater in comparison with rates in the root cap. The distribution of $RERG_1$ s obtained for the apex with a quiescent centre seem to be typical for angiosperms (Cloves 1975). The anisotropy of the growth in the cap can be relevant for forming the columella, although in the case of tangential planes (Fig. 3b) values of $RERG_1$ in the region of the columella could be higher than ones on the flank of the cap. Anticlinal growth in the peripheral part of the root-cap junction is significantly small in both apices but mainly in the apex with CQ. In the semi-cylindrical part of the apex with an apical cell, the growth "in width" is slow which can favour achievement of a constant radial dimension.

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*Rozmieszczenie szybkości wzrostu liniowego w różnych kierunkach
w merystemach apikalnych korzeni*

Streszczenie

Wzrost merystemów apikalnych u roślin opisywać można za pomocą tensora wzrostu. Hejnowicz (Envir. Exp. Bot. 1989, 29) określił dwa tensory wzrostu dla korzeni: jeden z minimum i drugi z maksimum względnej elementarnej szybkości wzrostu objętościowego w niewielkiej odległości od szczytu. Zastosował je do opisu dwu typów wierzchołków: jednego z komórką szczytową i segmentami (I), drugiego z ciągami komórek zbiegającymi się w strefie słabo rosnącej (quiescent centre, II). W niniejszej pracy pokazano i przedyskutowano rozmieszczenie względnej elementarnej szybkości wzrostu liniowego, $RER G_1$, w różnych kierunkach w obu wymienionych typach wierzchołków. Mapy $RER G_1$ wykonano dla dwóch typów płaszczyzn: osiowej i stycznej, tej ostatniej wyznaczonej przez dwa główne kierunki wzrostu: peryklinalny-podłużny i peryklinalny-obwodowy. W apikalnej części wierzchołka I, w miejscu gdzie jest maksimum szybkości wzrostu objętościowego, występuje również maksimum $RER G_1$ we wszystkich kierunkach. Poza

tym rejonem REG_1 stopniowo się zmniejsza. W obrębie ciała korzenia przeważa REG_1 w kierunku peryklinalnym-podłużnym, w obrębie czapeczki REG_1 w kierunku peryklinalnym-obwodowym „dorównuje” mu pod względem wielkości. W wierzchołku II REG_1 ma minimum w strefie słabo rosnącej, poza tą strefą zwiększa się stopniowo ale nierównomiernie w różnych kierunkach. Największe wartości osiąga w kierunku peryklinalnym-podłużnym w cylindrycznej części wierzchołka. W obu typach wierzchołków (ale wyraźniej w II), w miejscu zespolenia ciała korzenia z czapeczką REG_1 w kierunku antyklinalnym jest mały.