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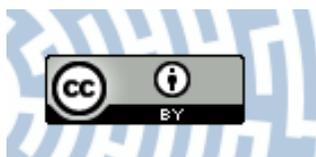
Trajectories of principal directions of growth, natural coordinate system in growing plant organ

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Abstract

In symplasticly growing organs the principal directions of growth, which are indicated by the eigenvectors of the symmetric part of the growth tensor, can be associated with each positional point and joined up to form a network of orthogonal trajectories, unless the growth is isotropic. The trajectories represent a natural coordinate system suitable for description of growing organs. These trajectories often can be recognized in patterns of nonrandom alignments in the cell wall network: these alignments are normal to anticlinal and periclinal walls. Coordinate systems that fit the trajectories in different types of growing organ are listed.

Key words: growth tensor, principal directions, growth modeling

INTRODUCTION

It has been shown that growth of plant organs is a tensorial attribute if that growth is symplastic (Hejnowicz and Romberger 1984). The growth tensor, t_p^q, is the covariant derivative of the field $\underline{V}$, where the vector $\underline{V}$ is the displacement velocity of a material point in the cell wall network. The tensor allows one to characterize the growing organ in terms of growth rates (linear, areal, and volumetric), rate of angular change between cell walls, vorticity, and the principal directions of growth. The latter are the directions in which the linear relative elemental rate of growth, $RERG_l$, attains extremal values (either maximal or minimal) around a considered point. For each position in the organ there are three such mutually orthogonal directions, unless the growth is isotropic. These directions are defined by the eigenvectors of the symmetric part of the growth tensor, T_{pq} represented by physical components (physical components are symbolized by capital letters in this paper). Line elements oriented along principal directions, and having a co-

inciding initial point, preserve their orthogonality during growth, i.e., the angles between them are not deformed during growth. In the case of line elements initially orthogonal but not aligned along the principal directions the right angles are deformed.

In a symplasticly and nonuniformly growing organ, we can associate principal directions with each point within the organ. We can then regard the principal directions as forming a network of orthogonal trajectories, the trajectories thus form a natural coordinate system. The symmetric part of the growth tensor, T_{pq}, represented in such a system is in the diagonalized form. The components (on the main diagonal) give the principal growth rates or principal $RERG_l$. The skew-symmetric part of the growth tensor, $T_{pq} = -T_{qp}$, where $p \neq q$, describes vorticities of the trajectories.

HOW TO RECOGNIZE THE PRINCIPAL DIRECTIONS OF GROWTH

As mentioned, the line elements oriented in the principal directions and including coinciding points preserve their orthogonality during growth. Inversely, if there exist orthogonal elements that preserve orthogonality during growth in an organ, and which increase in length (assuring that there is growth at their locations), then they are oriented in the principal directions.

It is known that wherever cells within plant organ are physically arranged with nearly complete surface contact, there is a pattern of hexagons (on the average) in section or in surface view (Dormer 1980). On it another pattern in the form of series of periclinal and anticlinal walls, or wall trajectories, can be superposed (Fig. 1). These wall trajectories are then mutually orthogonal and preserve their orthogonality during growth. This means that they coincide with the trajectories of the principal directions of growth.
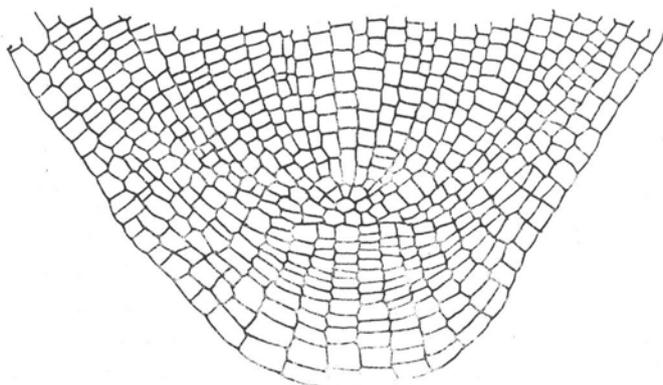

Fig. 1. Classical scheme of anticlinal and periclinal wall trajectories in a root tip already used by J. Sachs more than hundred years ago. The series of the periclinal walls form a zigzag in longisection. This zigzag is continuously rebuilt during growth, however it remains orthogonal to the anticlinal walls

It should be noted that the cell wall network can indicate the principal directions if the following conditions are fulfilled: A). That the principal directions exist not only in mathematical sense but are physically unambiguous. B) Newly formed partitions are normal to the principal directions. C) The pattern of principal direction trajectories is steady or is changing only slowly in comparison with the maximal $RERG_l$.

Condition A demands, firstly, that growth be nonuniform i.e. that $RERG_l$ is not the same in all directions at the considered point when that point is at various positions in the organ. If growth is uniform, the growth tensor has the same components on the main diagonal and zeros elsewhere, i.e. $T_{pq}=a\delta_{pq}$, where a represents $RERG_l$ of the isotropic growth and δ_{pq} is the Kronecker's symbol. In such case the growth causes only an increase of the scale factor for the organ. However, nonuniform growth is not a sufficient to fulfill the consition A, because if the difference between the growth rates in the several principal directions is small in comparison to the mean value of these rates, the physical situation is similar that of isotropic growth. The dependence of $RERG_l$ on direction must be great enough to distinquish the principal directions in an unambiquous physically manner. To provide a numerical measure of growth anisotropy, Erickson (1976) proposed an anisotropy ratio as the ratio of maximal $RERG_l$ to the minimal $RERG_l$ at a point. In the plane of a pair of principal directions of growth this is the ratio of the corresponding principal growth rates. Condition A demands that anisotropy ratio be high enough to allow anticlinal and periclinal wall trajectories to be visibly evident.

Condition B demands that the precursory phases of cell division "recognize" the principal directions of growth and orient the cell plates, and consequently the new-formed partitions, normal to one of the directions (in the plane of the two remaining). Such partitions being orthogonal to the smoothed outline of the mother cell wall can preserve this orthogonality during subsequent growth if the partition and the outline are normal to two principal directions (the partitions must be considered with regard to the smoothed outline of mother cell wall, because the contact angle on both sides of the partition subsequently increases from 90° to about 120° due to the tendency toward hexagonal pattern formation).

It is a working hypothesis that there is a tendency of cell divisions to be normal (in sense of cell plate orientation) to a principal direction of growth, and that this tendency is the higher the higher is the anisotropy ratio. This hypothesis is based on the observation that, within groups (packets) of cells of the same lineage all derived from one cell within a meristem, there is a relation between the degree of growth anisotropy of the group and the conformity of orientation of the partitions within it. The more pronounced is the maximal increment of one dimension of the group, say l_1, in comparison to increments of the dimensions orthogonal to l_1, the higher is the tendency of partition orientation to be normal to the extremal (maximal or minimal) increment of the group size. The majority of cell divisions are normal to the direction of maximal increment, however some are normal to that of minimal increment.

Condition C points out the importance of steadiness in the pattern of principal direction trajectories. Only steady or nearly steady patterns of principal trajectories are considered in this paper, but it should be noted that steadiness characterizes a very broad class of growing organs, as will be shown later.

Important hints about principal direction trajectories can be derived from inspection of the surface layer of an organ. Usually periclinal and anticlinal walls, which maintain mutual orthogonality during growth are evident in this layer. This indicates that one principal direction is normal to and the two remaining are tangent to the surface. There are no obvious deducible reasons that this must be so, in contrast to the principal directions of stress, however there is a good empirical basis to infere that it is so. On this assumption the shape of an organ provides important information about the trajectories of the principal directions of growth, at least in proximity to the surface. One trajectory is normal to, and the two remaining are tangent to the surface. Observe that this "rule" is already inherent in the statement that trajectories of principal directions of growth are manifested by the visible trajectories of the periclinal and anticlinal walls, because what is periclinal and anticlinal is defined with reference to organ surface.

The orientation of the two principal directions that are tangent to the surface can be recognized by epidermal cell patterns and/or by consideration of organ symmetry. If an organ is a figure of revolution around its axis, and if its tip does not rotate during growth, one principal direction at a point on its surface must be along the meridional line, the other along the latitudinal line crossing the point. Since the principal direction trajectories are continuous, their pattern when known at the surface can be extrapolated into the organ interior.

ORTHOGONAL CURVILINEAR COORDINATE SYSTEMS THAT CAN COINCIDE WITH THE TRAJECTORIES OF PRINCIPAL DIRECTIONS OF GROWTH

A coordinate system (y^1, y^2, y^3) such as we seek should obey two conditions. 1) One coordinate surface should coincide with organ surface, for instance, in the case of paraboloidal apical domes a paraboloidal coordinate system (u, v, φ) is appriopriate (Fig. 2a). The coordinate surface $v=$constant then represents the dome surface. 2) The eigenvectors of the symmetric part of the growth tensor T_{pq} represented in this coordinate system should coincide with the coordinate lines, which means that the tensor components, except those on the main diagonal, are skew-symmetric, i.e. $T_{pq} = -T_{qp}$ when $p \neq q$. What can be inferred from this concondition?

The physical component T_{pq} corresponding to the tensorial component $t_q^p = v_{,q}^p$ is $T_{pq} = \dfrac{\sqrt{g_{pp}}}{\sqrt{g_{qq}}} \, v_{,q}^p$ (without summation over p and q). The covariant derivative is $v_{,q}^p = \dfrac{\delta v^p}{\delta y^q} + \Gamma_{qr}^p \, v^r$ (summation over r). Thus the condition that the nondiagonal components must be skew symmetric can be written:*

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* $\dfrac{\delta v^p}{\delta y^q}$ denotes partial derivative and not intrinsic or absolute derivative

A. Paraboloidal coordinates (u, v, ϕ)

$$x = uv \cos\phi$$
$$y = uv \sin\phi$$
$$z = \frac{1}{2}(u^2 - v^2)$$
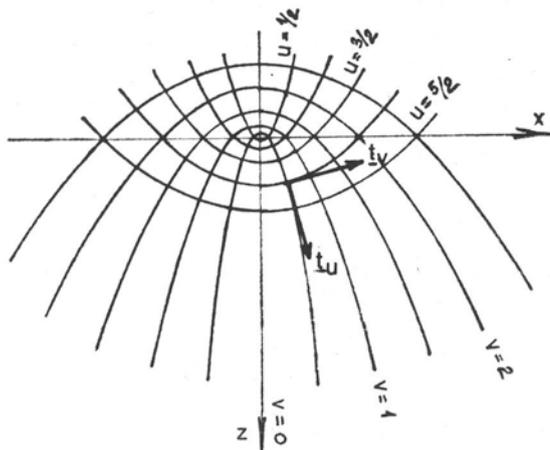
where $u \geqslant 0$, $v \geqslant 0$,
$$0 \leqslant \phi \leqslant 2\pi$$

$$h_u = h_v = \sqrt{u^2 + v^2}$$
$$h_\phi = u \cdot v$$

B. Prolate spheroidal coordinates (ξ, η, ϕ)

### B.1. for ellipsoidal dome

$$x = a \sinh\xi \sin\eta \cos\phi$$
$$y = a \sinh\xi \sin\eta \sin\phi$$
$$z = a \cosh\xi \cos\eta$$
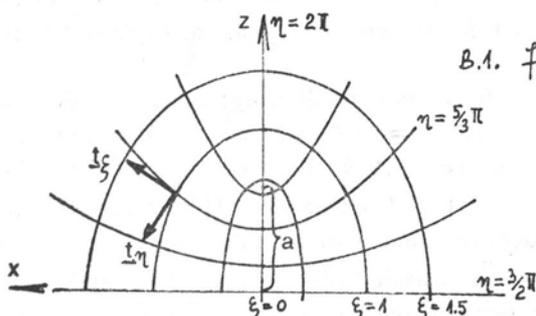
where $\xi \geqslant 0$, $0 \leqslant \eta \leqslant \pi$
$$0 \leqslant \phi \leqslant 2\pi$$

$$h_\xi = h_\eta = a\sqrt{\sinh^2\xi + \sin\eta}$$
$$h_\phi = a \sinh\xi \sin\eta$$

B.2. for hyperboloidal dome

Fig. 2. Natural coordinate systems for apical domes

$$\frac{\sqrt{g_{pp}}}{\sqrt{g_{qq}}}\left(\frac{\delta v^p}{\delta y^q} + \Gamma^p_{qr} v^r\right) = -\frac{\sqrt{g_{qq}}}{\sqrt{g_{pp}}}\left(\frac{\delta v^q}{\delta y^p} + \Gamma^q_{pr} v^r\right), \text{ when } p \neq q.$$

From this equation it follows that: (A) v^p cannot be a function of y^q if $p \neq q$, i.e.
$$\frac{\delta v^p}{\delta y^q} = \frac{\delta v^q}{\delta y^p} = 0 \quad \text{and (B) that } g_{pp} \Gamma^p_{qr} = -g_{qq} \Gamma^q_{pr} v^r, \text{ when } p \neq q. \text{ Condition (A)}$$

refers to the way of defining the field V and will be considered in next section. Condition (B) refers to the coordinate system alone, which we will consider now.

For orthogonal coordinate system $\Gamma^p_{qr} = \Gamma^q_{pr} = 0$, if p, q, r are all distinct. Thus we can conclude that in case of non-vanishing Christoffel's symbols, when $p \neq q, r$ is either equal to p or to q. For a specified r condition (B) can be written:

$$g_{pp} \, \Gamma^p_{qp} = -g_{qq} \, \Gamma^q_{pp} \, , \qquad \text{when } r = p,$$

$$g_{pp} \, \Gamma^p_{qq} = -g_{qq} \, \Gamma^q_{pq} \, , \qquad \text{when } r = q.$$

Since for orthogonal coordinate systems (Spiegel 1959):

$$\Gamma^p_{qp} = \frac{1}{2 \, g_{pp}} \, \frac{\delta g_{pp}}{\delta y^q} \quad \text{and} \quad \Gamma^p_{qq} = -\frac{1}{2 \, g_{pp}} \, \frac{\delta g_{qq}}{\delta y^p}$$

we see that condition (B) is fulfilled for these systems.

Several orthogonal coordinate systems have been selected for presentation by graphs and by equations that relate specific systems to rectangular coordinates. The scale factors $h_i = \sqrt{g_{ii}}$ (without summation over i) are given too, because they are important in specification of the field V for the growing organ, as explained in the next section.

The geometric meaning of a scale factor is the following: If we consider two neighboring coordinate surfaces $y^i = c$, and $y^i = c + \Delta c$, where c is a constant, then the physical distance between these surfaces is $\Delta c \, h_i$. For instance, h_u for paraboloidal coordinate system (u, v, φ) (Fig. 2a), is $h_u = \sqrt{u^2 + v^2}$. This means that the distance between the anticlinal surfaces $u = c$ and $u = c + \Delta c$ does not depend on φ but on u and v, and is $\Delta c \sqrt{u^2 + v^2}$. If we consider u-lines as periclines and v-lines as anticlines (Fig. 2a), the distance between the periclines $v = c$ and $v = c + \Delta c$ is also $\Delta c \sqrt{u^2 + v^2}$.

The coordinate systems are grouped according to the type of organ the surface of which conforms to the system (Figs. 2-6). The systems presented are those which will be applied in subsequent papers.

THE IMPORTANCE OF THE NATURAL COORDINATE SYSTEM FOR DESCRIPTION OF GROWTH

The natural coordinate system facilitates calculations of the field V for the whole organ from fragmentary data. Observe that the field cannot be defined arbitrary because the growth of all continuous elements must be compatible, i.e. the various organ parts must not be torn apart. Compatibility is secured if the field V is expressible by contravariant components, and if each component v^p is a function of p-coordinate only. The last condition is fulfilled if the eigenvectors of the growth tensor coincide with coordinate lines (condition A in the previous section, which means that we are dealing with the natural coordinate system).

A. Parabolic cylindrical coordinates (u, v, z)
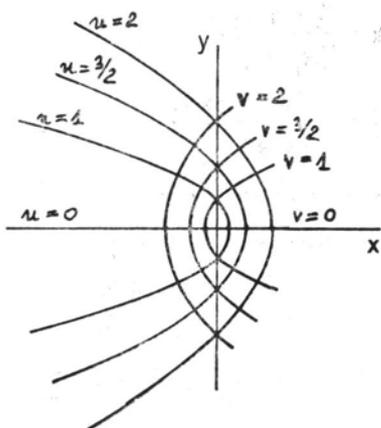

$$x = \tfrac{1}{2}(u^2 - v^2)$$

$$y = uv$$

$$z = z$$

where: $-\infty < u < \infty \quad v \geqslant 0$

$$h_u = h_v = \sqrt{u^2 - v^2}$$

$$h_z = 1$$

B. Elliptic cylindrical coordinates (u, v, z)
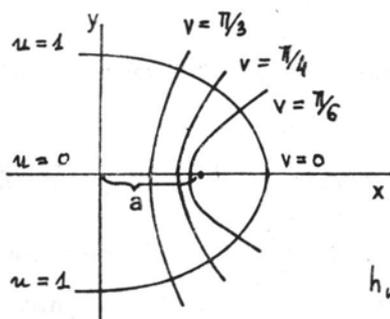
$$x = a \cosh u \cos v$$

$$y = a \sinh u \sin v$$

$$z = z$$

where: $u \geqslant 0 \quad 0 \leqslant v < 2\pi$

$$-\infty < z < \infty$$

$$h_u = h_v = a\sqrt{\sinh^2 u + \sin^2 v} \qquad h_z = 1$$

Fig. 3. Natural coordinate systems for marginal meristem of a leaf

Condition A implies that v^p is the same over the whole coordinate surface $y^p = a$. What is its implication with reference to the physical component V_p (whenever we deal with physical components we use capital letters as symbols). We have $V_1 = \sqrt{g_{11}}\, v^1 = h_1\, v^1$ where the component of the metric tensor, g_{11}, and also the scale factor, $h_i = \sqrt{g_{ii}}$, are functions of y^1, y^2 and y^3, while v^i is a function only of y^i. Expressions for V_2 and V_3 are analogous.

Let V^1 be known along the coordinate line y^1 such that $y^2 = a$, $y^3 = b$, where a, b are constants. Let us denote the physical component V_1 and the scale factor h_1 along the specified coordinate line by $\tilde{V}_1$ and $\tilde{h}_1$ respectively, i.e. $\tilde{V}_1$ means: $V_1(y^1, y^2 = a, y^3 = b)$. We thus have on the specified line: $\tilde{V}_1 = \tilde{h}_1\, v^1$ and in general: $V_1 = h_1\, v^1$. Introducing v^1 from the equation for the specified line into the last
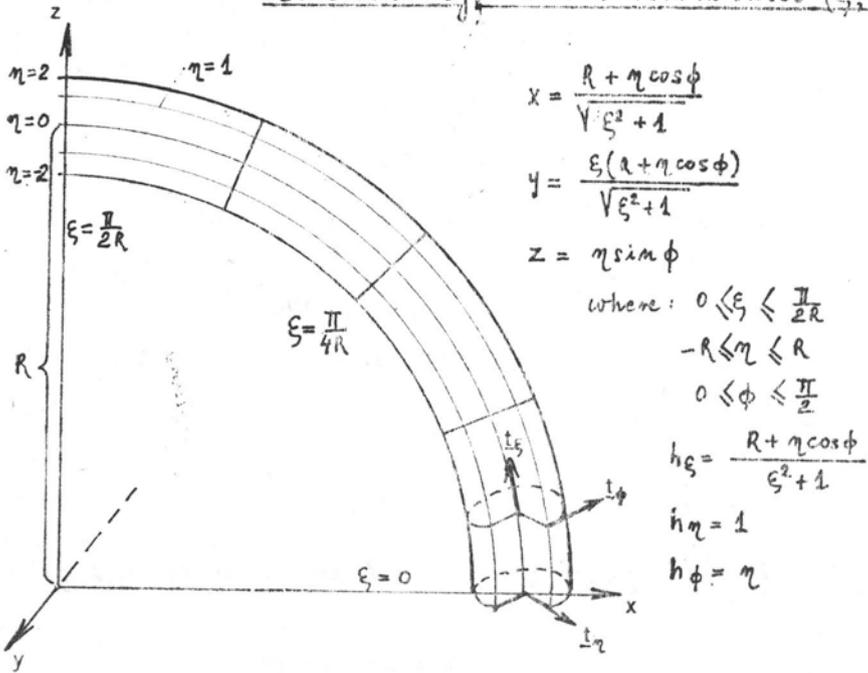
Fig. 4. Natural coordinate system for a circularly curved cylindrical axis (hook)

equation we obtain $V_1 = \dfrac{h_1}{\tilde{h}_1} \, \tilde{V}_1$. Similarly, if we now v^2 on one line y^2 specified

by $y^1 = c$, $y^3 = d$, the physical component V_2 is $V_2 = \dfrac{h_2}{\tilde{h}_2} \, \tilde{V}_2$. This procedure of

scaling of $\underline{V}$ for the whole organ agrees with that presented earlier (Hejnowicz

1982) according to which $V = \dfrac{(\mathrm{grad}\,G)_c^2}{(\mathrm{grad}\,G)^2}$ grad G, where c defines this

displacement line along which the vector $\underline{V}$ is known, and G is a scalar such that

$\dfrac{\mathrm{grad}\,G}{|\mathrm{grad}\,G|} = e_s$, where e_s is a unit vector tangent to the displacement line

running through the considered point, and $|\mathrm{grad}\,G|$ gives the magnitude of $\underline{V}$.

According to present notation $(\mathrm{grad}\,G_c) = \widetilde{\mathrm{grad}}\,G$. Namely, we have for the com-

ponent V_1, $V_1 \, t_1 = \dfrac{(\widetilde{\mathrm{grad}}\,G)^2}{(\mathrm{grad}\,G)^2}$ grad G. Now grad G is tangent to the co-

ordinate line y^1, i.e. $\dfrac{\mathrm{grad}\,G}{|\mathrm{grad}\,G|} = t_1$ (where $\underline{t}_1$ is the unit base vector), which

means that G is a function of y^1 only. In a curvilinear orthogonal coordinate sys-
tem we have:

Prolate spheroidal coordinates (ξ, η, ϕ)

/the same as in Fig. 2 B/
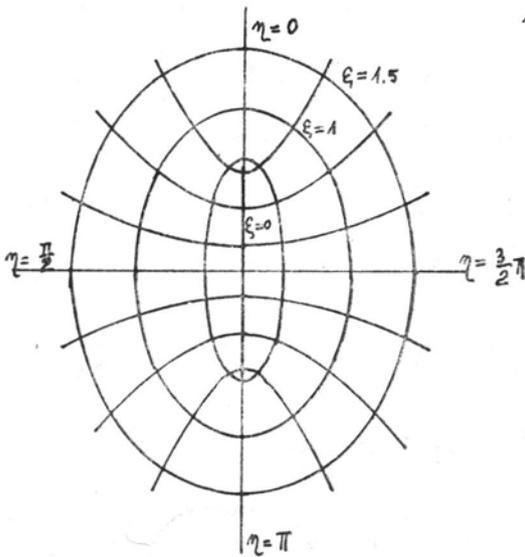
The sequence of shape change
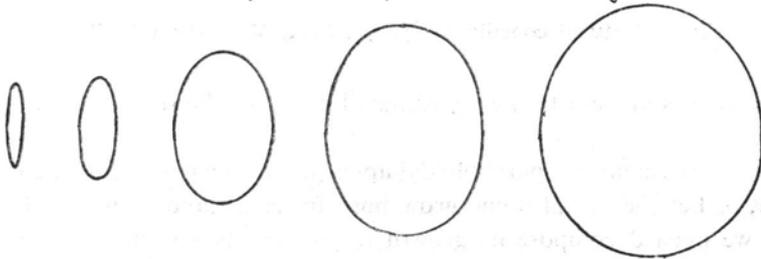
Fig. 5. Natural coordinate system for *Cucurbita*-type fruit

$$\text{grad } A = \frac{1}{h_1} \frac{\delta A}{\delta y^1} \underline{t_1} + \frac{1}{h_2} \frac{\delta A}{\delta y^2} \underline{t_2} + \frac{1}{h_3} \frac{\delta A}{\delta y^3} \underline{t_3},$$

thus $V_1 = \dfrac{(h_1)^2}{(\tilde{h}_1)^2} \dfrac{1}{h_1} \dfrac{\delta G}{\delta y^1}$ and $\tilde{V}_1 = \dfrac{1}{\tilde{h}_1} \dfrac{\delta G}{\delta y^1}.$

Introducing $\dfrac{\delta G}{\delta y^1}$ from the last equation into the previous one we obtain $V_1 =$

$= \dfrac{h_1}{\tilde{h}_1} \tilde{V}_1$, which is identical with the equation for V_1 derived from the contra-

variant component. The same procedure for V_2 starts with $V_2 t_2 = \dfrac{(\widetilde{\text{grad } G})^2}{(\text{grad } G)^2} \text{ grad } G$

Toroidal coordinates (ξ, η, ϕ)

$$x = \frac{a \sin \xi}{\cosh \eta - \cos \xi} \cos \phi$$

$$y = \frac{a \sin \xi}{\cosh \eta - \cos \xi} \sin \phi$$

$$z = \frac{a \sin h \eta}{\cosh \eta - \cos \xi}$$
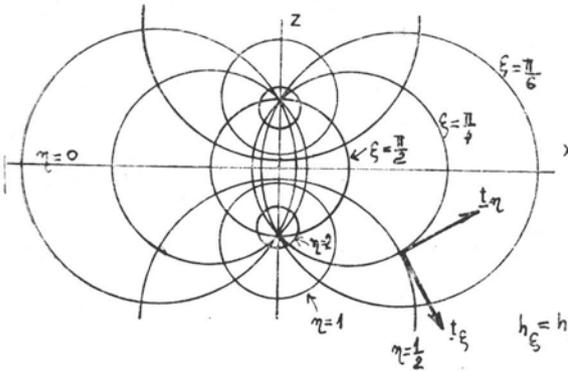
where $\quad 0 \leqslant \xi \leqslant 2\pi$

$-\infty < \eta < \infty \quad 0 \leqslant \phi \leqslant 2\pi$

$$h_\xi = h_\eta = \frac{a}{\cosh \eta - \cos \xi} \qquad h_\phi = \frac{a \sin \xi}{\cosh \eta - \cos \xi}$$

The sequence of shape change
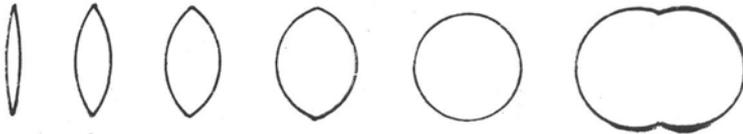
Fig. 6. Natural coordinate system for a *Malus*-type fruit

(but now grad *G* is tangent to the coordinate line y^2, so the *G* is not the same as previously).

Consider as an example, a paraboloidal apical dome in a paraboloidal coordinate system u, v, φ. Let the apical dome grow both in length and in width. To model its growth we must decompose its growth tensor into two parts, one for growth in length and another for growth in width, because we must specify the components of $\underline{V}$ separately. The growth in length is expressed by only the u-component of $\underline{V}$. The growth in width is expressed by only the v-component of $\underline{V}$.

Considering first the growth in length let, for instance, V_u be proportional to u on the axis which is defined by $v=0$. Thus the field V_u is $V_u = \dfrac{\sqrt{u^2 + v^2}}{\sqrt{u^2}} \quad ku =$

$= k\sqrt{u^2 + v^2}$. This V_u enters the growth tensor which describes the growth of the dome "in length" (Hejnowicz et al. 1984) and which is in paraboloidal coordinate system. Let us denote this tensor by U.

Consider now the growth "in width". The width of the dome corresponds to the v-coordinate line. An increase in the v-dimension of the dome requires a non-zero v-component of the field $\underline{V}$. Let the rate of width increase at the dome surface, i.e. when $v=s$, at a certain distance from the vertex, $u=b$, be 1, i.e. $V_v=1$ when $u=b$ and $v=s$. We need to know V_v as a function of distance from the axis. Imagine

that inspection of transections through the dome enables to make the assumption that V_v is proportional to v (unrealistic but simple) i. e. $V_y = \dfrac{1}{s} v$ when $u = b$.

Thus the field V_v for the whole dome is $V_v = \dfrac{\sqrt{u^2 + v^2}}{\sqrt{b^2 + v^2}} \dfrac{1}{s} v$. This field enters the growth tensor formulated for the paraboloidal coordinate system and describes the growth of the dome "in width" when $V_v = v \, 1/s$ at $u = b$. Let us denote this as tensor W.

Tensors of the same rank can be added. If we add the two growth tensors U and W we obtain the more general growth tensor which describes the growth of the apical dome both "in length" and "in width", i.e. the apical dome which remains paraboloidal but which width measured at certain distance from the vertex increases.

The considered example illustrates what relations or attributes are steady during the mode of organ growth considered in this paper. The pattern of principal direction trajectories is steady. The type of organ shape is steady. The geometry is not necessarily steady. The considered apical dome described by $U + W$ remains paraboloidal during growth, but becomes wider and wider.

Details of using the natural coordinate system in modeling of growth of plant organs will be illustrated in a subsequent paper (Hejnowicz et al. 1984).

THE IMPORTANCE OF PRINCIPAL DIRECTION TRAJECTORIES IN STUDIES OF ORIENTED MORPHOLOGICAL PHENOMENA

It is tempting to ask what might be the relationship between the principal direc" tions of growth and directions distinguished with regard to other phenomena and processes occurring in growing organs. The list of the phenomena could be ong, but let us examine two examples.

ORIENTATION OF CELL DIVISIONS

In many meristematic organs the periclinal and anticlinal walls can be recognized. Since they remain orthogonal during growth, we can infer that the new partitions produced by cell divisions are oriented in planes of principal directions of growth.

It is known that in organs growing mainly in one direction, s_{max} the orientation of cell divisions is quite regular; majority of the divisions result in partitions perpendicular to s_{max} and a rib meristem arises. Obviously s_{max} is in the principal direction having the maximal growth rate. The growth rates in the two remaining principal directions are much lower in such cases; yet there are some cell divisions, strictly normal to these directions also, though they are rare, for instance the divisions producing longitudinal partitions in root meristem cortex. It seems that the divisions are always normal to a principal direction when the principal growth

rate corresponding to this direction differs distinctly from the rates in the two remaining principal directions. A corollary hypothesis is that: a) there is a tendency for a newly formed partition to be normal to one of the principal directions of growth; b) that tendency is the stronger the more pronouced is the difference between the principal growth rates.

The plane of cell division is considered to be the plane of minimum shear stress, or shear-free plane (Lintilhac 1974). However, it is not clear exactly what the term "shear-free plane" means for a cell. Is it a sectioning plane determined by the stress status of the cell wall or of the cytogel inside the wall? The two planes do not necessarily coincide, because the stress state within the cytogel depends not only upon tractions exerted by cell wall but also upon arrangement of cytoplasmic filamants and distribution of the local stresses resulting from active interactions between the filaments. Perhaps the shear-free plane in Lintilhac's concept (1974) is equivalent to the plane element normal to a principal direction of growth.

ORIENTATION OF THE PRINCIPAL DIRECTIONS OF STRESSES WITHIN THE CELL WALL NETWORK

The growth of a plant organ is the result of the yielding of the cell walls to the tensional stresses generated by hydrostatic pressures of the protoplasts and by tensions occurring within the organ. The cell wall is in a state of tension which brings about elastic strain and plastic deformation. The latter depends on wall--loosening activity which is controlled by the protoplast (Green 1973). In the plane of the cell wall there are two principal directions of stress. The relation of these directions of stress to the principal direction of growth is complex when a cell wall is not in the plane of the two principal directions of growth. When it is, the principal directions of growth and of tensional stress probably often coincide. Even when the principal directions coincide, there are two possibilities; the maximal principal growth rate may coincide either with the maximal or with the minimal principal stress. It seems that the second alternation is often true: the maximal principal growth rate coincides with the minimal principal tension in the cell wall. Such relation seems to be typical for cells growing at their tips (Hejnowicz et al. 1977). In cylindrical rubber ballon undergoing inflation distention starts in the proximal part and the maximal principal stress is in the latitudinal direction. When the strain becomes hardened in this direction distention is propagated acropetally as additional gas is forced in. In a plant cell the strain "hardening" is actively reinforced by deposition of oriented cellulose microfibrils. If one principal direction of stress is reinforced, the loosening activity of the protoplast favors plastic expansion in another principal direction of stress, which is that of minimal stress (tension). If so, it is also the direction of maximal growth rate.

Stress can be recognized by the consequent elastic strain, thus a problem appears: How can a cell recognize the principal stress if the corresponding elastic strain is masked by plastic expansion? An appriopriate answer may be the oscillatory variation of elastic strain in which the stress determines the frequency of the oscillation.

Whatever the mechanism of control of cell wall reinforcing, the principal direc tions of growth must be related to the direction of reinforcing unless the wall is outside the plane of the principal directions. It is tempting to think that the major role in controlling growth directionality in an organ is played by those walls that are tangent to two principal directions of growth. Cell walls within a growing organ may or may not be in such planes. However, those plane elements that together make up the organ surface are favored to be in the plane of the two principal directions of growth. If this rational is valid then the epidermal tangential walls play an important role in controlling growth directionality, in accord with the suggestion made by Green (1980).

Acknowledgments

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Trajektorie głównych kierunków wzrostu, naturalny układ współrzędnych w rosnącym organie roślinnym

Streszczenie

Główne kierunki wzrostu określone są przez wektory własne symetrycznej części tensora wzrostu. W każdym punkcie istnieją trzy takie kierunki, wzajemnie ortogonalne. W przypadku wzrostu izotropowego, powodującego jedynie zmianę skali organu, nie można wyróżnić głównych

kierunków wzrostu, bowiem wszystkie kierunki wokół punktu są równoważne. Dwa albo trzy elementy liniowe, np. elementy siatki ścian, stykające się w rozważanym punkcie i ułożone w głównych kierunkach wzrostu zachowują ortogonalność. Natomiast kąt prosty między elementami nie ułożonymi w głównych kierunkach ulega zmianie w czasie wzrostu organu na kąt ostry albo rozwarty. Względna elementarna szybkość wzrostu liniowego wokół rozważanego punktu przyjmuje wartości ekstremalne (maksimum albo minimum) w głównych kierunkach wzrostu. Określamy te ekstremalne wartości jako główne szybkości wzrostu. Im bardziej różni się od jedności stosunek dwu głównych szybkości wzrostu tym wyraźniej wykształcone są główne kierunki wzrostu. W przypadku wzrostu izotropowego główne kierunki nie są wykształcone. Z połączenia elementów liniowych, które w kolejnych punktach organu są styczne do głównych kierunków wzrostu otrzymujemy system ortogonalnych trajektorii. Tworzą one naturalny układ współrzędnych. Tensor wzrostu wyrażony w tym układzie ma diagonalizowaną część symetryczną, co wynika z własności wektorów własnych tensora. Wykazano, że w naturalnym układzie współrzędnych kontrawariantne składowe wektora szybkości przesunięć punktów materialnych rosnącego organu są funkcjami tylko tych współrzędnych do których się odnoszą, t.zn. składowa v^1 jest funkcją tylko współrzędnej u_1. Właściwość ta umożliwia wyznaczenie pola wektorowego V w składowych fizycznych dla całego organu na podstawie fragmentarycznych danych o szybkości wzrostu na pojedynczej linii współrzędnych, a tym samym wyznaczenie tensora wzrostu. Główne kierunki wzrostu można rozpoznać w rosnącym organie na podstawie trajektorii ścian komórkowych zachowujących ortogonalność w czasie wzrostu. Trajektorie te znane są jako perykliny i antykliny. Istotnej informacji o typie naturalnego układu współrzędnych dostarcza kształt organu, bowiem na ogół jeden z głównych kierunków wzrostu jest normalny do powierzchni organu. Zestawiono krzywoliniowe ortogonalne układy współrzędnych, które mogą być naturalnymi układami dla kilku typów rosnących organów.