

## Growth Tensor of Plant Organs

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Analysis of the definition of the relative elemental rate of growth of a line element,  $RERG_l$ , in a growing plant organ leads to the dyadic  $\nabla V$  where  $V$  is the vector field of displacement velocities of material points in the organ. The components of this dyadic represent physical components of a tensor, which we propose to call the growth tensor. The latter can be derived directly from the definition of  $RERG_l$ . The growth tensor allows full characterization of the rate of growth in length, area, and volume, as well as rates of angular change between elements, and of vorticity in the growing organ. From the fact that anticlinal and periclinal walls of cells within the organ preserve their orthogonality during growth, we infer that the principal directions of the growth tensor coincide with periclinal and anticlinal. The definition of the growth tensor based on the dyadic offers an easy way to generate this tensor in different coordinate systems. An example is given of the use of the growth tensor in analyzing elongation growth of a cylindrical plant organ in two alternative modes: with and without rotation of the tip. It is shown that growth by the two modes yields the same relative elemental rates of growth in volume, but that the principal directions of the growth tensors are different. We infer that if growth is a tensorial attribute of an organ, then the controls of growth must also be tensorial attributes. The controlling tensors must have at least as high a rank as the growth tensors, but must be of a higher hierarchical level.

### 1. Introduction

Is the growth rate of a plant organ a scalar or a vector quantity? That depends on the level of rigor with which we scrutinize our perception of

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growth. It seems obvious that a rate of growth in volume, having no defined direction, is a scalar. Superficially it may appear that a growth rate pertaining only to increase in length in a specified direction is a vector. Upon close scrutiny, however, we detect that because of "frame of reference" problems, simple specification of growth direction cannot unequivocally distinguish the head from the tail of the "vector". A simple linear growth rate specification is in fact a scalar defined along a certain direction. If we consider and specify such a scalar for every direction at a particular point, then we are simulating a tensor.

By invoking accepted definitions and conventions, we can say that if  $R$  denotes a region in space, and if for each point  $(x, y, z)$  in  $R$  there exists a corresponding number or scalar  $N(x, y, z)$ , then  $N$  is a scalar point function. Going further, we can rigorously specify a vector point function  $\mathbf{V}(x, y, z)$  by requiring that for each point in  $R$  there must be not only a scalar  $V$  representing the magnitude of the vector, but also a corresponding unit vector  $\mathbf{e}_{(s)}$  which specifies the direction of  $\mathbf{V}$ . If for every direction from every point in  $R$  we define a corresponding vector, then we have defined a tensor point function in  $R$ . This is an intuitive explanation of a tensor.

Tensor fields have been applied to the characterization of plant organ growth by Silk & Erickson (1979). They made an analogy between organ growth and fluid flow and treated the growth pattern as a deformation pattern in a compressible fluid, which undoubtedly is an appropriate analogy. Since the deformation is known to be characterized by the strain (or rate-of-strain) and vorticity tensors, these tensors have been used to characterize the growth pattern. The treatment of growth as a type of deformation already answers the question posed above: The growth rate is not a scalar, and not a simple vector, but a tensor quantity.

One can readily understand the tensorial character of growth treated as a kind of deformation by first accepting an informal explanation of the meaning of the term "tensor point function". Let us suppose that within a growing organ we can determine the displacement, relative to a chosen point  $P_0$ , of the material points (microparticles in the cell wall network) located on the surface of a sphere of radius  $r$  centered on  $P_0$ . The initial position of any point on the sphere, with respect to  $P_0$ , can thus be represented by a position vector  $\mathbf{r}_s$  which equals  $r\mathbf{e}_{(s)}$ , where  $\mathbf{e}_{(s)}$  is the unit vector defining the direction. During a short time interval of growth,  $\Delta t$ , all points on the sphere are displaced with respect to  $P_0$ . As a consequence, for each vector  $\mathbf{e}_{(s)}$  there is generated another specific vector representing the change of position during  $\Delta t$  of the specific point toward which  $\mathbf{e}_{(s)}$  was initially directed. This procedure is valid for every point in the growing

organ; thus, according to our informal definition of a tensor point function, the growth is specified by such a function.

In this paper we will provide a rigorous rationale for the preceding statement by logical analysis of the definition of relative elemental rate of growth in length,  $RERG_l$ , of an element in a growing organ. This analysis leads to a tensor quantity describing the growth rate, which we will call the growth tensor. An example of the use of the growth tensor will be given for representation of the growth of a cylindrical organ in two alternative modes: with and without rotation of the tip. This example shows how understandable growth with rotation appears in this representation, though otherwise it is difficult to grasp.

The basic notations used herein are explained in Appendix A.

## 2. Derivation of the Growth Tensor

An assumption basic to the derivation of the growth tensor is that plant organs grow symplastically. Necessary corollaries are: (1) that cells maintain their mutual-contact neighborhoods during growth, and (2) that the displacement of definable points in the cell network (such as intersections of cell edges, or distinctive wall features) is ascribable only to growth. These conditions, we believe, are generally met in primary growth of plant organs. They may not be fully met in secondary growth of woody stems, especially if there is extensive intrusive growth of cambial initial cells and their differentiating derivatives. Such secondary growth, however, is beyond the scope of this discussion.

During primary growth every definable point within the organ moves with a velocity  $\mathbf{V}$  relative to some reference point. Accordingly  $\mathbf{V}$  is a vector point function and has three components,  $V_x$ ,  $V_y$ , and  $V_z$ , each of which is a scalar point function. Now consider two vicinal points,  $P^{(1)}$  and  $P^{(2)}$ , through which a straight line,  $s$ , is drawn. The line segment between the two points has a length of  $\Delta s$ . Let  $V_s^{(1)}$  and  $V_s^{(2)}$  represent the magnitudes of the velocities of points  $P^{(1)}$  and  $P^{(2)}$ , respectively. If  $V_s^{(1)}$  and  $V_s^{(2)}$  are unequal, the difference is the result of growth between these points along the direction  $s$ . The measure of this growth is the (local) relative elemental rate of growth of the line element in the direction  $s$ . This is abbreviated and mathematically defined as:

$$RERG_{l(s)} = \lim \frac{\Delta(\Delta s)}{\Delta s \Delta t} = \frac{d(ds/dt)}{ds} = \frac{dV_s}{ds}$$

(Richards & Kavanagh, 1943; Erickson, 1976; Hejnowicz, 1982). If the velocity vector field,  $\mathbf{V}$ , is known, the displacement velocity in the direction

$s$  is the scalar product (dot product) of  $\mathbf{V}$  at the point of calculation and the unit vector  $\mathbf{e}_{(s)}$ , which specifies the direction  $s$ . Thus we write:

$$\text{RERG}_{l(s)} = \frac{d(\mathbf{V} \cdot \mathbf{e}_{(s)})}{ds}.$$

Now the derivative of the scalar  $\mathbf{V} \cdot \mathbf{e}_{(s)}$  in the direction  $s$  can be determined from its gradient (grad, or  $\nabla$ , where  $\nabla$  is "nabla" and the bold type emphasizes its vectorial character):

$$\frac{d(\mathbf{V} \cdot \mathbf{e}_{(s)})}{ds} = \nabla(\mathbf{V} \cdot \mathbf{e}_{(s)}) \cdot \mathbf{e}_{(s)},$$

and necessarily then,

$$\text{RERG}_{l(s)} = \nabla(\mathbf{V} \cdot \mathbf{e}_{(s)}) \cdot \mathbf{e}_{(s)}.$$

In such representations the scalar  $\mathbf{V} \cdot \mathbf{e}_{(s)}$  depends both on position and direction. This is so because growth in organs generally is not uniformly distributed and  $\mathbf{V}$  is a function of position. Necessarily then,  $\nabla(\mathbf{V} \cdot \mathbf{e}_{(s)})$  is also a function of position as well as of the specified direction. However, by an extension of the rationale introduced above,  $\nabla(\mathbf{V} \cdot \mathbf{e}_{(s)})$  can be expressed as the product of an entity which is a function of position only and the vector  $\mathbf{e}_{(s)}$ . Namely

$$\nabla(\mathbf{V} \cdot \mathbf{e}_{(s)}) = (\nabla\mathbf{V}) \cdot \mathbf{e}_{(s)} + (\nabla\mathbf{e}_{(s)}) \cdot \mathbf{V} \quad (1)$$

where  $\nabla\mathbf{V}$  and  $\nabla\mathbf{e}_{(s)}$  are generalized vectors or dyadics. The dyadic  $\nabla\mathbf{V}$  is a function of position only. For example, in rectangular coordinates we can write the dyadic  $\nabla\mathbf{V}$  as the product of two three-term factors, or as an array of nine terms each consisting of a coefficient and a unit dyad:

$$\nabla\mathbf{V} = \left( \frac{\partial}{\partial x} \mathbf{i} + \frac{\partial}{\partial y} \mathbf{j} + \frac{\partial}{\partial z} \mathbf{k} \right) \cdot \left( V_x \mathbf{i} + V_y \mathbf{j} + V_z \mathbf{k} \right)$$

or

$$\begin{aligned} \nabla\mathbf{V} = & \frac{\partial V_x}{\partial x} \mathbf{ii} + \frac{\partial V_y}{\partial x} \mathbf{ij} + \frac{\partial V_z}{\partial x} \mathbf{ik} + \\ & \frac{\partial V_x}{\partial y} \mathbf{ji} + \frac{\partial V_y}{\partial y} \mathbf{jj} + \frac{\partial V_z}{\partial y} \mathbf{jk} + \\ & \frac{\partial V_x}{\partial z} \mathbf{ki} + \frac{\partial V_y}{\partial z} \mathbf{kj} + \frac{\partial V_z}{\partial z} \mathbf{kk} \end{aligned}$$

which may be abbreviated as

$$\nabla \mathbf{V} = \frac{\partial V_q}{\partial x_p} \mathbf{t}_p \mathbf{t}_q,$$

which in turn can be abbreviated to  $T_{pq} \mathbf{t}_p \mathbf{t}_q$ . In this equation  $\mathbf{t}_p$  represents the rectangular unit vectors in the directions  $p$ .

Correspondingly,

$$\nabla \mathbf{e}_{(s)} = \frac{\partial e_q}{\partial x_p} \mathbf{t}_p \mathbf{t}_q$$

where the values assigned to  $e_q$  are direction cosines of the unit vector  $\mathbf{e}_{(s)}$  defining the direction  $s$ . Because, for a particular direction, the direction cosines are constant, all coefficients of the dyadic  $\nabla \mathbf{e}_{(s)}$  are zeros and the second dyadic on the right side of equation (1) vanishes. Thus:

$$\nabla(\mathbf{V} \cdot \mathbf{e}_{(s)}) = (\nabla \mathbf{V}) \cdot \mathbf{e}_{(s)} \quad \text{and} \quad \text{RERG}_{l(s)} = (T_{pq} \mathbf{t}_p \mathbf{t}_q) \cdot \mathbf{e}_{(s)} \cdot \mathbf{e}_{(s)} = T_{pq} e_p e_q.$$

Similar formulas applicable to curvilinear orthogonal coordinates can be written. In such,  $T_{pq}$  represents the physical components of the dyadic;  $\mathbf{t}_i$  are unit vectors tangent to the coordinate curves; and  $\mathbf{e}_i$  are physical components of the unit vector in the direction  $s$ . Such formulas are dyadic expressions for the relative elemental rate of growth of a line element in the direction  $s$ . We propose to call the dyadic  $\nabla \mathbf{V}$  the growth dyadic.

It is known that a dyadic is equal to, or represents, a second rank tensor. Whether it actually equals or only represents the indicated tensor depends on (1) the coordinate system, and (in the case of a curvilinear system) on (2) the nature of the components by which the vectors are represented. In rectangular coordinates, there is only one type of component and a dyadic is a cartesian tensor. In curvilinear coordinates (which usually must replace rectangular coordinates in descriptions of plant organs) the dyadic is equal to a tensor only when its components are expressed in tensorial form rather than as physical components, i.e., expressed either as covariant or contravariant vectors.

Such expression is always possible if the metric tensor is known. Thus a tensor corresponding to the growth dyadic can always be calculated from the physical components of the dyadic. It can be shown, moreover, that a tensor also follows directly from the definition of  $\text{RERG}_{l(s)}$ . (We did not begin this section with such a direct tensor derivation, because that approach would require the reader to have a knowledge of tensor analysis.) To wit: If we have

$$\text{RERG}_{l(s)} = \frac{d(\mathbf{V} \cdot \mathbf{e}_{(s)})}{ds} = (\nabla \mathbf{V}) \cdot \mathbf{e}_{(s)} \cdot \mathbf{e}_{(s)},$$

but we also have

$$\frac{d\mathbf{V}}{ds} = (\nabla\mathbf{V}) \cdot \mathbf{e}_{(s)},$$

then

$$\text{RERG}_{l(s)} = \frac{d\mathbf{V}}{ds} \cdot \mathbf{e}_{(s)}.$$

Now  $d\mathbf{V}/ds$  can be expressed as the absolute derivative of  $\mathbf{V}$  with respect to the line  $s$ :

$$\frac{d\mathbf{V}}{ds} = \frac{DV^k}{ds}.$$

The absolute derivative in turn can be expressed by the covariant derivative

$$\frac{DV^k}{ds} = V^k_{,n} \frac{dy^n}{ds},$$

in which the  $n$  factors of  $dy^n/ds$  are contravariant components of the unit vector representing the direction  $s$ :

$$\frac{dy^n}{ds} = e^n.$$

Thus:

$$\frac{DV^k}{ds} = V^k_{,n} e^n.$$

To evaluate  $\text{RERG}_{l(s)}$ , which is a scalar, we must take the inner product of  $V^k_{,n} e^n$  and the vector  $\mathbf{e}_s$ . Because  $V^k_{,n} e^n$  is a contravariant vector, to find the inner product we must act on it with the vector  $\mathbf{e}_{(s)}$ , which is represented by its covariant components  $e_k$ . Thus:

$$\text{RERG}_{l(s)} = V^k_{,n} e^n e_k = T^n_k e^n e_k.$$

This is the tensor representation of  $\text{RERG}_{l(s)}$ . We propose to call the tensor  $T^n_k$  the growth tensor. This growth tensor is the covariant derivative of  $\mathbf{V}$ .

Now let us compare the two representations of  $\text{RERG}_{l(s)}$ : as  $T_{pq} e_p e_q$  (the dyadic form) and as  $T^q_p e^p e_q$  (the tensor form). The positions of the subscripts indicate that we are dealing with physical components in the dyadic representation and with tensorial components in the alternate representation. The physical components,  $T_{pq}$ , are generally not equal to the tensorial components,  $T^q_p$ , but for every set of values of one there is a corresponding

set for the other. In orthogonal coordinate systems

$$T_{pq} = \frac{\sqrt{g_{qq}}}{\sqrt{g_{pp}}} T_p^q$$

where  $g_{ii}$  are the components of the metric (or fundamental) tensor.

How can we calculate the physical components of the growth tensor? For someone skilled in tensor analysis, it is no great problem to calculate the covariant derivative of  $\mathbf{V}$  for a chosen coordinate system and then to recalculate these tensor components into the physical components of the growth tensor. For most biologists, however, the fundamentals of tensor analysis are more difficult to grasp than those of vector analysis, and the latter are adequate to calculate the physical components of the growth dyadic, which are identical with the physical components of the growth tensor. The calculation of the growth dyadic in terms of physical components is straightforward.

Let  $V_j$  represent the components of the vector  $\mathbf{V}$  in a chosen coordinate system. Let  $\mathbf{t}_j$  represent the unit vectors tangent to the coordinate lines  $u_j$  at  $P$ . We operate on the vector  $\mathbf{V} = V_j \mathbf{t}_j$  with the vector differential operator  $\nabla$  (nabla) expressed in the chosen system:

$$\nabla = \frac{\mathbf{t}_1}{h_1} \frac{\partial}{\partial h_1} + \frac{\mathbf{t}_2}{h_2} \frac{\partial}{\partial h_2} + \frac{\mathbf{t}_3}{h_3} \frac{\partial}{\partial h_3}$$

where  $h_i$ , the so-called scale factors, are given by

$$h_i = \left| \frac{\partial \mathbf{r}}{\partial u_i} \right|,$$

where  $\mathbf{r}$ , in turn, represents the position vector of point  $P$ . Therefore, the dyadic is

$$\begin{aligned} \nabla \mathbf{V} &= \left( \frac{\mathbf{t}}{h} \right)_i \frac{\partial}{\partial u_i} (V_j \mathbf{t}_j) \\ &= \left( \frac{\mathbf{t}}{h} \right)_i \left[ \frac{\partial V_j}{\partial u_i} \mathbf{t}_j + V_j \frac{\partial \mathbf{t}_j}{\partial u_i} \right] \\ &= \frac{1}{h_i} \frac{\partial V_j}{\partial u_i} \mathbf{t}_i \mathbf{t}_j + \frac{1}{h_i} V_j \mathbf{t}_i \frac{\partial \mathbf{t}_j}{\partial u_i}. \end{aligned}$$

After the differentiation of unit base vectors is performed, the resulting dyadic components are grouped into a matrix array with rows headed by  $i$  and columns headed by  $j$  of the unit dyads  $\mathbf{t}_i \mathbf{t}_j$ . For example, in cylindrical

coordinate systems  $(r, \phi, z)$  the matrix of the growth tensor has the form:

$$\begin{pmatrix} \frac{\partial V_r}{\partial r} & \frac{\partial V_\phi}{\partial r} & \frac{\partial V_z}{\partial r} \\ \frac{1}{r} \left( \frac{\partial V_r}{\partial \phi} - V_\phi \right) & \frac{1}{r} \left( \frac{\partial V_\phi}{\partial \phi} + V_r \right) & \frac{1}{r} \frac{\partial V_z}{\partial \phi} \\ \frac{\partial V_r}{\partial z} & \frac{\partial V_\phi}{\partial z} & \frac{\partial V_z}{\partial z} \end{pmatrix}.$$

Though in biological practice the calculations may be based on the growth dyadic concept, we will use the term "growth tensor" rather than "growth dyadic" for semantic reasons—because the former term emphasizes that growth ideally is expressible as a tensorial quantity.

### 3. The Meaning of Growth Rate Components—Rate-of-Strain and Vorticity Tensors

The general expression for  $\text{RERG}_i$  at a point  $P$  in a growing organ in a direction  $s$  specified by the unit vector

$$\mathbf{e}_{(s)} = \cos(s, u_1)\mathbf{t}_1 + \cos(s, u_2)\mathbf{t}_2 + \cos(s, u_3)\mathbf{t}_3$$

or

$$\mathbf{e}_{(s)} = \alpha\mathbf{t}_1 + \beta\mathbf{t}_2 + \gamma\mathbf{t}_3,$$

the components of which are direction cosines with respect to the local base vectors, is:

$$\begin{aligned} \text{RERG}_{i(s)} &= T_{pq}e_{(s)p}e_{(s)q} = \begin{bmatrix} T_{11}\alpha^2 + T_{12}\alpha\beta + T_{13}\alpha\gamma + \\ T_{21}\beta\alpha + T_{22}\beta^2 + T_{23}\beta\gamma + \\ T_{31}\gamma\alpha + T_{32}\gamma\beta + T_{33}\gamma^2 \end{bmatrix} \\ &= T_{11}\alpha^2 + T_{22}\beta^2 + T_{33}\gamma^2 + (T_{12} + T_{21})\alpha\beta + (T_{13} + T_{31})\alpha\gamma \\ &\quad + (T_{23} + T_{32})\beta\gamma. \end{aligned}$$

Now, when the direction  $s$  is tangent to the  $u_1$  coordinate line,  $\cos(s, u_1) = \alpha = 1$ , while  $\beta$  and  $\gamma = 0$ . Hence all terms of the above array, except the first, become 0. The same arguments obtain when  $s$  coincides with the  $u_2$  and  $u_3$  coordinate lines so that  $T_{11} = \text{RERG}_{i(u_1)}$ ,  $T_{22} = \text{RERG}_{i(u_2)}$ , and  $T_{33} = \text{RERG}_{i(u_3)}$ . Thus the diagonal component of the growth tensor represents  $\text{RERG}_i$  in the direction of the corresponding coordinate line. It is known that the sum of  $\text{RERG}_i$  in three orthogonal directions represents the relative



elemental growth rate in volume (Richards & Kavanagh, 1943). In orthogonal coordinate systems  $\text{RERG}_{\text{vol}} = T_{11} + T_{22} + T_{33} = T_{pp} = \text{div } \mathbf{V}$ . This reflects the invariance of the scalar  $T_{pp}$ .

We have already seen that the non-diagonal components contribute to the  $\text{RERG}_{l(s)}$  when  $s$  is not tangent to the coordinate line or lines. To facilitate further interpretation of the non-diagonal components of the growth tensor, let us consider two mutually perpendicular, infinitesimal line elements which originate from the initial point  $P$  in a growing organ. Let the elements be represented by infinitesimal vectors  $\mathbf{a}$  and  $\mathbf{b}$ . Initially  $\mathbf{a} \cdot \mathbf{b} = 0$ , or  $(\mathbf{a}, \mathbf{b}) = \pi/2$ . Then let  $\mathbf{a}$  be tangent to coordinate line  $u_1$ , and  $\mathbf{b}$  tangent to coordinate line  $u_2$ , at  $P$ . Thus the direction of  $\mathbf{a}$  is represented by the unit vector  $\mathbf{e}_{(a)} = \mathbf{t}_1$ , and that of  $\mathbf{b}$  by  $\mathbf{e}_{(b)} = \mathbf{t}_2$ . These elements undergo changes in both length and direction during growth. The vectorial relative rates of these changes,  $\mathbf{c} = \Delta\mathbf{a}/\mathbf{a}\Delta t$ , can be obtained by multiplying the growth tensor by the unit vectors specifying the directions of the elements (Appendix 2). Thus for the time unit  $\Delta t = 1$ ,

$$\mathbf{c}_{(a)} = \frac{\Delta\mathbf{a}}{\mathbf{a}} = T_{pq}\mathbf{e}_{(a)q} = T_{11}\mathbf{t}_1 + T_{21}\mathbf{t}_2 + T_{31}\mathbf{t}_3,$$

and

$$\mathbf{c}_{(b)} = \frac{\Delta\mathbf{b}}{\mathbf{b}} = T_{pq}\mathbf{e}_{(b)q} = T_{12}\mathbf{t}_1 + T_{22}\mathbf{t}_2 + T_{32}\mathbf{t}_3.$$

As the organ grows, the elements  $\mathbf{a}$  and  $\mathbf{b}$  are transformed, so that

$$\mathbf{a} \rightarrow \mathbf{a}' = \mathbf{a} + d\mathbf{a} = a(1 + T_{11})\mathbf{t}_1 + aT_{21}\mathbf{t}_2 + aT_{31}\mathbf{t}_3$$

and

$$\mathbf{b} \rightarrow \mathbf{b}' = \mathbf{b} + d\mathbf{b} = bT_{12}\mathbf{t}_1 + b(1 + T_{22})\mathbf{t}_2 + bT_{32}\mathbf{t}_3.$$

The angle between the vectors  $\mathbf{a}'$  and  $\mathbf{b}'$  is, in general, changed through a small  $\phi$  in comparison with the initial angle  $\pi/2$ . Thus:

$$\cos(\mathbf{a}', \mathbf{b}') = \cos\left(\frac{\pi}{2} \pm \phi\right) = \pm \sin \phi = \pm \phi.$$

We can calculate the angle  $\phi$  from the scalar product of  $\mathbf{a}'$  and  $\mathbf{b}'$  because

$$\cos(\mathbf{a}', \mathbf{b}') = \frac{\mathbf{a}' \cdot \mathbf{b}'}{a'b'}. \quad \text{Thus} \quad \phi \approx \frac{\mathbf{a}' \cdot \mathbf{b}'}{a'b'}.$$

Although the precise product is difficult to evaluate, we can ignore those terms that contain products of  $T_{pq}T_{sr}$  because these tensor components are

very small in comparison with unity. We can also say that  $a'b' = ab$ , then

$$\cos(\mathbf{a}', \mathbf{b}') \approx \phi \approx \frac{abT_{12} + baT_{21}}{ab} = T_{12} + T_{21}.$$

This means that the sum of the symmetrically located components determines the angular change (increase or decrease as indicated by the sign of the sum) of the angle between the line elements, which initially were tangent to corresponding coordinate lines in an orthogonal system. Since this angular change is expressed per time unit, it is a rate of change. Specifically, the sum  $T_{12} + T_{21}$  gives the rate of angular change between elements tangent to the  $u_1$  and  $u_2$  coordinate lines.

The angular change between two vectorial elements having a coincident initial point is not the only kind of orientation change occurring during growth. Another is pure rotation, which results in the same change of orientation of both elements. It is known from kinematics that the angular velocity of rotation around an axis normal to the plane  $u_p \times u_q$  in tensor notation is

$$\omega_q^p = \frac{1}{2} \left( \frac{\partial V^p}{\partial y^q} - \frac{\partial V^q}{\partial y^p} \right).$$

Thus in a growing organ the angular velocity is given by a tensor the components of which are differences (divided by 2) between symmetrically located components of the growth tensor. In terms of physical components the angular velocity of rotation is

$$\omega_{pq} = \frac{1}{2}(T_{pq} - T_{qp}).$$

If a curvilinear coordinate system is so adjusted that the displacement lines are along the coordinate lines  $u_1$  and  $u_2$ , and we observe the plane tangent to these coordinates at the considered point, then  $\omega_{12}$  gives the angular velocity of the rotation of the base vectors attached to the material point that is moving along a displacement line (the rotation is around an axis normal to the observation plane). For example, consider a growing apical dome in which displacement lines are along periclinal lines in axial planes, and which is described in a curvilinear orthogonal coordinate system such that  $u_1$  lines are along periclinal lines, and  $u_2$  lines represent anticlinal lines in axial longitudinal sections. In such a system  $\omega_{12} = T_{12} - T_{21}$  and denotes twice the angular velocity of an anticlinal wall at the point considered. This rotation results from the displacement of an anticlinal or periclinal wall from the vicinity of the vertex along an arched path, as for instance in the tunica of a shoot apical dome.

We have seen that the interpretation of the non-diagonal elements refers either to the sum or to the difference of symmetrically located components of the growth tensor. It is thus appropriate to separate the growth tensor into its symmetric and skew-symmetric parts according to the equation

$$T_{pq} = \frac{1}{2}(T_{pq} + T_{qp}) + \frac{1}{2}(T_{pq} - T_{qp}) = \varepsilon_{pq} + \omega_{pq}.$$

The resulting tensors,  $\varepsilon_{pq}$  and  $\omega_{pq}$ , are well known from elastomechanics and hydromechanics as the strain, or rate-of-strain, tensor and the vorticity tensor, respectively. These tensors have been introduced to growth analysis of plant organs in rectangular coordinates by Silk & Erickson (1979).

The vorticity tensor does not contribute to  $\text{RERG}_1$ , because  $\omega_{pq} e_p e_q = 0$ . Thus it is irrelevant whether in the determination of  $\text{RERG}_1$  we use the growth tensor or the rate-of-strain tensor. However, the interpretation of the meaning of the components of the rate-of-strain tensor (half of the sum of the symmetrically located components of the growth tensor) as well as those of the vorticity tensor (half of the difference of the components) is simpler than those of the growth tensor. In summary, when  $p = q$ ,  $\varepsilon_{pq}$  denotes  $\text{RERG}_1$  along a direction tangent to the coordinate line  $u_p$ ; when  $p \neq q$ ,  $\varepsilon_{pq}$  denotes half of the rate of angular change between the elements that were initially oriented along lines  $p$  and  $q$  and is analogous to shearing strain. The term  $\omega_{pq}$  denotes angular velocity of a material element around an axis normal to the plane  $u_p \times u_q$ .

#### 4. Principal Directions of the Growth Tensor

Consider an infinitesimal line element fixed at its center to a point  $P$  in a growing organ, and suppose that the direction  $s$  of the element is changed. Now let the element be represented by an infinitesimal vector  $ds = ds_q$ . What are the directions along which the infinitesimal vector does not change its orientation during growth, except for the change resulting from pure rotation? The problem is to find the direction in which there is only an increase in length of the element and no change of direction related to the rate of shearing strain. The growth tensor  $T_{pq}$  transforms the vector  $ds_q$  into a new vector  $T_p$  and

$$T_p = T_{pq} ds_q = (\varepsilon_{pq} + \omega_{pq}) ds_q.$$

As the effect of the skew symmetric tensor  $\omega_{pq}$  is only pure rotation of the element, we can ignore it. Thus our task of finding the direction  $s$  such that  $ds_q$  does not change in direction, but only in length, can be written as

$$\varepsilon_{pq} ds_q = \lambda ds_q$$

or (dividing both sides by the magnitude of the vector,  $ds_q$ ) as

$$\varepsilon_{pq}e_{(s)q} = \lambda e_{(s)q}$$

where  $e_{(s)q}$  are direction cosines of a unit vector in the same direction as  $ds_q$ . In this equation set (there are three equations, as  $p = 1, 2, 3$ ) the vector  $ds_q$  or  $e_{(s)q}$  is transformed by the tensor into a multiple of itself. Both  $e_{(s)q}$  and  $\lambda$  are unknown. The scalar  $\lambda$  and the corresponding vector  $e_{(s)q}$  which fulfill the equation are called the eigenvalue and the unit eigenvector of the tensor, respectively. It is known that the considered set of equations has a nontrivial solution only when  $\text{Det}(\varepsilon_{pq} - \delta_{pq}\lambda) = 0$ , which provides the clue to find  $\lambda$ . There are always three values of  $\lambda$  in the solution of the last equation.

The interpretation of eigenvalues and of eigenvectors is easiest in the case of orthogonal coordinate systems so adjusted to the pattern of displacement lines characterized by the field of unit vectors  $V/|V|$ , that there are non-zero components of  $\varepsilon_{pq}$  on the main diagonal only. Theoretically this is always possible. Practically the adjustment requires an "appropriate" curvilinear coordinate system (Hejnowicz, 1984; Hejnowicz, Nakielski, & Hejnowicz, 1984a). If non-zero components occur only on the main diagonal of the matrix of  $\varepsilon_{pq}$ , we have

$$\text{Det}(\varepsilon_{pq} - \delta_{pq}\lambda) = (\varepsilon_{11} - \lambda)(\varepsilon_{22} - \lambda)(\varepsilon_{33} - \lambda) = 0,$$

which means that  $\lambda_1 = \varepsilon_{11}$ ,  $\lambda_2 = \varepsilon_{22}$ , and  $\lambda_3 = \varepsilon_{33}$ . Thus in the diagonal form of the tensor, the eigenvalues are the components representing  $\text{RERG}_i$  in the directions corresponding to the coordinate lines. We also have

$$\varepsilon_{pq}e_{(1)q} = \varepsilon_{11}e_1 = \text{RERG}_{1(1)}e_1$$

where  $e_{(1)q} = e_1$ , which is the unit vector tangent to the  $u_1$  coordinate line. Similarly we have

$$\varepsilon_{pq}e_{(2)q} = \varepsilon_{22}e_2$$

and

$$\varepsilon_{pq}e_{(3)q} = \varepsilon_{33}e_3$$

where  $e_2$  and  $e_3$  are the unit vectors tangent to the  $u_2$  and  $u_3$  coordinate lines, respectively. This means that for the "diagonal" form of the tensor the eigenvectors are tangent to the coordinate lines.

To interpret fully the meaning of  $\text{RERG}_{1(1)}$ ,  $\text{RERG}_{2(2)}$ , and  $\text{RERG}_{3(3)}$  as components of the rate-of-strain tensor in diagonal form and also as eigenvalues, let us consider what happens to the components of the rate-of-strain tensor when the coordinate orthogonal system, in which the tensor is

calculated, is rotated in different directions with respect to the growing organ. Obviously, the values of the components change (only the sum of the diagonal components is invariant). It can be proved that the  $REG_i$  along coordinate lines in different orientations of the system (the diagonal components of the rate-of-strain, or growth tensor) attain extremal values, either maximal or minimal, when the coordinate lines become tangent to the eigenvectors, that is, when the tensor attains diagonal form. Thus the eigenvalues are the extremal values of  $REG_i$ .

It is customary in mechanics to designate the extremal values of strain as the principal strains. Thus we propose to call the directions (from a considered point in the growing organ) in which  $REG_i$  attains extremal values the principal directions. The  $REG_i$  in these directions we call the principal growth rates. Thus the eigenvalues of the rate-of-strain tensor are principal growth rates, and the eigenvectors indicate principal directions. From the fact that eigenvectors are tangent to coordinate lines of an orthogonal coordinate system it follows that the principal directions are mutually orthogonal. Since the eigenvectors, though calculated for a particular tensor, are not specific for the tensor but for the underlying  $V$ -field, the important inference about orthogonality of principal directions is valid in general, although we derived it for the special case when the rate-of-strain tensor is in the diagonal form.

When the rate-of-strain tensor is in the diagonal form, the non-diagonal components are zeros by definition. Since those components represent rates of angular change between the elements initially tangent to corresponding coordinate lines, we infer that there is no angular change between the elements oriented in the principal directions. Thus these elements remain orthogonal during steady growth. The inverse of the inference is also valid: When initially orthogonal elements remain orthogonal during steady growth they are oriented in the principal directions.

## 5. An Example of Application of the Growth Tensor

Let us consider that there are two variants of the mode of growth of a cylindrical organ that is elongating longitudinally: first with no rotation of the tip, and secondly with such rotation. The growth tensor is helpful in approaching the question: Wherein lies the difference between the two growth modes? Now recall that the growth tensor in a cylindrical coordinate system  $(r, \phi, z)$  was presented at the end of section 2.

In defining  $V$  for the above-mentioned growth modes we make two assumptions: (a) Growth is exclusively longitudinal with no radial thickening; and (b) the organ remains straight during growth so that  $V_z$  at all

points on a transverse section is the same. Consequently  $\partial V_z/\partial r = \partial V_z/\partial \phi = 0$ .

Now, in growth without tip rotation,  $V_\phi = 0$ , and in growth with rotation,  $V_\phi$  is proportional both to  $r$  (the distance from the axis) and to  $V_z$  (the magnitude of the longitudinal velocity). Thus in the latter mode, the linear velocity of rotation,  $V_\phi = raV_z$ , where  $a$  is a scalar which together with  $V_z$  defines the angular velocity,  $\omega = aV_z$ , at a level specified by  $z$ . Because the actual direction of rotation does not influence our argument we can, without prejudice, assume that rotation is in the positive direction of the unit vector  $t_\phi$  (anticlockwise). Accordingly then, the growth tensors applicable to our two assumed growth modes can be represented by the matrices below:

$$\begin{array}{cc} \left\{ \begin{array}{ccc} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \partial V_z/\partial z \end{array} \right\} & \left\{ \begin{array}{ccc} 0 & aV_z & 0 \\ -aV_z & 0 & 0 \\ 0 & ra \partial V_z/\partial z & \partial V_z/\partial z \end{array} \right\} \\ \text{without rotation} & \text{with rotation} \end{array}$$

If we now recall that the sum of the elements of the main diagonal gives  $\text{RERG}_{\text{vol}}$ , it is obvious that it is the same with and without rotation. Whatever causes the rotation does not change  $\text{RERG}_{\text{vol}}$ . What then is the difference between growth with and without rotation? We note that there is a difference between  $\text{RERG}_l$  in the two growth modes.

In growth without rotation  $\text{RERG}_{l(s)} = \partial V_z/\partial z \cos^2 \delta$ , where  $\delta$  is the angle between the direction  $s$  and the unit base vector in the  $z$  direction,  $t_z$ . The value of this function is maximal when  $\delta = 0$ ; that is, when the  $s$  direction coincides with the axial direction (Fig. 1(a)). However, when tip rotation accompanies longitudinal growth

$$\text{RERG}_{l(s)} = ra \frac{\partial V_z}{\partial z} \cos \beta \cos \delta + \frac{\partial V_z}{\partial z} \cos^2 \delta,$$

where  $\beta$  is the angle between  $s$  and the unit base vector  $t_\phi$ . In the axial plane  $\cos \beta = 0$ , the first term on the right side of the above equation vanishes, and the graph of the function (in this plane) is the same as it is without rotation. In the tangential plane, however,  $\cos \beta = \sin \delta$ , hence in this plane

$$\text{RERG}_{l(s)} = \frac{\partial V_z}{\partial z} (ra \cos \delta \sin \delta + \cos^2 \delta).$$

The extreme values of  $\text{RERG}_l$  are attained in the directions specified by  $\delta$  and  $\delta + 90^\circ$  such that  $\tan 2\delta = \pm ra$ . This means that, except at the center of the cylinder, the maximal value of  $\text{RERG}_l$  is not in the axial direction.

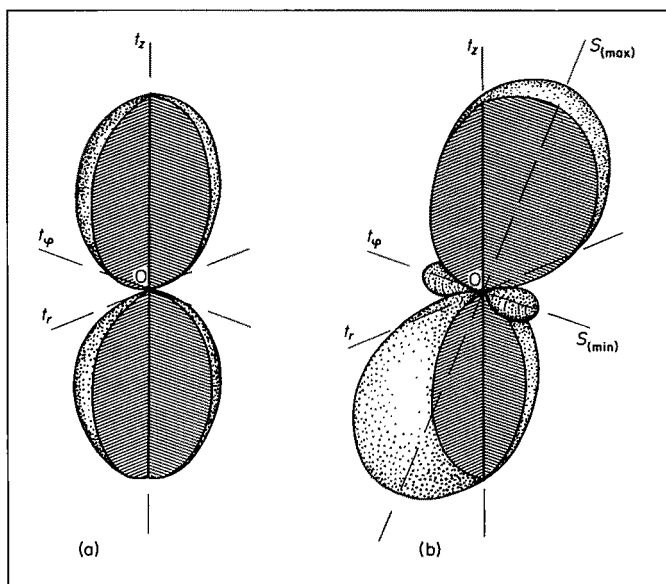


FIG. 1. The relative elemental rates of growth in length ( $RERG_i$ ) along infinitesimal line segments oriented in all possible directions, but centered on a point of origin,  $O$ , are represented as defining envelopes coincident with surfaces of solids of rotation. The distance along a straight line from  $O$  to any point on the envelope is the scalar magnitude of a growth vector in that specific direction. In this example, point  $O$  lies off the axis of a cylindrical organ growing longitudinally, either without (a) or with (b) rotation relative to a fixed base. Net radial growth is here assumed to be nil. The axial direction,  $t_z$ , is vertical. The radial and tangential directions, and the  $t_r$  and  $t_\phi$  axes, respectively, refer to the plane of cross section of the organ. In the drawing one quadrant of the solid of rotation around the vertical axis has been "cut" away. The "cut" surfaces in the radial and tangential planes are shaded. Note that the  $RERG$  values represented by the radial (left) faces of each "cut" are the same in (a) and (b), though the tangential faces are different. The bow-like lobes around the  $S_{(min)}$  direction in (b) represent negative values (shrinkage) of  $RERG_i$ , along that direction. Further interpretations are given in the text.

The angle at which the maximal value is found increases with  $r$ . Figure 1(b) represents  $RERG_i$  as a function of direction when  $a$  and  $r$  both equal unity. The graphed function  $RERG_i$  is symmetrical with regard to the direction  $s_{(max)}$  in which  $RERG_i$  is maximal and which is in its tangential plane. In this same plane, but in a direction orthogonal to  $s_{(max)}$ , there is an extreme of negative growth (shrinkage). This is the direction of  $s_{(min)}$ . The  $s_{(max)}$  and  $s_{(min)}$  represent the two principal directions. They are in a tangential plane. The third principal direction is the radial one, in which, in this example, there is no growth.

The principal growth rates  $\text{REG}_{l(s_{\max})}$  and  $\text{REG}_{l(s_{\min})}$  can be obtained by calculating  $\text{REG}_l$  from the equation

$$\text{REG}_{l(s)} = (\cos \delta \sin \delta + \cos^2 \delta) \frac{\partial V_z}{\partial z}$$

for different  $\delta$  and to find those  $\delta$  for which  $\text{REG}_l$  attains extremal values. More elegantly, the principal growth rates can be calculated as the eigenvalues of the corresponding rate-of-strain tensor. We can obtain the latter by decomposing the growth tensor into its symmetric and skew-symmetric parts,  $T_{pq} = \varepsilon_{pq} + \omega_{pq}$ . With our assumptions that  $ra = 1$  we have

$$\varepsilon_{pq} = \begin{Bmatrix} 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2} \partial V_z / \partial z \\ 0 & \frac{1}{2} \partial V_z / \partial z & \partial V_z / \partial z \end{Bmatrix}, \quad \omega_{pq} = \begin{Bmatrix} 0 & a V_z & 0 \\ -a V_z & 0 & -\frac{1}{2} \partial V_z / \partial z \\ 0 & \frac{1}{2} \partial V_z / \partial z & 0 \end{Bmatrix},$$

and

$$\text{Det}(\varepsilon_{pq} - \delta_{pq}\lambda) = \lambda^2 \left( \frac{\partial V_z}{\partial z} - \lambda \right) + \frac{1}{4} \left( \frac{\partial V_z}{\partial z} \right)^2 \lambda = 0.$$

One eigenvalue is thus zero; the two others are  $\frac{1}{2}(1 + \sqrt{2}) \partial V_z / \partial z$  and  $\frac{1}{2}(1 - \sqrt{2}) \partial V_z / \partial z$ . The diagonal form of the rate-of-strain tensor is:

$$\begin{Bmatrix} 0 & 0 & 0 \\ 0 & -0.2 \partial V_z / \partial z & 0 \\ 0 & 0 & 1.2 \partial V_z / \partial z \end{Bmatrix}$$

Accordingly the principal growth rate in the radial direction is zero, that in the direction  $s_{(\min)}$  is  $-0.2 \partial V_z / \partial z$ , and that in the direction  $s_{(\max)}$  is  $1.2 \partial V_z / \partial z$ , as is shown in Figure 1(b). Thus it can be inferred that growth with rotation differs from growth without rotation in the inclination of the principal directions at a point with respect to the axial direction, and also in occurrence of negative growth along lines which are contained within some cone around the principal direction  $s_{(\min)}$ . A stripe drawn on the cylinder surface along the line of maximal  $\text{REG}_l$  would become more narrow during growth. In a real cylindrical organ growing with tip rotation, this shrinkage is apparently compensated for by latitudinal growth accompanying the growth in the radial direction, which was assumed to be zero in this example.

## 6. Discussion

The utility of the growth tensor has been demonstrated in modelling of the growth of shoot apical domes (Hejnowicz *et al.*, 1984), leaf marginal meristems, rhizoids, and bent axes, in different curvilinear coordinate sys-



tems (Hejnowicz, unpublished). In presenting this theoretical work we are aware that tensor formalism may be difficult for the biologist, especially when complex curvilinear coordinate systems are used. We, therefore, elaborated the dyadic approach to the growth tensor. This approach does not require an extensive knowledge of tensor analysis and allows calculations of the growth tensor for a particular coordinate system relatively easily and directly in terms of physical components. However, completion of this presentation requires that some attention be given to the pure tensor approach and to tensor notations.

Rate-of-strain and vorticity tensors have already been introduced to kinematics of plant growth by Silk & Erickson (1979) who made analogies between growth and fluid flow or deformation of elastic bodies. It is not our aim here to introduce an improved tensor. Our intentions are: first, to show that the tensor concept is evoked by the very nature of growth, not merely by its analogy to deformation or strain; secondly, to explain the meaning of this concept, and of the tensor components, in descriptions of growth of plant organs; and thirdly, to introduce a series of papers which use these concepts in making growth rate calculations in those curvilinear coordinate systems that are most appropriate to descriptions of specific plant organs.

Is it appropriate to introduce a growth tensor instead of confining ourselves to the rate-of-strain and vorticity tensors? It is notable that in hydrodynamics the tensor which by decomposition produces the rate-of-strain and vorticity tensor has no special name—it is merely the second rank mixed tensor of the covariant derivative of a particle velocity field. Why then should we call the corresponding tensor in the kinematics of growth the “growth tensor”? One reason is that growth is of overriding importance in the biology of an organism. Growth can be considered in terms of strain and vorticity, but those terms cannot serve as synonyms for growth. There are good semantic reasons to advocate “growth tensor” as a general biological term, and the rate-of-strain and vorticity tensors as operational terms. (We return to the semantics of “growth tensor” at the end of this section.) It should also be noted that: first, in the derivation of the relevant tensors, the growth tensor is antecedent to the rate-of-strain and vorticity tensors, as the latter are the symmetric and skew-symmetric parts of the former; secondly, the rate-of-strain and vorticity tensors do not result directly from the analysis of the definition of the relative elemental growth rate (RERG), but only from the decomposition of the growth tensor, which arises directly from such an analysis. The present paper is a consequence of the introduction of the tensor concept to the kinematics of plant organ growth by Silk & Erickson (1979) and is not in itself such an introduction.

The rate-of-strain tensor is an extrapolation of the strain tensor, and the latter is based on assumptions about small deformations. Since growth seems related to large deformations, a question arises whether the rate-of-strain tensor, and therefore also the growth tensor, are appropriate to growth description. There is a simple answer: When we analyze growth, the displacement of one material point with respect to another, which is analogous to deformation, can be made extremely small simply by considering the displacement over an infinitesimally small time interval,  $\Delta t$ . This is so because the magnitude of displacement is the product of  $\Delta t$  and the difference of the displacement velocities.

The growth tensor "works" only in cooperation with the  $\mathbf{V}$  field. Can the latter be determined for the whole organ? The organ must grow in an integrated manner (symplastically) for we seldom observe rupturing between adjacent regions. It seems obvious that one cannot arbitrarily specify the components of  $\mathbf{V}$  as functions of the coordinates  $u_1$ ,  $u_2$ , and  $u_3$ . However, it is possible to determine the  $\mathbf{V}$  field for the whole organ if  $\mathbf{V}$  along one displacement line, for example along a line on the organ surface, is known (Hejnowicz & Nakielski, 1979; Hejnowicz, 1982). If we have the growth tensor for an orthogonal coordinate system with an unspecified  $\mathbf{V}$ , we do not even need to know  $\mathbf{V}$  along one displacement line. It is sufficient to know the ratio of  $T_{11} = \text{RERG}_{1(u_1)}$  to  $T_{33} = \text{RERG}_{1(u_3)}$  where  $u_1$  and  $u_3$  are meridional (or longitudinal) and latitudinal (or transverse) lines on the organ surface, respectively. The ratio  $T_{11}/T_{33}$  represents the allometric coefficient of directionality of expansion around a point on the organ surface (Green & King, 1966; Green, 1973). If we know this ratio, and it can be determined, then we can write a differential equation for  $V_1$ . This is possible because if the displacement line on an organ surface is coincident with the coordinate line  $u_1$ , then the only component of  $\mathbf{V}$  is  $V_1$ , and the ratio  $T_{11}/T_{33}$  contains  $V_1$  and  $\partial V_1/\partial u_1$ . Hence  $V_1$  can be determined, first along the displacement line on the organ surface, then for the whole organ (Hejnowicz, Nakielski, & Hejnowicz, 1984).

The tensor approach to analysis of growth of plant organs offers direct and important interpretation of the often observed fact that periclinal and anticlinal walls maintain their specific orientations, and therefore their orthogonality, during growth. The interpretation is that these walls are aligned along the principal directions of growth. This enlightens the hitherto perplexing problem of relation between growth rate of a cell (or tissue) in different directions and the orientation of its cell divisions. If cell divisions result in anticlinal and periclinal partitions that preserve their mutual orthogonal orientations, we can conclude that the divisions are aligned along planes in the principal directions of growth. Thus the tensor approach

to the problem of orientation of cell divisions in plant organs offers fresh perspectives which encourage further studies (Hejnowicz & Romberger, unpublished).

The general inference of our study is that growth is a tensorial attribute of an organ. Although we cannot yet construct a complete hierarchy of information, pattern, physiology, morphogenesis, geometry, and growth, we consider it necessary that the controls of growth rate distribution be at a higher hierarchical level than growth itself. The implication is that the factors controlling growth should also be characterized by tensor fields of the same rank as the growth tensor.

If this thinking is valid, then neither a scalar field (such as the concentration of a growth hormone), nor a vector field (such as the gradient of hormone concentration) would be competent to control growth except as mediated by a tensor field. What tensor fields are likely to be mediators? We can guess that they would be stresses, strains, and abilities to develop polarities (polarizabilities) when appropriate stimuli act. Such attributes are common to the cytoskeletal or microtrabecular systems within cells, and to the cell wall complex at the multicellular organ level. Which of them may be at a higher hierarchical level than growth itself? Perhaps the best candidate is polarizability—as it is heavily dependent upon organism history. An example is the hoop-reinforcement of a whole cylindrical organ mainly by the cellulose in the outer epidermal wall (Green, 1980).

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## APPENDIX A

### Basic Notations

In three dimensional space any vector **A** can be specified by a set of three numbers representing the components of **A** in the rectangular coordinate system, *x*, *y*, *z*, or more generally in an orthogonal curvilinear coordinate

system,  $u_1, u_2, u_3$ . Thus:

$$\mathbf{A} = a_x \mathbf{i} + a_y \mathbf{j} + a_z \mathbf{k} = a_1 \mathbf{t}_1 + a_2 \mathbf{t}_2 + a_3 \mathbf{t}_3 = \sum_p^3 a_p \mathbf{t}_p$$

where  $a_x, a_y, a_z$  or  $a_1, a_2, a_3$  are sets of components in the system, and  $\mathbf{i}, \mathbf{j}, \mathbf{k}$  or  $\mathbf{t}_1, \mathbf{t}_2, \mathbf{t}_3$  are rectangular unit vectors or unit base vectors tangent to the coordinate curves, respectively. In matrix form a vector can be represented as

$$\mathbf{A} = \begin{Bmatrix} a_1 \\ a_2 \\ a_3 \end{Bmatrix} \{\mathbf{t}_1, \mathbf{t}_2, \mathbf{t}_3\}.$$

When we work with a particular coordinate system, only the set of components need be given to specify a vector, thus we can write

$$\mathbf{A} = \begin{Bmatrix} a_1 \\ a_2 \\ a_3 \end{Bmatrix}$$

which conventionally is further abbreviated to  $\mathbf{A} = a_p$ , where it is understood that the suffix  $p$  successively represents the several coordinates of the system in which the components are taken.

The rationale of representation of a tensor follows from the way in which the vector  $\mathbf{A}_{(s)}$ , defined by the tensor (point function) and the direction  $s$ , is obtained. The  $\mathbf{A}_{(s)}$  vectors which correspond to the directions of the base vectors are in general not parallel to these base vectors. In case of the directions specified by the coordinate axes of rectangular systems:

$$\mathbf{A}_{(x)} = a_{xx} \mathbf{i} + a_{yx} \mathbf{j} + a_{zx} \mathbf{k}$$

$$\mathbf{A}_{(y)} = a_{xy} \mathbf{i} + a_{yy} \mathbf{j} + a_{zy} \mathbf{k}$$

$$\mathbf{A}_{(z)} = a_{xz} \mathbf{i} + a_{yz} \mathbf{j} + a_{zz} \mathbf{k}.$$

(Note that  $\mathbf{A}_{(x)}$  is not an  $x$  component of  $\mathbf{A}$ , but a vector defined by the tensor and the direction  $x$ .) Now consider how we obtain the vector  $\mathbf{A}_{(s)}$  corresponding to the direction defined by the unit vector  $\mathbf{e}_{(s)}$ , represented by its direction cosines, as:

$$\mathbf{e}_{(s)} = e_x \mathbf{i} + e_y \mathbf{j} + e_z \mathbf{k}.$$

The vector  $\mathbf{e}_{(s)}$  is the resultant of the rectangular unit vectors taken in proportion to their direction cosines. Similarly,  $\mathbf{A}_{(s)}$  can be obtained as the resultant of the vectors  $\mathbf{A}_{(x)}, \mathbf{A}_{(y)}, \mathbf{A}_{(z)}$  each taken in proportion to its

corresponding cosine:

$$\mathbf{A}_{(s)} = \mathbf{A}_{(x)}e_x + \mathbf{A}_{(y)}e_y + \mathbf{A}_{(z)}e_z \\ = (a_{xx}e_x + a_{xy}e_y + a_{xz}e_z)\mathbf{i} + (a_{yx}e_x + a_{yy}e_y + a_{yz}e_z)\mathbf{j} + (a_{zx}e_x + a_{zy}e_y + a_{zz}e_z)\mathbf{k}.$$

This means that the vector  $\mathbf{A}_{(s)}$  is specified by the equations for its components  $A_x$ ,  $A_y$ , and  $A_z$ :

$$A_x = a_{xx}e_x + a_{xy}e_y + a_{xz}e_z$$

$$A_y = a_{yx}e_x + a_{yy}e_y + a_{yz}e_z$$

$$A_z = a_{zx}e_x + a_{zy}e_y + a_{zz}e_z.$$

When the direction changes, the direction cosines change, whereas the set of nine numbers,  $a_{pq}$ , remains the same. In matrix form the equations for the components  $A_p$  of the vector  $\mathbf{A}_{(s)}$  can be written as:

$$\begin{Bmatrix} A_x \\ A_y \\ A_z \end{Bmatrix} = \begin{Bmatrix} a_{xx} & a_{xy} & a_{xz} \\ a_{yx} & a_{yy} & a_{yz} \\ a_{zx} & a_{zy} & a_{zz} \end{Bmatrix} \begin{Bmatrix} e_x \\ e_y \\ e_z \end{Bmatrix}.$$

This matrix with its  $a_{pq}$  components represents a tensor. A more concise representation of the tensor is simply  $a_{pq}$ . Hence the above set of equations can be written as  $A_p = a_{pq}e_q$ . In the latter notation we adopt the summation convention (Einstein's convention) that whenever an index appears exactly twice in the same term, we are to sum over that index, in this case from  $x$  to  $z$ , or from 1 to 3 if the coordinates were so numbered.

## APPENDIX B

### Vectorial Relative Elemental Rate of Change of a Line Element

Consider an infinitesimal vector  $\Delta\mathbf{s}$  joining two material points  $P_1$  and  $P_2$  in a growing organ. This vector represents the line element  $P_1P_2$  oriented in the direction  $s$ . During growth this element not only increases in length but usually also changes its direction. The rate of the increase in length and directional change is represented by the rate of change of the vector  $\Delta\mathbf{s}$ . Let the position of the material points at instant  $t$  be defined by the position vectors  $\mathbf{R}(t)$  and  $\mathbf{R}(t) + \Delta\mathbf{s}$ . The points undergo displacement in the field  $\mathbf{V}$ . Thus at instant  $(t + \Delta t)$  the position of  $P_1$  is

$$\mathbf{R}(t + \Delta t) = \mathbf{R}(t) + \mathbf{V}(P_1)\Delta t$$

and that of  $P_2$  is

$$\mathbf{R}(t + \Delta t) + \Delta\mathbf{s}(t + \Delta t) = \mathbf{R}(t) + \Delta\mathbf{s}(t) + \mathbf{V}(P_2)\Delta t.$$

By subtraction and rearrangement we obtain

$$\Delta \mathbf{s}(t + \Delta t) - \Delta \mathbf{s}(t) = \Delta \mathbf{V} \Delta t.$$

Dividing both sides by the magnitude of  $\Delta \mathbf{s}$  and by  $\Delta t$  then gives

$$\frac{\Delta \mathbf{s}(t + \Delta t) - \Delta \mathbf{s}(t)}{\Delta s \Delta t} = \frac{\Delta \mathbf{V}}{\Delta s}.$$

Now the limit when  $\Delta s \rightarrow 0$  and  $\Delta t \rightarrow 0$  is  $d\mathbf{V}/ds$ , thus the relative change of the vector  $\Delta \mathbf{s}$  caused by growth is the derivative of  $\mathbf{V}$  in the direction  $s$ . We denote this vectorial change by  $\mathbf{c} = d\mathbf{V}/ds$ . From section 2 we have

$$\begin{aligned} \text{RERG}_{l(s)} &= \frac{d(\mathbf{V} \cdot \mathbf{e}_{(s)})}{ds} = \frac{d\mathbf{V}}{ds} \cdot \mathbf{e}_{(s)} + \mathbf{V} \frac{d\mathbf{e}_{(s)}}{ds} \\ &= (\nabla \mathbf{V}) \cdot \mathbf{e}_{(s)} \cdot \mathbf{e}_{(s)} \\ &= (T_{pq} \mathbf{t}_p \mathbf{t}_q) \cdot \mathbf{e}_{(s)} \cdot \mathbf{e}_{(s)}. \end{aligned}$$

Thus

$$\mathbf{c} = \frac{d\mathbf{V}}{ds} = (\nabla \mathbf{V}) \cdot \mathbf{e}_s = (T_{pq} \mathbf{t}_p \mathbf{t}_q) \cdot \mathbf{e}_s.$$

In tensor notation this becomes

$$c^p = V^p_{,r} e^r = T^p_r e^r.$$

If, for example,  $s$  is in the direction of  $t_1$ , then

$$\mathbf{c} = T_{11} \mathbf{t}_1 + T_{21} \mathbf{t}_2 + T_{31} \mathbf{t}_3.$$