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THE DEFORMATION OF A ROD OF GROWING BIOLOGICAL MATERIAL UNDER LONGITUDINAL COMPRESSION†

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The deformation of a three-dimensional growing elastic cylinder under the action of an axially compressive load is considered, taking into account the influence of the stress on the growth rate. To analyse the stability of exact axially symmetric solutions, approximate differential relations were obtained, valid for objects with small transverse dimensions. The statement of the problem of the evolution of perturbations takes into account the variability of the rheological and geometric properties of the rod whilst it is being deformed. The physical meaning of the results obtained is discussed by comparing the time-scales for the development of perturbations and the unperturbed process.

Mathematical modelling of the growth and development of living organisms requires one to take into account how the growth rate depends on mechanical stresses [1–3], which is known from observation and experiment. The simple model that is investigated below enables us to study explicitly the consequences of this basic biological fact. The presence of feedback, governed by the dependence of the manner and rate of growth of material on its stress–strain state, fundamentally distinguishes the problem of biological growth from related problems dictated by technological applications [4].

Consider the mechanical deformation of thin objects (the human spine, the stalk and root of a plant) growing under conditions of axial compression. Here we will model this common phenomenon [1] (the best-known example of which is scoliosis) in its most general form by analysing mechanisms present in all the above systems. Estimation and refinement of the results obtained, taking into account the specific factors of actual processes, is an independent problem in each case.

1. The model of growing biological tissue as an effectively "visco-elastic" medium was first postulated directly in [5] and is obtained by coarsening the assumptions of more detailed analysis [6, 7].

We will confine ourselves to linear constitutive equations and use the following system of governing equations

$$\boldsymbol{\epsilon}^e = \mathbf{K}\boldsymbol{\sigma}, \quad \mathbf{e}^i = \mathbf{A} + \mathbf{M}\boldsymbol{\sigma}, \quad \mathbf{e} = \mathbf{e}^e + \mathbf{e}^i \tag{1.1}$$

Here $\boldsymbol{\epsilon}^e$ is the elastic strain tensor, $\mathbf{e}$, $\mathbf{e}^i$, $\mathbf{e}^e$ are the velocity tensors for total, inelastic (growth) and elastic strains, respectively, $\boldsymbol{\sigma}$ is the stress tensor, and $\mathbf{K}$ is the elastic coefficient tensor. In the second formula of (1.1) the tensor $\mathbf{A}$ describes the "proper" growth of the material (when there are no stresses) and the tensor $\mathbf{M}$ corresponds to the influence of stresses on the growth deformation.

We shall take the elastic (though not the growth) deformations to be small, so that it is unnecessary to specify the type of the time derivative when specifying the relation between the tensors $\boldsymbol{\epsilon}^e$ and $\mathbf{e}^e$, so that one can take the simplest dependence (in components) $e^e_{kl} = d\varepsilon^e_{kl}/dt$ and obtain the following differential relation

$$e_{kl} = \nabla_{(k}\upsilon_{l)} = A_{kl} + M_{klmn}\sigma^{mn} + \frac{d}{dt}(K_{klmn}\sigma^{mn}) \tag{1.2}$$

where υ_l are the components of the velocity vector, parentheses denote symmetrization over the appropriate indices, and the symbol d/dt denotes differentiation with respect to time for fixed comoving coordinates. Replacement of the operator d/dt in (1.2) by, for example, the Oldroyd derivative, leads to the appearance of additional negligibly small terms (of order $e\varepsilon^e$). Here and below summation is over repeated subscripts and superscripts.

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From Eqs (1.1) and (1.2) it is clear that there is an important difference between the model under consideration and the classical visco-elastic (Maxwellian) medium: the possibility of deformation when there is no stress. The relation between the deformation rate and the stress is governed by the mediating chemical (metabolic) processes. Hence any thermodynamic inequalities restricting the possible values of components of the tensor **M** cannot be written down for the general case. Equations (1.1) and (1.2), together with the momentum equations, form a closed system of equations if the tensors **A**, **K** and **M** are given. The slowness of the growth changes predetermines the negligible smallness of both the momentum flux due to mass inflow into an element of the medium and inertial effects; processes that are rapid compared with the growth can be taken into account by being averaged with respect to slow ("growth") time [1, 2].

2. Consider the growth of an object which initially has the shape of a rectangular cylinder. We choose a fixed Cartesian system of coordinates (Fig. 1) with the origin at the base of the cylinder and the x-axis directed along the initial direction of the generators. (If necessary, we further specify: $x = x^1, y = x^2, z = x^3$.) We will assume the material to be isotropic in its elastic properties and denote its Young's modulus, Poisson's ratio and shear modulus by E, σ and μ, respectively. The growth is assumed to be transversally isotropic, the plane of isotropy being initially perpendicular to the x-axis, and after deformation being perpendicular at each point to the fibre that was initially directed parallel to the x-axis.

In a fixed Cartesian system of coordinates oriented along the plane of isotropy (the chosen Eulerian system of coordinates satisfies this condition at least at the initial time) Eqs (1.2) take the form

$$\begin{aligned}
e_x &= w + \frac{1}{\theta}\sigma_x + \alpha_{12}(\sigma_y + \sigma_z) + \frac{d}{dt}\left(\frac{\sigma_x}{E}\right) - \frac{d}{dt}\left(\frac{\sigma}{E}(\sigma_y + \sigma_z)\right) \\
e_y &= w_s + \frac{1}{\theta_s}\sigma_x + \alpha_{22}\sigma_y + \alpha_{23}\sigma_z + \frac{d}{dt}\left(\frac{\sigma_y}{E}\right) - \frac{d}{dt}\left(\frac{\sigma}{E}(\sigma_x + \sigma_z)\right) \quad (y \leftrightarrow z) \qquad (2.1) \\
e_{xy} &= \alpha\sigma_{xy} + \frac{d}{dt}\left(\frac{\sigma_{xy}}{2\mu}\right) \; (y \to z), \quad e_{yz} = \beta\sigma_{yz} + \frac{d}{dt}\left(\frac{\sigma_{yz}}{2\mu}\right)
\end{aligned}$$

The subscripts x, y, z, xy, xz, yz replace the subscripts 11, 22, 33, 12, 13 and 23, respectively. The coefficients θ (growth "viscosity" along the x direction), θ_s, α_{kl}, α, β are expressed using the symmetry of the tensors **e** and $\boldsymbol{\sigma}$ [8] in terms of five parameters. (For example, eliminating the coefficients governing the shear deformation, we obtain $\beta = \alpha_{22} + \alpha_{23}$, $= \alpha = (1/\theta - \alpha_{12} - 1/\theta_s + \alpha_{22})/2$.)

We take $w > 0$ and $w_s > 0$, which ensure positive growth deformation when there are no stresses, which is typical for tissue undergoing intensive growth. To be consistent with observations of many biological objects over a wide range of loads which show the accelerating effect of tensile axial stresses

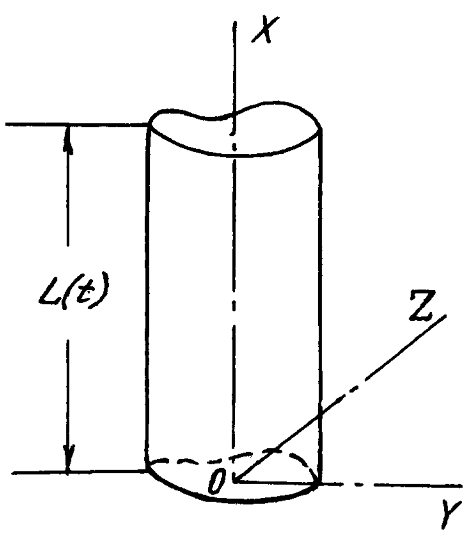

Fig. 1

(and, conversely, the slowing effect of compressive stresses) on growth, we shall always require the inequality $\theta > 0$ to be satisfied. The signs of the remaining coefficients associated with growth will neither be required nor discussed below.

For small changes in the comoving coordinate lines relative to their initial directions (which does not exclude large displacements, e.g. along the x-axis) formulae (2.1) can be applied directly in the Eulerian system of coordinates shown in Fig. 1, but already as an approximation.

In this Cartesian system the equilibrium equations have the form

$$\partial\sigma^{kl} / \partial x^l + F^k = 0 \tag{2.2}$$

where $F^2 = F^3 = 0$, while $F^1 = \rho g$ is the distribution of the volume force of gravity (with the x-axis being assumed to be directed perpendicularly). We shall assume the lateral surface of the object to be unloaded, while on the face ($x = L$) we set the conditions $\sigma_{xy} = 0$, $\sigma_x = -P/S(t, L)$, where $S(t, x)$ is the area of the section normal to the x-axis and $P = P(t) \geqslant 0$ is the axial load applied to the face.

If the weight of the object can be neglected compared with the external force P (so that we can put $F^k = 0$) and all rheological coefficients depend only on time, then the system of equations (2.1) and (2.2), taking kinematic relations into account, has an exact solution. It corresponds to growth without changes in the cylindrical shape with a spatially homogeneous distribution of stresses and deformation rates, which is governed by the following easily solvable finite and differential relations between functions of time only

$$\begin{aligned}
&\sigma_x = -\frac{P}{S}, \quad \sigma_y = \sigma_z = \sigma_{xy} = \sigma_{xz} = \sigma_{yz} = 0 \\
&e_x = w - \frac{1}{\theta}\frac{P}{S} - \frac{d}{dt}\left(\frac{P}{ES}\right), \quad e_{xy} = e_{yz} = e_{xz} = 0 \\
&e_y = e_z = w_s - \frac{1}{\theta_s}\frac{P}{S} + \frac{d}{dt}\left(\frac{\sigma P}{ES}\right), \quad \frac{1}{S}\frac{dS}{dt} = e_y + e_z = 2e_y
\end{aligned} \tag{2.3}$$

For the rate components there is a linear dependence on the coordinates: $\upsilon_x = e_x x$, $\upsilon_y = e_y y$, $\upsilon_z = e_z z$(choosing obvious and unimportant attachment conditions).

The solution (2.3) keeps its form (neglecting changes in the section geometry due to small elastic deformations) for vertical growth when the intrinsic weight is taken into account, when the condition $1/\theta_s = 0$ is satisfied (the axial loads have no effect on the sideways growth). In this case one must put

$$P = P(x,t) = P_0 + \int_x^L \rho g S dx \tag{2.4}$$

in (2.3), where P_0 is the face load. The variables $\sigma_x, e_x, e_y, e_z, S$ are now governed by (2.3) for a density ρ that is known as a function of t and x. Relations (2.3) can also be used as an approximation when $1/\theta_s \neq 0$ for sufficiently short times, when the inhomogeneity in the thickness does not lead to any substantial change in the stress distribution.

Omitting the small elastic deformations, which are insignificant when there are no perturbations of uniform growth, we obtain (for loads of general form) from (2.3) an equation giving the length of the cylinder

$$\dot{L} - wL + \frac{\tilde{p}(L,t)}{\theta} = 0, \quad \tilde{p}(L,t) = \int_0^L \frac{P}{S} dx \tag{2.5}$$

where the dot denotes differentiation with respect to time (of functions of time only).

Suppose that the coefficients w, w_s, θ, θ_s are constant. If the load is then restricted to just a constant pressure on the face ($P = P_0 = p_0 S; p_0 = \text{const}$), then Eqs (2.5) produce exponential growth in length (when $p_0 < \theta_w$) and thickness (when $p_0 > \theta_s < w_s$). The compressive stress $p_0 = \theta_w$ halts the axial growth, and for $p_0 > \theta_w$ shortening occurs and $L \to 0$ as $t \to \infty$. To obtain results that are physically meaningful at long times it is necessary to use a non-linear extension of Eqs (1.1) or take into account the time dependence of the rheological coefficients.

The coordinate lines of the comoving system of coordinates are not deformed for a concentrated load: in the general case within the limits of applicability of formulae (2.3) such a distortion can be ignored. Using (2.3) the relation is found between the Eulerian coordinate x and the comoving coordinate

ξ which initially coincides with x. For a load applied only at the upper end ($P = P_0$) this relation takes the form

$$x = LL_0^{-1}\xi \tag{2.6}$$

corresponding to uniform extension (L_0 being the length of the object at $t = 0$). Formula (2.6) is also approximately true in the case when the stresses have little effect on the axial growth ($P/(S\theta) \leqslant w$).

We also consider the isometric problem corresponding to constant cylinder length L; such a formulation is dictated by experiments with rigid restrictions on growth. Specifying zero axial displacement and free tangential slip on the face ($\sigma_{xy} = \sigma_{xz} = 0$) and assuming non-loading of the lateral surface, we have, in the case of insignificant mass forces, the exact solution

$$e_x = e_{xy} = e_{xz} = e_{yz} = 0, \quad \sigma_y = \sigma_z = \sigma_{xy} = \sigma_{xz} = \sigma_{yz} = 0$$

$$w + \frac{1}{\theta}\sigma_x + \frac{d}{dt}\left(\frac{\sigma_x}{E}\right) = 0, \quad e_y = e_z = w_s + \frac{1}{\theta_s}\sigma_x - \frac{d}{dt}\left(\frac{\sigma\sigma_x}{E}\right) = 0 \tag{2.7}$$

characterized by the absence of axial deformation and uniform axial stress $\sigma_x = \sigma_x(t)$. System (2.7) describes the growth of axial compression accompanied by variation in the sideways growth rate. Relation (2.6) remains formally valid: $L = L_0, x = \xi$. For constant coefficients in (2.7) the axial compressive stress $\sigma_x = -\theta w$ becomes constant exponentially with characteristic time $\tau_m = \theta/E$.

3. To analyse the stability of the steady-state growth process we consider a small deformation of a very extended object ($\delta/L \ll 1$, where δ is the characteristic transverse size). Approximate equations describing the deformations of the object (rod) in a quasisteady process will be obtained by averaging the equilibrium equations (2.2) and equations of state (2.1) together with moment equations constructed from the latter over the cross-section area. We will confine ourselves to the case of plane bending, which occurs when the initial deviation of the rod axis lies in the plane of one of the principal axes of the moment of inertia tensor of the cross-section. By the condition of transversal isotropy and using the approximation considered below this assumption ensures that the deviation remains in the same plane (the equations governing the bending in the perpendicular plane are satisfied automatically and will not be considered further). In the linearized problem the general three-dimensional distortion can be obtained as the superposition of solutions describing bending in the two principal planes.

We introduce the system of coordinates $\bar{x}, \bar{y}, \bar{z}$ as follows: $\bar{x}$ is the length of the arc along the distorted axis, $\bar{y}$ is measured in the plane of bending from the axis along the perpendicular to the latter, and $\bar{z}$ is measured along the perpendicular to this plane. The averaged value of a variable is its integral over the section normal to the deformed axis, divided by the area of cross-section. Such averages are denoted by angular brackets. The earlier notation (with x, y, z subscripts) are kept for the physical vector and tensor components in the new system of coordinates; $y = u(x, t)$ is the equation of the displaced axis in the fixed two-dimensional Cartesian system of coordinates of the observer lying in the plane of the bend (Fig. 2). The procedure for obtaining equations presupposes that terms of order δ/L and u/L, small compared to unity, will be neglected.

The averaging of the equilibrium equations and the moment equation obtained by multiplying the axial projection of the momentum equation by the $\bar{y}$ coordinate leads to the traditional relations

$$N' - p = 0 \tag{3.1}$$

$$Q = M' \tag{3.2}$$

$$M'' + (Nu')' = 0 \tag{3.3}$$

$N = \langle\sigma_{xy}\rangle S$ and $Q = \langle\sigma_{xy}\rangle S$ are the tensile and shear forces, respectively, and $M = \langle\sigma_x\bar{y}\rangle S$ is the bending moment acting over the cross-section. The primes denote differentiation with respect to the axial coordinate x in the observer system of coordinates. The presence of a distributed compressive load $p \geqslant 0$ is assumed, which includes both the weight of the rod itself and, possibly, loading across the lateral surface. During bending the load preserves its direction relative to the observer system of coordinates.

We will consider the averaging of the equations of state in more detail. Preserving the required degree of accuracy, the original dependences in the new system of coordinates are identical with (2.1), while σ_y and σ_z can now be ignored because of their smallness compared with σ_x.

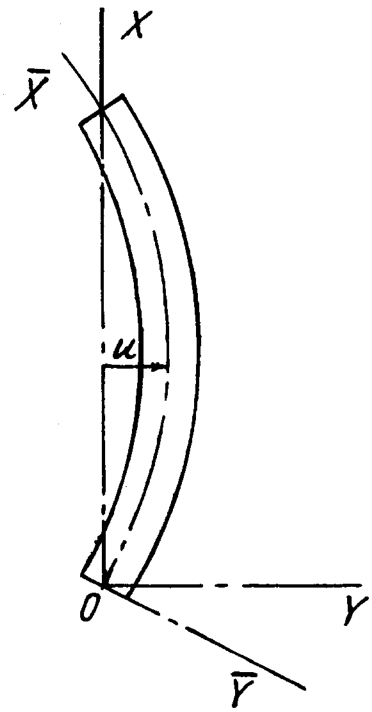

Fig. 2.

For the components of the tensor **e** we have

$$e_x=\frac{\partial \upsilon_x}{\partial \bar{x}},\quad e_y=\frac{\partial \upsilon_y}{\partial \bar{y}},\quad 2e_{xy}=\frac{\partial \upsilon_x}{\partial \bar{y}}+\frac{\partial \upsilon_y}{\partial \bar{x}}+\upsilon_x u'' \tag{3.4}$$

If in the first approximation we confine ourselves to linear distributions of the variables with respect to $\bar{y}$, we obtain the following relations as a result of averaging Eqs (2.1) and the moment equation formed by multiplying the first equation in (2.1) by $\bar{y}$

$$\langle \upsilon_x\rangle'=w+\frac{1}{\theta}\frac{N}{S}+\frac{d}{dt}\left(\frac{N}{ES}\right) \tag{3.5}$$

$$\frac{1}{I}\frac{dI}{dt}=\frac{2}{S}\frac{dS}{dt}=4\left[w_s+\frac{1}{\theta_s}\frac{N}{S}+\frac{d}{dt}\left(\frac{N}{ES}\right)\right] \tag{3.6}$$

$$\langle \upsilon_y\rangle'=-\frac{\langle \upsilon_x\bar{y}\rangle S}{I}-\langle \upsilon_x\rangle u''+2\alpha\langle\sigma_{xy}\rangle+\frac{d}{dt}\frac{\langle\sigma_{xy}\rangle}{\mu} \tag{3.7}$$

$$\left(\frac{\langle \upsilon_x\bar{y}\rangle S}{I}\right)'=\frac{M}{I\theta}+\frac{d}{dt}\left(\frac{M}{IE}\right) \tag{3.8}$$

where I is the moment of inertia of the cross-section with respect to the transverse axis, and the operator d/dt denotes differentiation with respect to time for fixed comoving axial coordinate ξ. We eliminate the parameter $\langle \upsilon_x\bar{y}\rangle$ from (3.7) and (3.8) using (3.2)

$$\langle \upsilon_y\rangle''=-\frac{M}{I\theta}-\frac{d}{dt}\left(\frac{M}{IE}\right)-(\langle \upsilon_x\rangle u'')'+\left(2\alpha\frac{M'}{S}\right)'+\left\{\frac{d}{dt}\left[\frac{1}{\mu}\left(\frac{M'}{S}\right)\right]\right\}' \tag{3.9}$$

On the right-hand side of (3.9) the last term is of order (δL^2) when compared with the second; if $|\alpha| \leqslant 1/\theta$ the penultimate term is at least as small when compared with the first. The last two terms in (3.9) are therefore neglected.

From simple geometrical considerations we obtain the constraint

$$du/dt=\langle \upsilon_y\rangle+\langle \upsilon_x\rangle u' \tag{3.10}$$

Relations (3.1), (3.3), (3.5), (3.6), (3.9) and (3.10) form a closed system of equations. To determine the axial displacement of individual points we also need $dx/dt = \langle \upsilon_x \rangle$.

4. The system of equations obtained has (if this does not contradict the boundary conditions) a solution describing the bending deformation of a rod for which $u = 0$, $\langle \upsilon_y \rangle = 0$, $M = 0$. The remaining variables N, $\langle \upsilon_x \rangle$, S, I are defined by Eqs (3.1), (3.5) and (3.6) which require, apart from initial conditions and an assumption specifying a fixed point (for example, $\langle \upsilon_y \rangle(0, t) = 0$), just one physically interesting condition. When $N(L, t) = -P_0(t)$ or $\langle \upsilon_x \rangle(L, t) = 0$ we obtain extensions of the exact solutions considered in Section 2, where all the relations from that section which link corresponding variables in the exact solutions, remain valid for the averages, including formulae (2.5) and (2.6) (under the hypotheses specified in Section 2).

We will now consider the problem of the development of a small perturbation of the solution, describing undistorted growth when the rod is bent. To do this we analyse the system of equations (3.3) and (3.9) (with the last two terms on the right-hand side omitted) and (3.10), in which we replace $\langle \upsilon_x \rangle$, N, S and I by functions obtained from the solution of the unperturbed problem, and the operator $\partial/\partial x$ previously denoted by a prime is replaced by the operator $\xi_x \partial/\partial x(\xi)$, where the variable $\xi_x = \partial\xi/\partial x$ is also determined from the unperturbed process. To solve this system, four boundary conditions are required as well as the initial conditions. If one can assume that the deformation of the axial growth during bending is small, the operators $\partial/\partial x$ and $\partial/\partial\xi$ can be identified. This formulation of the problem of the evolution of an initial perturbation is formally no different from that known for a rod of linearly creeping material [9] and was used in [10] for a growing rod.

In the example considered below the coefficients θ, E, θ_s, w_s and the moment of inertia I are taken to be functions of time only. (For I this condition imposes an implicit restriction on the formulation of the unperturbed problem and is satisfied exactly for a concentrated facial load.) We also assume that (2.6) holds, which we recall is true not only for a concentrated load, but also when the inequality $P/(S\theta) \ll w$ is satisfied, which does not exclude a significant influence of stresses on the lateral distortion.

We introduce dimensionless variables $\tilde{\xi} = \xi/L_0$ (here $L_0 = L(0)$) and $\tilde{u} = u/L$ (the relative transverse bending), keeping the time dimensional. The system now reduces to the single equation

$$\frac{1}{L} u_t^{\prime \mathrm{v}} - \frac{L}{I\theta}(Nu')' - \left[\frac{L}{IE}(Nu')'\right]_t = 0 \tag{4.1}$$

where the tildes over the dimensionless variables have been omitted. (Below these quantities are only required in their dimensionless form.) Henceforth primes and Latin letters denote differentiation of appropriate multiplicity with respect to the dimensionless comoving coordinate ξ, and the subscript t indicates differentiation with respect to time (with $\xi = \text{const}$). If one ignores the extension of the rod over the distortion period ($L = L_0$) and considers θ and I to be constant, and N to be a function of time, (4.1) turns into a version of the equation considered in [9] (using boundary conditions applied in [9]). The relation investigated in [10] is obtained if one also ignores the elastic deformations ($1/E = 0$) and puts $N = \text{const}$.

We consider the problem with boundary conditions

$$\partial_k^0 u(0,t) = 0, \quad \partial_k^1 u(1,t) = 0 \tag{4.2}$$

where k takes the values 1, 2, and $\partial_k^i u$ are homogeneous linear forms in u, u', u'', u'''. Conditions of this form are obtained, for example, from purely geometrical assumptions of the absence of lateral displacements of the ends ($u = 0$) or of rigid constraints ($u = 0, u' = 0$). Using Eqs (3.9) and (3.10), traditional-looking relations of the form (4.2) are derived from the assumption of non-restraint at one of the ends ($u'' = 0, u''' = 0$) or the bending moment M being set equal to zero ($u'' = 0$). (Strictly speaking, in these cases more general conditions are obtained at the boundary: $u''' = C_1$ and/or $u'' = C_2$, allowing arbitrary specification of the constants C_1 and C_2 determined, in particular, by the geometry of the initial non-elastic deformation of the rod. When these constants are non-zero the absence of a stationary solution $u = 0$ excludes the problem considered below.)

Suppose that the force $N(\xi, t)$ can be represented in the form $N = -N_0(\xi)P(t)$. We put $P > 0$; then in the case of a compressive load $N_0(\xi) > 0$ when $\xi \in (0, 1)$. If the load is concentrated at the upper end, $N_0 = 1$; when the load is just the total weight $P(t)$ of the rod (with the dependence of the area of cross-section area on ξ being negligible), $N_0 = 1 - \xi$.

Using separation of variables we seek solutions of problem (4.1), (4.2) in the form

$$u_n(\xi,t) = u_{1n}(\xi)u_{2n}(t) \quad (n = 1, 2, \ldots) \tag{4.3}$$

Each of the eigenfunctions $u_{1n}(\xi)$ is a solution of the equation

$$u_{1n}^{\prime v} + \lambda_n (N_0 u_{1n}')' = 0 \tag{4.4}$$

under conditions (4.2), where the functions u are replaced by u_{1n}; λ_n are the eigenvalues of the problem. The functions $u_{2n}(t)$ are solutions of the equation

$$\frac{PL}{I\theta} u_{2n} + \left(\frac{PL}{IE} u_{2n} \right) = \frac{\lambda_n}{L} \dot{u}_{2n} \tag{4.5}$$

given by the formulae

$$u_{2n} = u_{2n}(0) \exp \int_0^t \Lambda_n dt, \quad \Lambda_n = L \left[\frac{PL}{I\theta} + \left[\frac{PL}{IE} \right] \right] \left(\lambda_n - \frac{PL^2}{IE} \right)^{-1} \tag{4.6}$$

If the functions $u_{1n}(\xi)$ form a complete system, the solution of problem (4.1), (4.2) has the form

$$u = \sum_{n=1}^{\infty} u_{0n} u_n(\xi, t) \tag{4.7}$$

where u_{0n} are coefficients of the expansion of the initial perturbation $u_0 = u(0, \xi)$ in terms of the functions $u_{1n}(\xi)$ (when $u_{2n}(0) = 1$). All the $\lambda_n > 0$, and the completeness condition is satisfied if, in particular, amongst the constraints (4.2) we have the equalities $u(0) = u(1) = 0$, and a second condition $u' = 0$ or $u'' = 0$ at each end [11]. Another example which satisfies the above requirements is the problem of a rod loaded by its own weight, with a fixed lower end and a free upper end. Below we investigate the development of individual modes when $\lambda_n > 0$.

Taking the stability condition for the rod as an elastic object (after Euler) at each instant of time with the same boundary conditions and the same load, considered to be quasisteady, we obtain $\lambda_n > PL^2/(IE)$. Taking this restriction into account, according to formula (4.6) the perturbations grow if the condition

$$\frac{PL}{I\theta} + \left(\frac{PL}{IE} \right) > 0 \tag{4.8}$$

is satisfied.

The first term in (4.8) is positive because of the assumptions made above ($P > 0$, $\theta > 0$); the sign of the second is undetermined. In particular, when the radius of the section increases rapidly compared with the extension and growth of the load, this term can be negative. In the case when condition (4.8) is satisfied, all the modes grow, and the mode with greatest wavelength allowed by the boundary conditions develops fastest, which basically corresponds to the observed change of shape.

Growth processes in biological objects diminish over a finite timescale t^* (smaller, in general, than the lifetime). This formally means that $1/\theta(t) \to 0$ and $w(t) \to 0$ when $t \to \infty$, and the largest relaxation times of these functions is t^*. Then $L(t)$ and $l(t)$ approach finite limits. What is significant for estimating the deformation of an object is not the existence of growing perturbations, but the level of their development over the growth time, computed from formula (4.6) when $t \to \infty$ (or when $t = t^*$). The characteristic time of the unperturbed process τ^* is governed by the problem an can turn out to be smaller than t^* (for the example of isometric loading given in Section 2 $\tau^* = \theta/E$). Nevertheless the development of instability should, in general, be estimated over the time t^* because the growth of the perturbations when $\tau^* < t < t^*$ can also be prolonged due to the preservation of the possibility of growth ($w \neq 0$, $1/\theta \neq 0$).

At an unknown level of the initial deformation the physically decisive comparison is between the characteristic time τ of development of the perturbation, estimated from (4.6), and the time of growth activity t^*. If these times have the same order, $\tau \sim t^*$, we have slow deformation, which can be significant for large initial perturbations, but does not lead to catastrophic deformation of the object; if, however, $\tau \gg t^*$, the process should be considered to be physically completely stable. One can only speak of a physically significant instability in the case when the perturbation develops rapidly compared with the growth process: $\tau \ll t^*$.

It is easy to write down sufficient conditions for "stability" in the sense explained above for growing perturbations (when condition (4.8) is realized)

$$1/\Lambda_1 \gg t^* \tag{4.9}$$

(λ_1 is the least eigenvalue). The structure of condition (4.9) ensures its violation near the limiting Euler stability of the rod if the left-hand side of inequality (4.8) is bounded from below by a positive constant.

The mechanism by which stability is lost due to the effect of stress on growth was first noted by Yentov [10] (1978 preprint). The analysis given here produces a more complicated scenario than that described in [10]. Even in an elementary formulation this scenario does not reduce to simple instability of axisymmetric growth under compression. The symmetry-breaking mechanism investigated here can participate in the shaping of biological systems and, together with other mechanical and chemical factors, should be taken into account when developing physical theories of morphogenesis [3, 12–15].

Some of results presented above have previously appeared in preliminary form [16, 17].

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