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Morpho-elastodynamics: the long-time dynamics of elastic growth

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As elastic tissues grow and remodel, they generate stresses that influence their mechanical states which influence the way growth proceeds. This complex feedback leads to a dynamic evolution of growth and stresses which can be modelled within the theory of exact nonlinear elasticity. Here, we first review the different theoretical results considering growth laws and then, we present a new approach to look at morphoelasticity as a continuous dynamical process. These evolution laws lead to new dynamical systems that can be studied by the classical methods of dynamical systems theory.

Keywords: biomechanics; growth and developmental biology

1. Introduction

Morphoelasticity is the theory of growth in elastic tissues [25]. When a biological tissue undergoes a growth process, its deformation is the result of both growth itself and possible elastic deformations of the tissue due to the stresses. In many physiological, biological, and pathological systems such as bones [14], arteries [57], cartilage [44], plants [16,36,43], and solid tumours [11,15,59,62], growth depends on the stress field and, *vice versa*, the stress generated in the tissue depends on growth [28]. While there are many outstanding questions in the biology of growth, from a mechanical standpoint the central problem of morphoelasticity is to include the effect of growth and remodelling within the framework of nonlinear elasticity and explore its consequences. The basic idea is to consider deformations of a body under mechanical loads and analyse the long-time evolution of such a body when either the mass or volume changes or its material properties evolve. For instance, when considering the evolution of a solid tumour in a tissue, the growth process depends on many different factors including mechanical stresses [67], which may induce a negative (controlling growth) [23,59] or positive (enhancing growth) [55,66] feedback mechanism. Therefore, without a proper analysis, there is no intuitive way to predict the final size of a tumour, even in a very simplified theoretical model, and the problem is to understand the long-time behaviour of such a system when subject to external stresses and remodelling.

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The evolution of either mass or material properties requires a new set of laws, the *evolution laws* which complement the *constitutive laws* describing the response of a material under load. The theoretical formulation of such evolution laws and their validation through experiments is a field that is by and large in its infancy. The purpose of this article is to first review the basic theoretical results concerning evolution laws and to formulate a simple theory of evolution equations for long-time behaviour in morphoelasticity.

2. Background

We consider deformations of a material body from a reference unstressed configuration $\mathcal{B}_0$ to another current configuration $\mathcal{B}$. The deformation is given by $\mathbf{x} = \boldsymbol{\chi}(\mathbf{X}, t)$, where $\mathbf{X}$ (respectively $\mathbf{x}$) is the material coordinate of a point in the reference (respectively current) configuration of a body $\mathcal{B}_t$ (respectively $\mathcal{B}_0$). The main postulate in morphoelasticity follows from early work in elastoplasticity [48,57] and was first described in [58]. It states that the deformation gradient $\mathbf{F}(\mathbf{X}, t)$ can be decomposed into a product of a growth tensor[1] $\mathbf{G}(\mathbf{X}, t)$ by an elastic tensor $\mathbf{A}(\mathbf{X}, t)$, so that

$$\mathbf{F}(\mathbf{X}, t) = \mathbf{A}(\mathbf{X}, t) \cdot \mathbf{G}(\mathbf{X}, t). \tag{1}$$

This decomposition is not trivial and not without controversy [12,32,33] (Figure 1). Nevertheless, it has been applied successfully to many different systems, such as solid tumours [3,4,6,7], plants [26], heart [49,53,66], arteries [41,63,65], muscles [64], and cartilage [44]. Similarly, in the last few years there has been considerable theoretical work to put the theory of elastic growth on a rigorous foundation [10,17,21,22,50] and to develop numerical tools to simulate the time-evolution of growing tissues [29,40,42,52]. Before we proceed with further discussions on the meaning of the decomposition, we consider it as a basic postulate, that is, we assume that at any time t, the mapping is well-defined and proceed with the derivation of the balance equations.

Let ρ be the mass density of the material of body $\mathcal{B}$ at a point $\mathbf{x}$, then the rest of the mass reads

$$\frac{\mathrm{d}\rho}{\mathrm{d}t} + \rho \operatorname{div}(\mathbf{v}) = \rho c, \tag{2}$$

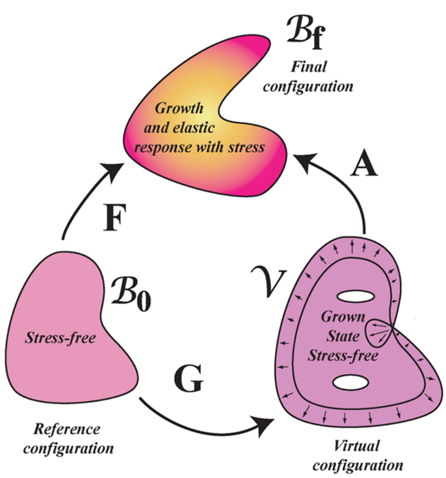

Figure 1. The one-step decomposition of finite morphoelastcity.

where $\mathbf{v}(\mathbf{x}, t) = \dot{\chi}(\mathbf{X}, t)$ is the velocity vector and c is a mass growth function [37] describing the local evolution of mass and will be related to the growth tensor. The forces distributed on a body $\mathcal{B}$ include a contact-force density $\mathbf{t}_n$ and a body-force density $\mathbf{b}$. In accordance with Euler's laws of motion, the balance of linear momentum is given by

$$\int_{\mathcal{B}} \rho(\mathbf{x}, t)\mathbf{b}(\mathbf{x}, t)\mathrm{d}v + \int_{\partial\mathcal{B}} \mathbf{t}_n \,\mathrm{d}a = \int_{\mathcal{B}} \rho(\mathbf{x}, t)\dot{\mathbf{v}}(\mathbf{x}, t)\,\mathrm{d}v, \tag{3}$$

where $\dot{\mathbf{v}}$ is the time derivative of the velocity vector. For the purpose of simplicity, the density is assumed to be constant during the growth process. According to Cauchy's theorem, the contact-force density depends linearly on the unit normal $\mathbf{n}$, given by $\mathbf{t}_n = \mathbf{Tn}$, where $\mathbf{T}$ is referred to as the Cauchy stress tensor. Using the Cauchy's theorem and applying the divergence theorem to Equation (3), the usual local equilibrium equation is obtained

$$\mathrm{div}(\mathbf{T}^{\mathrm{T}}) + \rho b = \rho\dot{\mathbf{v}}, \tag{4}$$

where the divergence is obtained with respect to $\mathbf{x}$ in the current configuration. A similar localization of the angular momentum balance reveals that the stress tensor is symmetric, that is $\mathbf{T}^{\mathrm{T}} = \mathbf{T}$. We have included in Equation (4) the dynamics associated with the inertial response of an elastic material. The typical time-scales associated with the growth processes are of the order of hours to days or years and are the orders of magnitude larger than the time-scales of elastic response (related to wave propagation in the material, that is no larger than seconds). Therefore, both the time-scales are widely separated and it is reasonable to assume that for the growth process, the elastic response of the material can be modelled as a quasi-static process. Implicit in this assumption is the existence of a viscous process that brings the elastic material to a static configuration with an associated time-scale much smaller than the growth process. Within this *slow growth assumption*, we assume that the body returns to a state of elastic static equilibrium fast enough and the equation for mechanical equilibrium becomes

$$\mathrm{div}(\mathbf{T}) + \rho\mathbf{b} = 0. \tag{5}$$

The solutions to the equilibrium equations must satisfy the conditions imposed on the boundary which can be in the form of dead-loading, rigid-loading, or mixed-loading, that is, in general, a function of $\mathbf{F}$ and $\mathbf{T}$ at the boundary:

$$\mathcal{F}(\mathbf{F}|_{\partial\mathcal{B}}, \mathbf{T}|_{\partial\mathcal{B}}) = 0. \tag{6}$$

Dead-loading prescribes the normal components of the stresses at the boundary, rigid-loading forces a fixed deformation at the boundary, and mixed-loading imposes fixed deformations on some part of the body and stresses on the remaining boundaries.

We assume the existence of a response function relating locally the stress tensor to the elastic tensor

$$\mathbf{T} = \mathcal{H}(\mathbf{A}, t), \tag{7}$$

where the explicit time-dependence refers to the possibility of the moduli to remodel in time. A common assumption is that the body is hyperelastic [27]. That is, the response function can be related to a strain energy function, $W = W(\mathbf{A}, t)$, so that

$$\mathbf{T} = J\mathbf{A}\frac{\partial W}{\partial \mathbf{A}} - p\mathbf{1}, \tag{8}$$

where p is a Lagrange multiplier associated with the incompressibility constraint and $J = \det(\mathbf{A})$ represents the change of volume due to the elastic deformation. For an incompressible material, $J = 1$ and p is the hydrostatic pressure. If the material is compressible, then $p = 0$.

3. Evolution laws for growth

At a superficial level, the decomposition $\mathbf{F} = \mathbf{A} \cdot \mathbf{G}$ seems reasonable and, with sufficient hand-waving, almost intuitive. One could easily argue that there is a continuous adjustment of growth and elastic deformation so that at all time, the deformation gradient is decomposed as a product of both the effects. The decomposition is more puzzling when one tries to apply it and understand the long-time effect of growth [35]. Assume for instance that growth takes place in time in such a way that it depends on the state of stress in the current configuration. Then, the values that the tensor $\mathbf{G}(\mathbf{X}, t)$ takes depend continuously on the configuration $\mathcal{B}$ at time t, which has not, been attained yet. Moreover, the growth tensor is defined from an unstressed configuration $\mathcal{B}_0$ but takes values that depend on the stressed configuration $\mathcal{B}$. Clearly, proper care must be taken to ensure that this decomposition makes sense. The basic solution to this problem is that an evolution law for $\mathbf{G}$ is postulated as a differential equation for $\mathbf{G}$ in the form

$$\dot{\mathbf{G}} = \mathcal{G}(\mathbf{T}, \mathbf{F}, \mathbf{G}, \boldsymbol{\mu}; t, \mathbf{x}, \mathbf{X}), \tag{9}$$

where the function $\mathcal{G}$ may be a function of the stress tensor, the geometric deformation, the growth tensor itself, the external loads, or other fields $\boldsymbol{\mu}$. A possible way to think about a growth process is to consider the differential Equation (9) and, following the original proposal of Rodriguez *et al.* [58], discretize it forward in time to obtain a sequence of growth increments

$$\mathbf{G}(t + \delta t) = \mathbf{G}(t) + \delta t \mathcal{G}(\mathbf{T}, \mathbf{F}, \mathbf{G}, \boldsymbol{\mu}; t, \mathbf{x}), \tag{10}$$

where all the arguments in the left-hand side are evaluated at time t. That is, initially, the growth tensor depends on the states of the configuration $\mathcal{B}_0$, and one can define $\mathbf{G}_1 = \mathbf{G}(\delta t)$, which corresponds to a small time increment δt. Computing the residual stress field and elastic deformations due to loading leads to a geometric deformation tensor $\mathbf{F}_1$ mapping the initial configuration $\mathcal{B}_0$ to $\mathcal{B}_1$. From the configuration $\mathcal{B}_1$, we can define a new growth tensor, $\mathbf{G}_2 = \mathbf{G}(2\delta t) = \mathbf{G}_1 + \delta t \mathcal{G}$. Once the virtual configuration $\mathcal{V}_2$ is obtained, the elastic deformation tensor $\mathbf{A}_2$ can be obtained to satisfy the proper boundary conditions. The process can be iterated as shown in Figure 2. The cumulative effect of all the growth increments can be computed to obtain the overall growth process. We see from this incremental decomposition that the growth law gives the evolution of the reference configuration by updating the growth tensor based on the values of the stress and geometric deformation tensors. Therefore, there is no causality issue and the continuous limit is well-defined. It is standard to use the discrete process when computing the evolution of growth. In general, this is necessary because at each incremental time, a non-trivial boundary value problem needs to be solved. Once this is done, the geometric deformation tensor is known and the reference

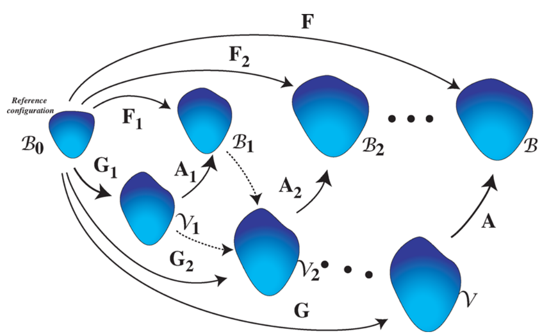

Figure 2. Evolution of the virtual grown state. The reference configuration evolves with time. To compute $\mathbf{G}_2$, we need the information contained in the state $\mathcal{V}_2$ and $\mathcal{B}_2$ as indicated by the dashed lines.

configuration is updated before a new boundary value problem is solved. However, in the case where the boundary value problem is sufficiently simple further progress can be achieved. In this case, one can use the differential equation to obtain a continuous description of the effects of growth with no time discretization.

4. More on evolution laws

Before we proceed with some examples of morphodynamics, we review what is known about evolution laws.

4.1. *Theoretical results*

To date, there is no thermodynamic theory of growth. That is, there is no rational way to derive evolution laws from general principles. Nevertheless, different authors have argued for some particular forms of the growth tensor. If we use the polar decomposition theorem [27], we can write

$$\mathbf{G} = \mathbf{G}_{\mathrm{R}}\mathbf{G}_{\mathrm{U}}, \tag{11}$$

where $\mathbf{G}_{\mathrm{R}}$ is a rotation tensor and $\mathbf{G}_{\mathrm{U}}$ is a positive definite symmetric tensor. Usually, the rotation part of the growth tensor is assumed to be identity or, equivalently, that the elastic deformation tensor contains the part of the deformation related to rotation [12,13,61]. We can now define a *growth velocity tensor* as

$$\mathbf{D}^{G} = \frac{1}{2}\left[\dot{\mathbf{G}}_{\mathrm{U}}\mathbf{G}_{\mathrm{U}}^{-1} + \mathbf{G}_{\mathrm{U}}^{-1}\dot{\mathbf{G}}_{\mathrm{U}}\right], \tag{12}$$

which is related to the mass increase by

$$c = \mathrm{Tr}(\mathbf{D}^{G}), \tag{13}$$

where c is the growth mass function appearing in the mass balance Equation (2).

Epstein and Maugin [17] argue on thermodynamic principles that the driving force behind the growth is either the Eshelby or the Mandel stress tensor defined on the virtual configuration [51]. Explicitly, the evolution law [34] for growth should be

$$\mathbf{G}_{\mathrm{U}}\dot{\mathbf{G}}_{\mathrm{U}} = \psi_0\mathbf{1} + \psi_1\mathbf{B} + \psi_2\mathbf{B}^2, \tag{14}$$

where $\mathbf{B} = J\mathbf{A}^{-1}\cdot\mathbf{T}\cdot\mathbf{A}$ is the Mandel stress tensor, that is the product of the second Piola-Kirchho. stress tensor $J\mathbf{A}^{-1}\cdot\mathbf{T}\cdot\mathbf{A}^{-\mathrm{T}}$ by the right CauchyGreen tensors $\mathbf{A}^{\mathrm{T}}\cdot\mathbf{A}$ with respect to the virtual configuration, and ψ_0, ψ_1, ψ_2 are the material parameters defining growth. Following this idea, Ambrosi *et al.* [1,2,5] propose that the evolution law should be

$$\dot{\mathbf{G}} = -\mathbf{K}\cdot(\mathbf{E} - \mathbf{E}^{*})\cdot\mathbf{G}, \tag{15}$$

where $\mathbf{E} = \mathbf{A}^{\mathrm{T}}\cdot\mathbf{T}\cdot\mathbf{A}^{-\mathrm{T}} - W\mathbf{1}$ is the Eshelby stress tensor and $\mathbf{K}$ is a second-order tensor and $\mathbf{E}^{*}$ represents the homeostatic value of the Eshelby stress tensor.

Despite the theoretical interest of these formulations, there is clearly a difficulty in relating some of these quantities (the Mandel or Eshelby stress tensors) to physical experiments and much theoretical work on a rigorous theory for evolution laws remains to be done.

4.2. *Some plausible models*

Here, we mention a few phenomenal models that have been used in the literature for evolution laws based on the heuristic and experimental findings. The simplest choice for $\mathcal{G}$ is to take it as a vanishing tensor, in which case, the growth tensor is constant in time. If we further assume that it is constant in space, analytical results can be obtained [9,10,38], and the residual stress can be computed explicitly. If we keep the growth tensor constant in time but non-homogenous, we can model the processes where growth depends on the position in the material. This effect is particularly important in systems undergoing differential growth. Explicitly, the growth tensor is a function of the reference position **X** (in the case where different cells or tissues are involved) or **x** (if growth depends on the relative position with respect to the boundary of the body) [24,25].

Following the experimental findings dating back to the nineteenth century, it has been widely recognized experimentally that one of the main biomechanical regulators of growth is stress and many authors have used simplified evolution laws based on a relation between the growth tensor and the Cauchy stress tensor [20,28,31,51,58,64,65]. Stress applied on cell walls could even play the role of a pacemaker for the collective regulation of tissue growth [60]. Simplified models of growth-stress evolution laws will now be considered.

5. Morpho-dynamics

We first collect here all the relevant equations describing the morphodynamic process. Assuming that the mass density remains constant, that the body is in elastic equilibrium at all times and in the absence of body force, we have

$$\mathbf{F} = \mathrm{Grad}\boldsymbol{\chi}(X), \tag{16}$$

$$\mathbf{F} = \mathbf{A} \cdot \mathbf{G}, \tag{17}$$

$$\dot{\mathbf{G}} = \mathcal{G}(\mathbf{T}, \mathbf{F}, \mathbf{G}), \tag{18}$$

$$\mathbf{T} = \mathcal{H}(A), \tag{19}$$

$$\mathrm{div}(\mathbf{T}) = 0, \tag{20}$$

where explicit dependence in some of the fields have been omitted, but are implicitly assumed. These are complemented by the initial conditions

$$\boldsymbol{\chi}(t = 0) = \mathbf{0}, \tag{21}$$

$$\mathbf{F}(t = 0) = \mathbf{A}(t = 0) = \mathbf{G}(t = 0) = \mathbf{I}, \tag{22}$$

$$\mathbf{T}(t = 0) = \mathbf{0}, \tag{23}$$

and the boundary conditions

$$\mathcal{F}(\mathbf{F}|_{\partial\mathcal{B}}, \mathbf{T}|_{\partial\mathcal{B}}) = 0. \tag{24}$$

Note that auxiliary equations for the evolution of elastic moduli to describe remodelling may also be needed. Equations (16)–(20) form a system of 36 partial algebraic-differential equations to solve the three components of the vector $\boldsymbol{\chi}$ and the nine components of each of the tensors **F, A, G**, and the six components of **T** (due to the symmetry $\mathbf{T}^{\mathrm{T}} = \mathbf{T}$). No obvious analytical progress can be made at this level without further assumptions.

5.1. *Dynamics of homogeneous deformations*

Here, we consider the simple but informative case where the elastic deformations are homogeneous. In such a case, the Cauchy Equation (20) is trivially satisfied. Furthermore, since there is no spatial dependence, the boundary conditions provide a global relationship. Using Equations (17) and (19), all dependence on **F** and **T** is removed and the system can be written as a set of 18 equations for **A** and **G**

$$\dot{\mathbf{G}} = \hat{\mathcal{G}}(\mathbf{A}, \mathbf{G}), \tag{25}$$

$$\mathbf{0} = \hat{\mathcal{F}}(\mathbf{A}, \mathbf{G}), \tag{26}$$

where

$$\hat{\mathcal{G}}(\mathbf{A}, \mathbf{G}) = \mathcal{G}(\mathcal{H}(\mathbf{A}), \mathbf{A} \cdot \mathbf{G}, \mathbf{G}), \tag{27}$$

$$\hat{\mathcal{F}}(\mathbf{A}, \mathbf{G}) = \mathcal{F}(\mathbf{A} \cdot \mathbf{G}, \mathcal{H}(\mathbf{A})). \tag{28}$$

This set of algebraic-differential equations can be converted into a system of differential equations for **A, G** by using the time-derivative of the second equation to obtain

$$\dot{\mathbf{G}} = \hat{\mathcal{G}}(\mathbf{A}, \mathbf{G}), \tag{29}$$

$$\hat{\mathcal{F}}_{\mathbf{A}} : \dot{\mathbf{A}} + \hat{\mathcal{F}}_{\mathbf{G}} : \dot{\mathbf{G}} = -\frac{\partial \hat{\mathcal{F}}}{\partial t}, \tag{30}$$

where $\hat{\mathcal{F}}_{\mathbf{A}} = \partial \hat{\mathcal{F}} / \partial \mathbf{A}$ and $\hat{\mathcal{F}}_{\mathbf{G}} = \partial \hat{\mathcal{F}} / \partial \mathbf{G}$ are the fourth-order tensors. For a given constitutive law and imposed boundary conditions, the solution of this system predicts the evolution of stresses, growth, and strains. We will consider some simple examples and explore various growth evolution laws to help us develop insights into the growth processes. Note that if the material is incompressible, we have both an additional constraint and an extra variable p for the evolution of the hydrostatic pressure.

5.2. *A one-dimensional example*

To gain some intuition on the dynamics of growth, we revisit the case of the growth of a rectangular block subject to constant compression along one of its axes and allowed to grow in the two other directions [58]. The growth evolution is a function of the stress and we assume the existence of a state of homeostatic stress along the compression in the z-axis (taken to be vertical), that is, when the body is compressed along the longitudinal axis, the corresponding longitudinal stress may be different from a predetermined equilibrium stress. Therefore, the material will grow or resorb along the x and y directions until the equilibrium is restored. We assume that growth and elastic tensors are diagonal and that the block is hyperelastic, incompressible, and under uniaxial loading, so that

$$\mathbf{A} = \begin{bmatrix} \alpha_x & 0 & 0 \\ 0 & \alpha_y & 0 \\ 0 & 0 & \alpha_z \end{bmatrix} = \begin{bmatrix} \alpha & 0 & 0 \\ 0 & \alpha & 0 \\ 0 & 0 & \dfrac{1}{\alpha^2} \end{bmatrix}, \quad \mathbf{G} = \begin{bmatrix} \gamma & 0 & 0 \\ 0 & \gamma & 0 \\ 0 & 0 & 1 \end{bmatrix}, \quad \mathbf{F} = \begin{bmatrix} \lambda_x & 0 & 0 \\ 0 & \lambda_y & 0 \\ 0 & 0 & \lambda_z \end{bmatrix}, \tag{31}$$

and the kinematics relationship, $\mathbf{F} = \mathbf{A} \cdot \mathbf{G}$ implies that $\lambda_x(t) = \lambda_y(t) = \gamma(t)\alpha(t)$, $\lambda_z = 1/\alpha^2$. The Cauchy stresses are given by

$$T_x = \alpha W_x(\alpha, \alpha, 1/\alpha^2) - p, \tag{32}$$

$$T_y = \alpha W_y(\alpha, \alpha, 1/\alpha^2) - p, \tag{33}$$

$$T_z = \frac{1}{\alpha^2} W_z(\alpha, \alpha, 1/\alpha^2) - p, \tag{34}$$

where $W_x(\alpha, \alpha, 1/\alpha^2) = \partial W/\partial \alpha_x$ evaluated at $\alpha_x = \alpha, \alpha_y = \alpha, \alpha_z = 1/\alpha^2$ and W_y and W_z are similarly defined. Here, we adopt the evolution law

$$\dot{\gamma} = k(T_z - T_*), \tag{35}$$

where T_* is a given homeostatic stress. The boundary conditions on the block are no traction on the four vertical faces of the block and constant compressive force F_* on the horizontal faces. Since the deformation is homogeneous, we have

$$T_x(t) = T_y(t) = 0, \tag{36}$$

$$F_* = A(t)T_z = A(0)\lambda_x\lambda_y T_z = \alpha^2\gamma^2 T_z, \tag{37}$$

where $A(t)$ is the surface area of the horizontal faces at time t and $A(0) = 1$ is chosen without loss of generality. Note that since $T_x(t) = T_y(t) = 0$, we have $p(t) = \alpha W_x$, which implies

$$T_z = f(\alpha) = -\frac{\alpha}{2}\hat{W}'(\alpha), \tag{38}$$

where $\hat{W}(\alpha) = W(\alpha, \alpha, 1/\alpha^2)$ is assumed to be in C^3. The two equations for T_z, α, γ can be rewritten in terms of γ and α by using the constitutive relationships to obtain

$$\dot{\gamma} = k(f(\alpha) - T_*), \tag{39}$$

$$0 = F_* - g(\alpha)\gamma^2, \tag{40}$$

where $g(\alpha) = \alpha^2 f(\alpha)$. These last equations are a particularly simple example of the general relationships (25) and (26). From these equations, a single differential equation for α can be obtained

$$\dot{\alpha} = -2k\alpha^2 f(\alpha)\left[\frac{f(\alpha)}{F_*}\right]^{1/2} \frac{f(\alpha) - T_*}{2f(\alpha) + \alpha f'(\alpha)}. \tag{41}$$

The dynamics can be directly inferred from this equation. Assume that F_* is chosen so that the equation $f(\alpha_*) = T_*$ has at least one solution (depending on the particular choice of potential W and T_* there may be more than one solution as will be shown shortly). This fixed point α_* is an equilibrium solution that corresponds to a growth $\gamma_* = \sqrt{F_*/\alpha_*^2 T_*}$. The stability of such a fixed point is determined by the sign of the linear stability exponent μ given by

$$\mu_\alpha = -2k\frac{\partial}{\partial \alpha}\left[\alpha^2 f(\alpha)\left[\frac{f(\alpha)}{F_*}\right]^{1/2} \frac{f(\alpha) - T_*}{2f(\alpha) + \alpha f'(\alpha)}\right]_{\alpha=\alpha_*}. \tag{42}$$

As usual, a positive value of μ corresponds to an unstable fixed point and a negative value to a stable fixed point. More elegantly, the stability analysis can be applied directly to Equations (25)

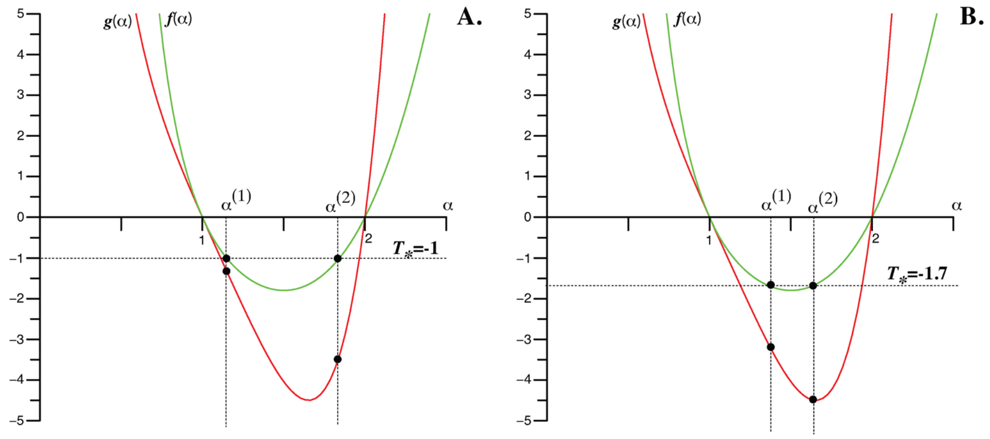

Figure 3. Stability of fixed points for a Mooney-Rivlin strain–energy function with $A = 1$, $B = 1/4$. While the fixed point $\alpha^{(1)}$ is always stable since both f and g have the same slope, the stability of the fixed point $\alpha^{(2)}$ depends on the value of F_*.

and (26) by setting $\gamma = \gamma_* + \epsilon\tilde{\gamma}$, $\alpha = \alpha * + \epsilon\tilde{\alpha}$, and expanding both the equation to first order in $epsilon$ to obtain, after simplification

$$\dot{\tilde{\gamma}} = \mu_\gamma \tilde{\gamma}, \tag{43}$$

where

$$\mu_\gamma = -2k\alpha_*^3 T_* \sqrt{\frac{T_*}{F_*}\frac{f'(\alpha_*)}{g'(\alpha_*)}}. \tag{44}$$

We conclude that the stability of the fixed point depends only on the respective sign of k, $f'(\alpha_*)$, $(\alpha_*^2 f(\alpha_*))'$. In particular, if $f'(\alpha_*) < 0$ and since $T_* < 0$, $f'(\alpha_*) < 0$, we have $f'(\alpha_*)/g'(\alpha_*) > 0$ which implies that the fixed point is stable if $k < 0$.

As an example, we consider the Mooney-Rivlin strain-energy function

$$W = A(\alpha_x^2 + \alpha_y^2 + \alpha_z^2 - 3) + B(\alpha_x^{-2} + \alpha_y^{-2} + \alpha_z^{-2} - 3), \tag{45}$$

In Figure 3 we show the existence of two fixed points for $A = 1$, $B = 1/4$ and $F_* = 1$. For $k < 0$, depending on the value of T_*, the second fixed point $\alpha^{(2)}$ is either stable or unstable depending on the relative slopes of f and g at $\alpha = \alpha^{(2)}$. This simple example, which reduces to a one-dimensional dynamical system, already shows the complexity of the growth process. For non-trivial strain-energy functions, as growth proceeds, an increase in volume can have non-intuitive effects on the stress. We further study the effect of the boundary conditions by considering the rigid boundaries.

5.3. *On the influence of boundaries*

Now suppose a rectangular block is constrained on its horizontal face and is allowed to grow along the z-direction, while the vertical faces are free of traction. This setup requires mixed-loading bounding conditions so that the deformation is fixed along the z-direction and the stresses in the x and y directions vanish. The rigid-loading on the ends requires that the longitudinal stretch remains one, that is $\lambda_z = 1$. Using the kinematics relationship $\lambda_z = \alpha_z\gamma$, the rigid-loading condition $\lambda_z = 1$ is given by

$$\frac{\gamma}{\alpha^2} = 1, \tag{46}$$

where γ is the longitudinal growth and $1/\alpha^2$ is the elastic response in the z direction as defined in Equation (31). The other boundaries are stress-free ($T_x = T_y = 0$) which provides an equation for the hydrostatic pressure, $p = \alpha W_x$ which, again, implies $T_z = -\alpha/2\hat{W}'(\alpha)$. The growth rate is given by

$$\dot{\gamma} = \mathcal{E}(T_z) = k(T_z - T_*). \tag{47}$$

The system for (α, γ) reads

$$\dot{\gamma} = k(f(\alpha) - T_*), \tag{48}$$

$$\gamma - \alpha^2 = 0, \tag{49}$$

where $f(\alpha) = -\alpha/2\hat{W}'(\alpha)$, as before. The differential equation for α is

$$\dot{\alpha} = \frac{k}{2\alpha}(f(\alpha) - T_*). \tag{50}$$

The linear eigenvalues (μ_α, μ_γ) associated with the stability of (T_*, α_*) are

$$\mu_\alpha = k\frac{2T_* - \alpha^2\hat{W}''(\alpha_*)}{4\alpha^2}, \tag{51}$$

$$\mu_\gamma = \frac{k}{2\alpha_*}f'(\alpha_*), \tag{52}$$

and, since $\alpha_* > 0$, the fixed point is stable if $kf'(\alpha) < 0$. In particular, if $f'(\alpha) < 0$, the fixed point is stable for $k > 0$. This example shows the influence of the boundary conditions. Depending on the type of boundary that is applied, the system will not settle on the same homeostatic stress.

5.4. *A two-dimensional example*

A more general formulation is now discussed in which growth can occur at different rates in the x, y, and z directions. Growth and elastic tensors are assumed to be diagonal and the material is assumed to be incompressible. The elastic tensor, growth tensor, and total deformation tensor are given by

$$\mathbf{A} = \begin{bmatrix} \alpha_x & 0 & 0 \\ 0 & \alpha_y & 0 \\ 0 & 0 & \alpha_z \end{bmatrix} = \begin{bmatrix} \alpha_x & 0 & 0 \\ 0 & \alpha_x & 0 \\ 0 & 0 & \dfrac{1}{\alpha_x\alpha_y} \end{bmatrix}, \quad \mathbf{G} = \begin{bmatrix} \gamma_x & 0 & 0 \\ 0 & \gamma_y & 0 \\ 0 & 0 & \gamma_z \end{bmatrix}, \quad \mathbf{F} = \begin{bmatrix} \lambda_x & 0 & 0 \\ 0 & \lambda_y & 0 \\ 0 & 0 & \lambda_z \end{bmatrix} \tag{53}$$

and the Cauchy stresses are given by

$$T_x = \alpha_x W_x - p, \tag{54}$$

$$T_y = \alpha_y W_y - p, \tag{55}$$

$$T_z = \frac{1}{\alpha_x\alpha_y}W_z - p. \tag{56}$$

Assume there are constant compressive forces F_x, F_y, and F_z on each of the vertical faces, which implies

$$F_x = A_x(t)T_x = A_x(0)\lambda_y\lambda_z T_x, \tag{57}$$

$$F_y = A_y(t)T_y = A_y(0)\lambda_x\lambda_z T_y, \tag{58}$$

$$F_z = A_z(t)T_z = A_z(0)\lambda_x\lambda_y T_z, \tag{59}$$

where $A_x(t)$, $A_y(t)$, and $A_z(t)$ are the surface areas of the faces perpendicular to the x, y, and z axes, respectively, at time t. The surface areas at $t = 0$ are all chosen to be one. Equations (57) and (58) are used to find a relationship between α_x and α_y and therefore, the elastic tensor can be written in terms of a single variable, α, given by

$$\mathbf{A} = \begin{bmatrix} \alpha & 0 & 0 \\ 0 & \alpha\dfrac{(\gamma W_x - \gamma_x F_x)}{(\gamma W_y - \gamma_y F_y)} & 0 \\ 0 & 0 & \dfrac{(\gamma W_y - \gamma_y F_y)}{\alpha^2(\gamma W_x - \gamma_x F_x)} \end{bmatrix}, \tag{60}$$

where $\gamma = \gamma_x\gamma_y\gamma_z$ and Equation (59) can be written as

$$F_z = \gamma_x\gamma_y W_z - \frac{\alpha_x^3}{\gamma_z}\frac{(\gamma W_x - \gamma_x F_x)}{(\gamma W_y - \gamma_y F_y)}(\gamma W_x - \gamma_x F_x). \tag{61}$$

Assume a general growth law of the form

$$\begin{bmatrix} \dot{\gamma}_x \\ \dot{\gamma}_y \\ \dot{\gamma}_z \end{bmatrix} = \mathbf{K}\left(\begin{bmatrix} T_x \\ T_y \\ T_z \end{bmatrix} - \begin{bmatrix} T_x^* \\ T_y^* \\ T_z^* \end{bmatrix}\right), \tag{62}$$

where $\mathbf{K}$ is the growth coefficient matrix and T_x^*, T_y^*, and T_z^* are prescribed homeostatic stresses. Equations (61) and (62) result in four equations for α, γ_x, γ_y, and γ_z.

Further progress can be made if the growth and applied forces are symmetric in the x and y directions, that is $\gamma_x = \gamma_y$ and $F_x = F_y$. The components of the elastic tensor are now given by $\alpha_x = \alpha_y = \alpha$, $\alpha_z = 1/\alpha^2$ and the applied force in the x direction is now given by

$$F_x = \frac{\gamma_x\gamma_z}{\alpha}T_x. \tag{63}$$

The relationship $\lambda_x = \lambda_y = \alpha\gamma_x$ and the axial stress $T_z = W_z/\alpha^2 - p$ are substituted in Equation (59) to provide an equation for p, $p = (\gamma_x^2 W_z - F_z)/(\alpha^2\gamma_x^2)$. Therefore, the Cauchy stresses are given by

$$T_x = f(\alpha) + g(\alpha, \gamma_x) = \left(\frac{\alpha}{2}\hat{W}_\alpha + \frac{F_z}{\alpha^2\gamma_x^2}\right), \tag{64}$$

$$T_z = g(\alpha, \gamma_x) = \frac{F_z}{\alpha^2\gamma_x^2}. \tag{65}$$

Using these equations for T_x and T_z, three equations are obtained for α, γ_x, and γ_z given by

$$\begin{bmatrix} \dot{\gamma}_x \\ \dot{\gamma}_z \end{bmatrix} = \mathbf{K}\cdot\left(\begin{bmatrix} f(\alpha) + g(\alpha, \gamma_x) \\ g(\alpha, \gamma_x) \end{bmatrix} - \begin{bmatrix} T_x^* \\ T_z^* \end{bmatrix}\right), \tag{66}$$

$$0 = F_x - \frac{\gamma_x\gamma_z}{\alpha}(f(\alpha) + g(\alpha, \gamma_x)). \tag{67}$$

From these equations, a system of differential equations can be obtained

$$\begin{bmatrix}\dot{\gamma}_x\\ \dot{\gamma}_z\end{bmatrix} = \mathbf{K}\left(\begin{bmatrix} f(\alpha)+g(\alpha,\gamma_x)\\ g(\alpha,\gamma_x)\end{bmatrix} - \begin{bmatrix}T_x^*\\ T_z^*\end{bmatrix}\right), \tag{68}$$

$$\dot{\alpha} = \frac{(\dot{\gamma}_x\gamma_z+\gamma_x\dot{\gamma}_z)(f(\alpha)+g(\alpha,\gamma_x))+\gamma_x\gamma_z g_{\gamma x}(\alpha,\gamma_x)\dot{\gamma}_x}{F_x-\gamma_x\gamma_z f_\alpha(\alpha)-\gamma_x\gamma_z g_\alpha(\alpha,\gamma_x)}, \tag{69}$$

where the subscripts α and γ_x denote the derivative with respect to α and γ_x, respectively. Recall that T_x^* and T_z^* are prescribed homeostatic states, yet the structure can relax to equilibrium states, denoted by T_x^e and T_z^e, which may or may not be equal to the prescribed equilibrium states. This can be seen by setting Equation (66) equal to zero and solving for the equilibrium values α^* and γ_x^*. Once α^* and γ_x^* are known, Equation (67) is used to solve for γ_z^*,

$$\dot{\gamma}_x = K_{11}(f(\alpha)+g(\alpha,\gamma_x)-T_x^*)+K_{12}(g(\alpha,\gamma_x)-T_z^*)=0, \tag{70}$$

$$\dot{\gamma}_z = K_{21}(f(\alpha)+g(\alpha,\gamma_x)-T_x^*)+K_{22}(g(\alpha,\gamma_x)-T_z^*)=0, \tag{71}$$

$$\dot{\gamma}_z = \frac{\alpha F_x}{\gamma_x(f(\alpha)+g(\alpha,\gamma_x))} \tag{72}$$

Consider a simple example where $K_{12}=K_{22}=0$ and $K_{11}, K_{21}<0$. Then, $f(\alpha^*)+g(\alpha^*,\gamma_x^*)=T_x^*$. However, $f(\alpha^*)+g(\alpha^*,\gamma_x^*)$ is equivalent to T_x^e so that the relaxed equilibrium stress is always equal to the prescribed equilibrium stress in the x and y directions. The axial stress equilibrium, T_z^e, on the other hand, will depend on the applied forces. The system in Equations (68) and (69) can be solved numerically and the results are shown in Figure 4 as the growth coefficient matrix $\mathbf{K}$ is varied. Note that for certain cases, the equilibrium stress states may change as the initial conditions vary, and for other cases the equilibrium stress states are independent of the applied forces.

Depending on the values of K_{ij}, Equations (66) and (67) can produce other interesting dynamics, such as the occurrence of oscillations. For example, Figure 5 shows dampened oscillations in the stresses and the corresponding stable spiral in the γ_x, γ_z phase plane. The structure is shown to oscillate between growth states even in the case of a rather simple growth law. Note that oscillation during growth is frequently encountered in biological systems ranging from fungi [45], pollen tubes [19,30], and plants [18,39] to invertebrates [8] and even humans [46,47]. However, a proper modelling of the phenomenon of growth oscillation requires the coupling with other important fields (such as calcium concentration for pollen tubes). The goal of our example is merely to show the possibility of interesting dynamics related to the structure of equations for elastic growth.

5.5. *A general stability result*

We can now return to the general form of Equations (25) and (26), and study the stability of a fixed point for growth given that there exists a pair of constant tensors (G_*, A_*), such that $\hat{\mathcal{G}}(\mathbf{A}_*,\mathbf{G}_*)=\hat{\mathcal{F}}(\mathbf{A}_*,\mathbf{G}_*)=0$. The question is now to assess the stability of such a state for the growth dynamics. We assume that if the inverse $\hat{\mathcal{F}}_{\mathbf{A}}^{-1}$ of the fourth-order tensor exists, $\hat{\mathcal{F}}_{\mathbf{G}}$ exists, then the linearized equation for $\tilde{G}$ is

$$\dot{\tilde{G}} = \mathcal{M} : \tilde{G}, \tag{73}$$

where $\mathcal{M}=\hat{\mathcal{G}}_{\mathbf{A}} : \hat{\mathcal{F}}_{\mathbf{A}}^{-1} : \hat{\mathcal{F}}_{\mathbf{G}}+\hat{\mathcal{G}}_{\mathbf{G}}$ is evaluated at the fixed point. This is now a regular spectral problem with an associated matrix of eigenvalues $\boldsymbol{\mu}_{\mathbf{G}}$ and assuming that the real part of each entry does not vanish, the fixed point is hyperbolic and its stability (or lack thereof) is simply given by the sign of the entries of $\boldsymbol{\mu}_{\mathbf{G}}$.

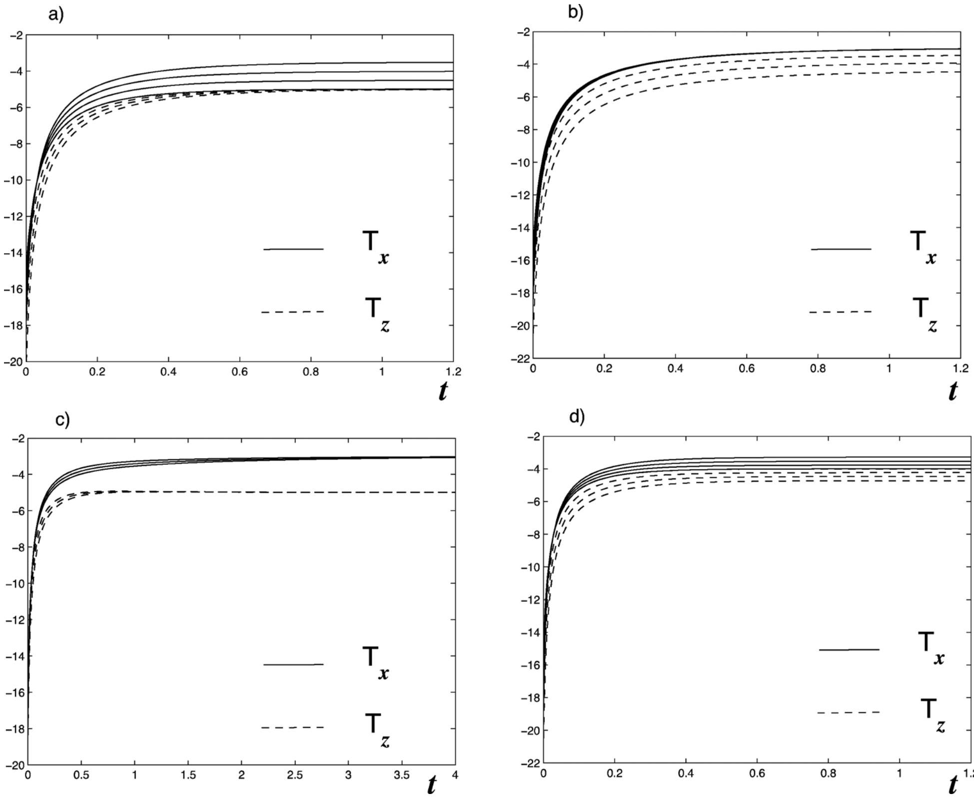

Figure 4. The stresses in the x and z directions are plotted for $T_x^* = -3$, $Tz^* = -5$ and $F_x = -15$. The curves are shown for various applied loads, $F_z = -16, -22, -29$. (a) $K_{11} = K_{21} = 0$ and $K_{12} = K_{22} = -1$, (b) $K_{12} = K_{22} = 0$ and $K_{11} = K_{21} = -1$, (c) $K_{11} = K_{22} = 0$ and $K_{12} = K_{21} = -1$, (d) $K_{11} = K_{21} = K_{12} = K_{22} = -1$.

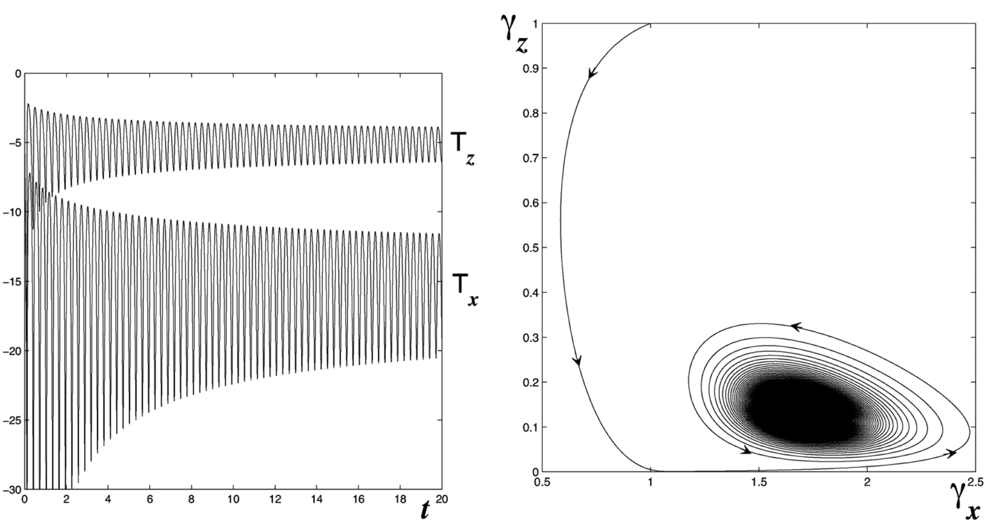

Figure 5. The oscillating stresses are shown to dampen in (a) and the corresponding growth phase plane is shown in (b) where $K_{11} = -1$, $K_{12} = 0.1$, $K_{21} = -0.1$, $K_{22} = 1$, $T_x^* = -15$, $T_z^* = -5$, $F_x = -5$, $F_z = -6.44$.

6. Conclusions

Growth is a process of infinite complexity. Here, we have only considered the possible role of mechanical feedback in the growth process in simple geometries and for homogeneous deformations. Growth can generate stresses in the tissue which influence their mechanical states, which in turn affect the way the tissue grows creating a complex feedback. Whereas previous studies have focused on incremental (and therefore numerical) growth processes, in the setting proposed here, morphodynamics can be written as a continuous dynamical system and studied for long-time behaviour. In the case of a simple growth law, a classical stability analysis can be performed and the asymptotic dynamics can be fully elucidated (the case of multiple homeostatic states competing in a one-dimensional process as proposed by Fung [20] can be treated similarly).

Here, we have considered an evolution law function of the stresses and we have not taken into account the possible dependence on the geometric deformation, external loads, or other fields. However, a general framework was formulated for the evolution equations which can be easily generalized to include other forms of the evolution law. Although a simple stress-dependent growth evolution law was used, interesting dynamics are observed including the existence of multiple growth equilibrium states, equilibrium states different from homeostatic stresses, and oscillating growth states.

This paper focuses on evolution equations in cartesian coordinates, but a similar formulation in cylindrical coordinates can be derived and applied to a cylindrical structure which is a relevant geometry in many physiological and biological systems, such as the growth of arteries and plants. It is clear that there are many more interesting applications to be studied in which the use of morpho-elastodynamics could prove to be quite useful.

Notes

1. Note that most authors use the notation $\mathbf{F} = \mathbf{Fe} \cdot \mathbf{Fg}$ by analogy with the elastoplastic decomposition $\mathbf{F} = \mathbf{Fe} \cdot \mathbf{Fp}$. Here following previous works [9,24,25], Cowin's notation for the growth tensor [13] and Ogden's notation for elastic strains [54], we use the decomposition $\mathbf{F} = \mathbf{A} \cdot \mathbf{G}$ which is not well established, but has the greater advantage to identify $\mathbf{G}$ has a central object and allows for various subscripts.

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