TRUSS MODEL FOR STRESS CONTROLLED MORPHOGENESIS

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ABSTRACT

We resort to the usual decomposition of the deformation gradient into an active and a passive component, and deduce the constitutive law and equilibrium equations when the two components are not independent. In the model described here the active part of the deformation is related to the hyperelastic passive part through a control function that simulates a feedback mechanism that has been experimentally observed during embryo development. Using a variational approach, we first write the equations for continua and study the effects of the control function in these equations. We particularise the results for a system of trusses, which allows us to obtain a simplified set of equations. In our derivations, we apply special attention to the conditions that a thermodynamically compliant formulation should satisfy.

We particularise these equations and conditions for the relevant elements of the cytoskeleton, namely, microfilaments and microtubules. We apply the model to simulate the shape changes observed during invagination of the Drosophila Melanogaster embryo. As a salient result, the model reveals that the incompressibility constraint of the yolk furnishes a necessary pressure on the epithelium that eventually eases its internalisation.

Key Words: *Morphogenesis, Development, Drosophila, Growth, Trusses, Invagination*

1 INTRODUCTION

Mesodermal invagination is one of the first movements with large deformations of the epithelium cells during embryo development. It has been experimentally tested that the genetical expression of the main genes involved in this process may be mechanically induced and expressed[1,5]. This feedback

mechanism has strongly motivated the development of models where the active mechanisms are stress-controlled [1]. We here apply these ideas in a continuum approach and in a thermodynamically consistent manner, and particularise them to a system of truss elements, which will eventually represent the relevant elements of the cytoskeleton, namely microfilaments and microtubules. The resulting model is an improvement to the author's previous two-[3] and three-dimensional models [4].

2 CONTINUUM MODEL

We will resort to the usual decomposition of the deformation gradient $\boldsymbol{F}$ into an active component $\boldsymbol{F}$ and an elastic component $\boldsymbol{F}_e$ (see Figure 1). Consistent expressions of the elastic and active stresses, denoted by $\boldsymbol{P}_e$ and $\boldsymbol{P}$ respectively, can be deduced from reduced dissipation inequality, which in the present case reads,

$$\mathcal{D} := \boldsymbol{P}_e : \boldsymbol{L}_e + \boldsymbol{P} \ : \boldsymbol{L} \ - \rho^0 \dot{\psi} \geq 0,$$

with $\mathcal{D}$ the dissipated energy, and $\boldsymbol{L}_e = \dot{\boldsymbol{F}}\boldsymbol{F}^{-1}$, and $\boldsymbol{L} \ = \dot{\boldsymbol{F}} \ \boldsymbol{F}^{-1}$ the kinematic conjugates to $\boldsymbol{P}_e$ and $\boldsymbol{P}$, respectively.

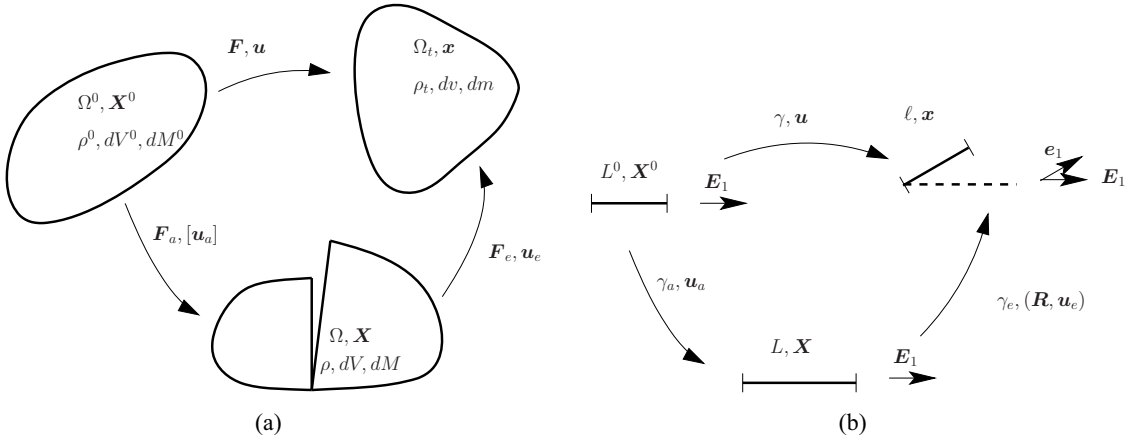

Figure 1: Maps between the reference configuration, the relaxed configuration, and the deformed configuration for the continuum model (a), and the truss model (b).

Two sets of equilibrium equations are deduced by minimising the following functional,

$$\Pi \ \boldsymbol{u} \ , \boldsymbol{u}_e \ = \int_\Omega \rho\psi \ \boldsymbol{u} \ , \boldsymbol{u}_e \ \ V + \Pi_{ext}$$

with respect to *independent* variations $\delta\boldsymbol{u}$ and $\delta\boldsymbol{u}_e$. After inserting the following dependence between active and elastic deformations,

$$\dot{\boldsymbol{F}} \ = \boldsymbol{\beta} \ \boldsymbol{F}_e \ . \tag{1}$$

with $\boldsymbol{\beta}$ a general stress-control function, we may couple the two sets of equilibrium equations into a single equation.

3 TRUSS MODEL

Motivated by the mechanism in the actin-myosin complex depicted in Figure 2, and the simplicity to measure the material properties in the cytoskeleton elements rather than in the continuum cell, we have

particularised the previous model to a system of trusses. The equivalent maps are given in Figure 1b, where the tensors $\boldsymbol{F}$, $\boldsymbol{F}$ and $\boldsymbol{F}_e$ have been replaced by γ, γ and γ_e, respectively. Due to the linear interpolation of the total displacements $\boldsymbol{u}$, the latter may be expresses as,

$$\gamma = 1 + u \; X_1^0{}' = \frac{\ell}{L^0}, \quad \gamma \; = 1 + u \quad X_1^0{}' = \frac{L}{L^0}, \quad \gamma_e = 1 + u_e \; X_1{}' = \frac{\ell}{L},$$

where L^0, L and ℓ are the reference, relaxed and deformed length of the truss, respectively (see Figure 2 for the physical representation of these lengths).

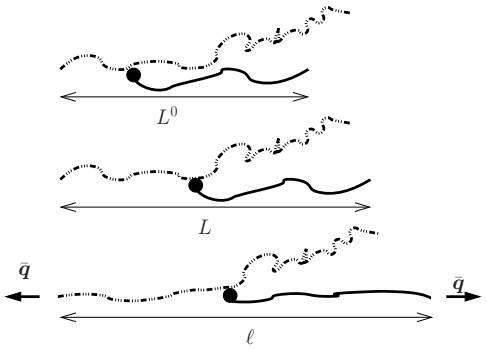

Figure 2: Scheme of the physical representation of the growth process in the actin-myosin complex.

we particularise our mode to a total stored free energy density given by $\psi = \frac{1}{} \quad u_e' \quad = \frac{1}{} \; \left(\frac{\ell - L}{L}\right)$, with a material parameter, assumed constant for each truss. The dependence in (1) between the active deformations and the elastic deformations is now replaced by the following linear relationship:

$$\dot{u} \; = \beta \quad u_e' - \sigma \tag{2}$$

with β a material parameter, and σ the target stress at which homeostatic equilibrium takes place.

4 NUMERICAL RESULTS

We have modelled the cross-section of the Drosophila Melanogaster embryo, and applied a stress controlled active deformation (non-zero parameter β in Eqn. (2)) to the apical elements of the mesoderm (cells at the bottom in Figure 3), and to the radial trusses. For some combinations of the stiffness , consistent with experimental measurements, we have obtained the deformed configurations in Figure 3. We note that the cytoplasm and the yolk have been modelled through an incompressibility condition for each cell unit, and for the whole inner volume of the cross-section. Interestingly, when the yolk is not modelled, no invagination could be achieved.

5 CONCLUSIONS

We have applied the common gradient decomposition to the cellular structural elements, in conjunction with a stress controlled growth process. The method has allowed us to identify some of the key mechanisms that trigger invagination. In this regard, it has been found that the internal pressure furnished by the yolk of the embryo has a determinant role in the invagination of the mesoderm in the Drosophila embryo.

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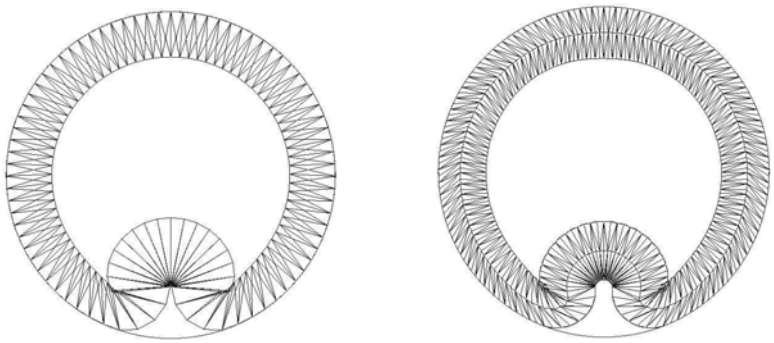

(a) (b)

Figure 3: Deformed cross-section of the embryo using different typologies of the cytoskeleton.

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