Journal of the Mechanics and Physics of Solids 59 (2011) 863–883

Contents lists available at ScienceDirect

Journal of the Mechanics and Physics of Solids

journal homepage: www.elsevier.com/locate/jmps

Review Article

Perspectives on biological growth and remodeling

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ARTICLE INFO

Article history:
Received 31 January 2009
Received in revised form
15 December 2010
Accepted 19 December 2010
Available online 28 December 2010

Keywords:
Mechanotransduction
Chemo-mechanics
Morphogenesis
Thermodynamics
Computational mechanics

ABSTRACT

The continuum mechanical treatment of biological growth and remodeling has attracted considerable attention over the past fifteen years. Many aspects of these problems are now well-understood, yet there remain areas in need of significant development from the standpoint of experiments, theory, and computation. In this perspective paper we review the state of the field and highlight open questions, challenges, and avenues for further development.

Contents

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0022-5096/$ - see front matter
doi:10.1016/j.jmps.2010.12.011

1. Introduction

Biological growth occupied the minds of students of evolutionary and organismic biology in the early twentieth century. Foremost among them were D'Arcy Thompson and Julian Huxley. Their classics, "On Growth and Form" (Thompson, 1917) and "Problems of Relative Growth" (Huxley, 1932), put forth the idea of growth as a change in form. The focus then was on the recurring observation that certain organisms and their sub-parts grew into well-defined geometric forms. As in other aspects of life science, however, the advent of molecular and cell biology subsequently over-shadowed this organism-level morphological view. The dominant view today is that molecular interactions drive biological processes. Perhaps as a natural outcome of this view, the contemporary classic "The Molecular Biology of the Cell" (Alberts et al., 2008) describes growth as an increase in mass driven primarily by the biochemistry. Both of these viewpoints—growth as changes in form or changes in mass—have found acceptance within the continuum mechanics community.

Early work by Skalak et al. (1982) introduced the kinematic treatment of continuum mechanics to describe surface growth (see also Cowin and Van Buskirk, 1979). It was followed by a more comprehensive discussion (Skalak et al., 1997) of growth velocities and velocities of generating cells that shape antlers, horns, tusks, and shells. Among continuum mechanicians there remain adherents to the view that the important effects of growth are explained by induced changes in form. The other opinion, that of growth as a change in mass, has drawn from the thermodynamics of open systems and more specifically in some cases, from the continuum theory of mixtures. It too has numerous adherents.

Modern continuum mechanical treatments of growth as a change in mass do not ignore the related change in form, however, as do some quarters of the mathematical biology community. How to translate gain and loss of mass into non-uniform changes in form is a central question for continuum mechanics. A common approach has been to treat local changes in mass via variations in concentrations, and to allow stress, or alternately the elastic part of the deformation gradient, to be driven by these variations in concentration. This approach is predicated upon a decomposition of the deformation gradient tensor into elastic and growth components, mathematically isomorphic to the multiplicative decomposition that is a cornerstone of finite strain plasticity. The coupled solution of balances of mass and linear momentum then governs changes in form: An increase in mass is accompanied by an increase in volume and *vice versa* for a decrease in mass. This simple approach (some would say simple-minded) successfully models residual stress in growing tissues. Indeed, a series of seminal studies by Fung and co-workers (Liu and Fung, 1988; Omens and Fung, 1990) on residual stress in arteries and the heart was interpreted in terms of continuum growth theories (and remodeling—see below). In the 1990s Fung also introduced the concept of a "mass–stress relation" for growth, a generalization to unmineralized tissues of a concept developed for mineralized tissue (bone) growth (Pauwels, 1980; Kummer, 1972; Firoozbakhsh and Cowin, 1981). Another general approach to modeling growth (and remodeling) has stemmed from Fung's suggestion, that is, by incorporating biologically driven mass density productions and survival functions within constitutive relations for stress response based on simple rule of mixture formulations (Humphrey and Rajagopal, 2002).

"Remodeling", a term often used jointly with growth, has been employed to describe changes in properties, such as the anisotropy, stiffness and strength, that result from fine changes in microstructure as well as coarse changes such as thickening and fibrosis (Taber, 1995). However, the last two processes are also manifestations of growth at lower spatial scales. This example suggests that although growth and remodeling can be distinct cell driven biological processes, they often interact. One example occurs in the growth of long bones. The cartilaginous growth plate near the ends of a long bone provides an increment of length to the bone before the growth plate closes (endochondral ossification).