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Alain Goriely

The Mathematics and Mechanics of Biological Growth

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Alain Goriely

The Mathematics and Mechanics of Biological Growth



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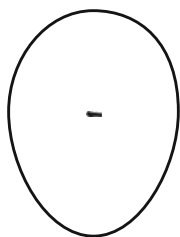
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This book is dedicated to the 3Z:

Zébulon, Zakkai, and Zéphyr.

*Not as an acknowledgement of their patience or help,
as they have none and gave me little,
but for the daily joy and chaos that they create
and for the fabulous examples of growth processes
that they generated over the last seventeen years.
My interest in growth conveniently coincided
with their birth and childhood.*

Preface



To the nature lover, there is a distinct feeling of awe and beauty when observing the gradual development of a child, the slow growth of trees, the fine structure of a seashell, or the opening of a flower. Throughout human cultures and civilizations, philosophers, artists, and scientists have marveled and pondered at the cycle of life, the changes from an embryonic form to a newborn, the maturation of the newborn, and the constant physiological renewal of the adult. All these processes can be summarized by a single concept: growth. Growth provides an organism with the ability to adapt and control its environment through its life and through time. Growth is at the very core definition of life itself.

The problem of growth has been traditionally central to all aspects of biological research but of marginal interest to physicists, engineers, and mathematicians. However, in the last thirty years with the rise of medical bioengineering, biophysics, and mathematical biology, the problematic of describing and understanding growth quantitatively has become a main topic of multidisciplinary research.

Writing a book in an active field, spanning centuries of knowledge and covering multiple disciplines, is a risky proposition. The idea for this monograph came to me more than ten years ago when I realized that the general topics of mathematics of growth was becoming a central theme of research for many scientists in different communities. There was a clear need to bridge different concepts and ideas originating from multiple communities and, in particular, create a common language to

describe phenomena appearing in different scientific disciplines. This monograph is an attempt in this direction.

Following my own interests and limited abilities, there is a strong bias in the choice of topics presented in this monograph.

First, most of the descriptions are at the continuum level, essentially from tissues to organs with very little discussion on cellular processes responsible for growth. Whereas much is known at the cellular level, our understanding of transduction mechanisms, linking cellular processes to tissue and organ growth, is still in infancy.

Second, the emphasis is on physical and mechanical aspects of growth at the level of organs and organisms but not at the population level. The mathematics of evolving populations of cells or individuals, and their coupling with chemical fields is well developed. It can be found in classic textbooks of mathematical biology and will not be repeated here.

Third, the theory is developed around modern concepts of solid mechanics and illustrated through the use of reduced simplified models that can be analyzed by the methods of applied mathematics. Unavoidably, the concepts may be advanced but the models are often simple. The hope is that these models provide some insight into the mechanisms governing growth and the interplay between growth, mechanics, and geometry. More realistic models would typically require both an extensive discussion of the underlying biological system and extensive computational analyses. I leave these tasks to the experts in these different fields.

Fourth, the emphasis is on the consequences of growth rather than on its origin. The discussion is mostly restricted to the analysis of tissue and organs made out of a single elastic component rather than the more general theory of mixtures that takes into account the coupling between fluids and various tissue components. These advanced theories for growth and remodeling have been used to develop realistic models but cannot be easily analyzed mathematically. They also require a more general computational framework that is still in development. My general philosophy is that little progress can be made for models with multiple components unless we have a thorough understanding of the simpler problems studied here.

Fifth, whereas I try to provide general introductions to different topics and key references to many authors, most of the topics presented here have come about through my own research projects. I have worked on these with various collaborators over the last twenty years. Therefore, this monograph is not an exhaustive review of the field as much as my personal views on the subject. I do not believe that it is the only approach or even that it is superior to other points of view. I would like to encourage other researchers to provide alternative, complementary, or contradictory approaches as it will only enrich the debate and help develop a general theory of growth. While I have tried to be thorough in citing relevant works in the literature, I have undoubtedly missed important references and, I can only apologize to the colleagues that I have offended in the process.

This book is designed to be at the quadruple interface of mathematics, biology, physics, and mechanics. Life at the interface is particularly rich and exciting as it takes advantage of ideas, concepts, and methods from different fields. It is also

particularly dangerous as it is the ideal ecological zone for highly specialized predators. I expect that biologists will find the biological modeling over-simplistic and focussing on questions of little interest to them. I believe that many mathematicians will find the mathematical description too informal and lacking the rigor expected in various well-established disciplines ranging from partial differential equations to differential geometry. Some engineers may lament at the lack of finite-element simulations and detailed mechanical measurements. And, I fully expect that many physicists will view the treatment of mechanics as being too technical and unnecessarily complicated. These criticisms are all valid. It is the curse of interdisciplinarity to always fall short of the expectations required by disciplinary purity. But, it is only when these opprobriums will be bestowed on me that I will know that I have managed to reach different communities and that I may have attained some measure of success.

A Reader's Map

This book was conceived to be read at different levels, depending on the reader's interests and background. The difficulty is that a mathematical and mechanical theory of growth naturally combines aspects of biology, mathematics, and mechanics. The bio-mechanician with a good grip of solid mechanics may not always be familiar with some methods of applied mathematics. Similarly, many applied mathematicians and physicists, while often well trained in fluid mechanics, are not typically exposed to advanced concepts of solid mechanics. For the biologically trained but mathematically inclined readers, mathematics and mechanics may be appealing but may present technical difficulties. Accordingly, topics are presented in order of conceptual and mathematical difficulties.

Inspired by the structure of the excellent textbook "Nonlinear Dynamics and Chaos" by Steven Strogatz, I organized this monograph according to the dimensionality of the problem, starting in dimension one before considering problems in dimension two and only then presenting the general theory in three dimensions. Indeed, the coupling of growth and mechanics can be illustrated in simplified geometries where the fundamental concepts can be easily understood. Once these concepts are understood, they are progressively generalized.

Part I presents a general introduction to growth, hopefully accessible to all readers. It presents basic aspects and classification of growth processes and, more or less, use historical developments and abundant examples from biology and physiology to introduce key concepts relating biological growth to physical cues.

Part II was specifically developed for this monograph, both to introduce basic mechanical ideas such as elasticity, viscoelasticity, and plasticity; but also to illustrate the interplay between growth processes and mechanics. In the first chapter, I discuss the simplest instances of growth by restricting deformations along a line. In the process of writing this book, I realized that there was no general theory of growth for filamentary structures. With Derek Moulton and Thomas Lessinnes,

we filled this gap and showed how to generalize the theory of elastic rods to include the effects of growth and remodeling. These ideas are used to model many interesting systems, mostly taken from the world of plants.

Part III further generalizes these concepts in simple two-dimensional geometries with applications to accretive growth problems such as seashells and microbial systems exhibiting tip growth. Most of the discussion of two-dimensional elastic surfaces is restricted to axisymmetric membranes and shells. The general problem of deriving a general theory of morphoelastic shells would require a few more chapters and only a short introduction to the general problem is given.

Part IV presents a general theory of growth for three-dimensional bodies based on the twin concept of evolving reference configuration and the multiplicative decomposition of the deformation gradient. This part starts with a brief description of the classic theory of nonlinear elasticity so that readers not versed in the language of large deformations mechanics can learn the basic tools. An extensive discussion on the kinematics of growth viewed as evolving configurations is presented. It is followed by a general discussion on growth laws, dynamics, and stability. The two last chapters are devoted to detailed examples and applications in spherical and cylindrical geometries.

Rather than providing a final conclusion to a field that is still blooming, I conclude, in Part V, with a list of ten challenges. It is my hope that these challenges will motivate other researchers and help move the field forward.

Oxford, UK
2016

Alain Goriely

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I am deeply indebted to a number of friends and collaborators. First, it is with great pleasure that I acknowledge the influence of Michael Tabor on both my professional and intellectual life. Twenty years ago, tired of playing with problems in the theory of integrability, Michael and I decided to look at problems related to growth and mechanics. At that time, we knew next to nothing about rods, membranes, nonlinear elasticity or growth. All we had were a few questions that we thought deserved to be investigated and a few methods from applied mathematics that people did not seem to be using in mechanics. We taught each other the basics and tried to model simple systems, inching our way to a better understanding. Many of the basic ideas and applications presented in this book were born out of these discussions.

Another major influence on this work was my collaboration with Martine Ben Amar. During a sabbatical in Paris, we learned the foundations of rational mechanics and developed together the theory of growth-induced instabilities for nonlinear elastic systems. It was an exciting time of scientific discovery and it remains one of the best academic years of my life.

I would also like to acknowledge the many striking contributions of Derek Moulton through our years of collaboration. In his own work, Derek has been exploring the consequences of growth in many different settings and, doing so, has systematically propelled the field forward. We have been partners in crime for many years, shared the meager rewards of our malfeasance, and paid the price for our idiosyncratic interests. I hope that his punishment will be lighter than mine.

Many of the ideas discussed in this monograph are also the product of many years of work, discussions, reflection, and meetings with my collaborators. In particular, I have tremendously benefited from my interactions with Jon Chapman, Régis Chirat, Michel Destrade, Marcelo Epstein, Krishna Garikipati, Ray Goldstein, Andrew Hausrath, Ellen Kuhl, Thomas Lessinnes, John Maddocks, Angela Mihai, Sébastien Neukirch, Giuseppe Saccomandi, Dominic Vella, Sarah Waters, John Wettlaufer, and Arash Yavari. I take this opportunity to let them know that their intellect and friendship are precious to me.

Central to all academic endeavors is the training and interactions with students. I have been very lucky to be able to supervise several bright students whose hard work features prominently here: Alexandre Erlich, Georgina Lang, Tyler McMillen, Andrey Melnik, Joe McMahon, and Rebecca Vandiver.

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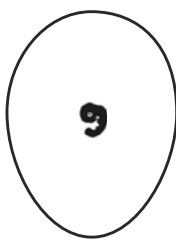
Part I

Introduction: Where It All Starts

*At first the infant,
Mewling and puking in the nurse's arms.
Then, the whining school-boy with his satchel
And shining morning face, creeping like snail
Unwillingly to school...*

Chapter 1

Basic Aspects of Growth



Growth is a generic term that describes processes in which the mass of a body changes over time. In biology, the problem of growth is fundamental to all aspects of life, with realizations as diverse as cell division, morphogenesis, development, maintenance, cancer, and aging. All life forms experience growth to some appreciable degree and one of the ultimate challenges of modern biology is to understand the role of the genetic code in transforming cells into fully mature organisms and explaining how these organisms manage to regulate shape and function through growth and remodeling.

Growth processes also appear in some physical processes where new material is added to an evolving system. For instance, in epitaxial growth, a thin layer of crystal is produced by depositing raw material on an existing crystalline substrate. Growth is also associated with phase transition phenomena, where an interface evolves in time to produce new structures such as crystals [81, 687, 765]. These free boundary problems are controlled by diffusion and, unlike biological systems, the interface is a line of discontinuity with no particular material property. The swelling of gels is arguably the closest nonbiological process that mimics growth as it is non-diffusive and occurs in the bulk of the material. It can be used as a physical analog to gain insight into the role of mechanics in biological pattern formation [116, 663, 904].

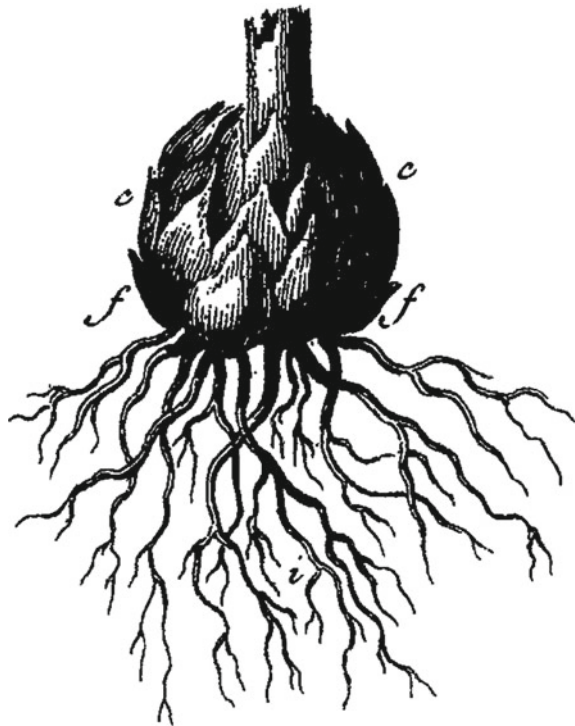
Our study of growth will mostly be limited to non-diffusive processes relevant to biological systems.

1.1 Classification

Aspects of growth and remodeling occur during the entire life of an organism. Therefore, growth fulfills many purposes and, accordingly, is associated with qualitatively different processes. Traditionally, a first classification is obtained by considering the way growth alters a body, either by changing its volume, its material properties, or by rearranging the relative position of material points. The three main growth processes are:

- **Growth.** The term *growth* by itself refers to a change in mass. It is colloquially understood as an increase in mass, but the concept extends naturally to describe mass reduction or shrinking. Change in mass can be created either by addition of mass at constant density, as found in the development of soft tissues, a change in density at constant volume, as in the case of bone densification, or both as found in a developing bone. Mathematically, a theory of growth must allow for changes in mass, volume, and density and must be flexible to account for mass permeating through the boundary of the body, accumulating at the boundary, or occurring within the body itself.
- **Remodeling.** It is well known that in the process of aging, tissues may become stiffer or softer. The term *remodeling* refers to an evolution of material properties in a system without change of mass such as stiffness, fiber orientation, fiber strength, and so forth. These remodeling processes are due to a change in the microstructure that determines the overall behavior of the tissue. For instance, the typical composition of soft tissues in many animals is a mixture of collagen fibers within an elastin matrix. Whereas elastin content remains mostly unchanged over many years, there is a continuous turnover of collagen that depends on the local biochemical and mechanical stimuli acting on the cells. The relative content of different types of collagen fibers and elastin determines the overall response of the tissue [635]. This process can occur without a change of mass, but it is crucial to understand the response of a tissue under mechanical loads. From a mathematical perspective, the variation of material properties can either be modeled by considering a separate evolution of the material parameters of a system or, at a lower scale, by taking into account the evolution of separate tissue components.
- **Morphogenesis.** Early in embryonic life, new tissues and organs are formed. In this process, major reorganization and differentiation of cells take place after cell division, and, importantly, there is a restructuring of material elements. This reorganization process can only happen if the adhesion between different components is weak enough so that they can separate and reattach. This simple observation has important consequences for modeling as tissues undergoing morphogenesis exhibit rapid elastic stress relaxation and plastic-like flow. Mathematically, this

Figure 1.1 Growing root as depicted by Duhamel in 1758 [898].



evolution is often described by modeling tissues as fluid or viscoelastic rather than elastic, even though these two points of views are equivalent, as we will show.

Growth can be further classified by the location of material addition. It can occur at the tip, on the surface, or in the bulk. We consider these processes in more detail next.

1.1.1 Tip Growth

In his book, “The Physics of Trees” published in 1758, Duhamel du Monceau describes the following discovery: “*The observations that I made in plants that grow in water helped me discover another peculiar phenomenon; that is, roots only grow at the tip.*” [898, p. 83] (see Figure 1.1). *Tip* or *apical growth* describes growth processes that take place in a small region at the tip of a filamentary structure. As shown in Figure 1.2, it is the main growth mechanism used by many microbial organisms and plant systems such as fungi, filamentary bacteria, pollen tubes, and root hair [431, 457, 479, 480, 482, 541, 625, 714, 715, 899, 1073]. In these organisms, there is a small active growing zone located near the tip where the outer shell is constantly remodeled and new material is consistently added.

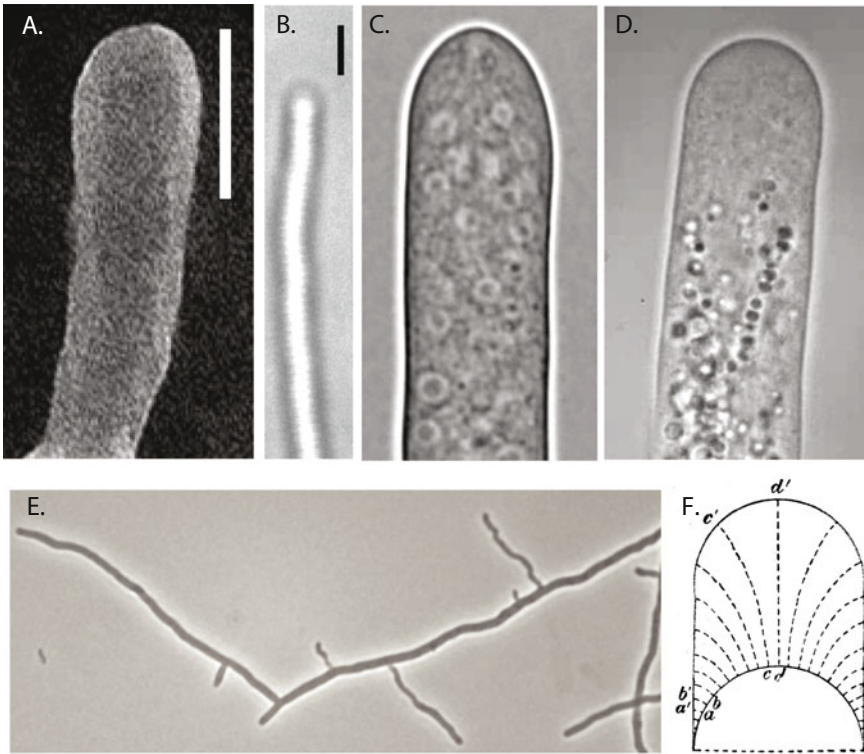


Figure 1.2 Tip growth. A. microbacterial filament, (bar is $1\ \mu\text{m}$) (*Kitasatospora setae* source: Society for Actinomycetes Japan, photograph by Y. Takahashi and Y. Iwai); B. microbacterial filament (*Streptomyces coelicolor* A3(2)), (bar is $1\ \mu\text{m}$); C. *Allomyces*; D. lily root hair (typical diameter $15\text{--}20\ \mu\text{m}$) (images courtesy of Jacques Dumais). E. Branching in *streptomyces* A3(2). F. First theoretical description of tip growth by Reinhardt in 1892 for the growth of fungus [1073].

For sufficiently small organisms, such as filamentary bacteria, the newly added material is transported to the tip by diffusion processes whereas for larger organisms, such as fungi and pollen tubes, active transport processes which require a complex internal structure are required for propagation.

Typically growth occurs in a region that maintains a constant size. Therefore, the typical scaling of mass with time is linear, as shown in Section 4.3. However, many filamentary structures also undergo repeated branching as shown in Figure 1.2E. These branches allow for one-dimensional structures to explore three-dimensional volume for nutrients. This branching process transforms the scaling of mass from being linear to exponential with respect to time since each new branch adds mass linearly and can branch again, leading to an intricate, fractal-like, geometry.

Tip growth is sometimes referred to as *primary growth* in plants. Once a stem or root is large enough, it may also undergo *secondary growth*, sometimes referred to as *growth in the cambium*, by the addition of external layers to thicken itself.

Cambial growth in trees takes place between the old wood and the bark of the tree, and seasonal variations lead to the formation of tree rings.

Mechanically, the main issue is to understand the interaction of the tip with its environment and to determine its shape, internal stresses, and how a filamentary structure evolves based on different laws for material addition.

1.1.2 Accretive Growth

Accretive, *surface*, or *appositional growth* describe mechanisms, such as deposition in hard tissues, where new material is added to the boundary of an existing body. It is the typical mechanism responsible for the formation of teeth, seashells, horns, and corals [4, 914, 915, 1173]. At the microscopic level, surface growth is also found in bones where changes in bone density occur by deposition or resorption of new material on the surface of trabeculae, or the walls of canals excavated by osteoclasts [1230].

Mathematically, many problems in accretive growth can be modeled geometrically by studying the evolution of the boundary as a function of accreted mass. For instance, the shell of the ammonite in Figure 1.3 is the result of material being accreted with different velocities at different points of the opening. This velocity gradient is necessary for coiling since the outer ridge requires more material than the inner ridge. In general, if the boundary is known at time t , an accretion vector, giving the local velocity of material accretion, can be defined at each point on the boundary as shown in Figure 1.4D. The new boundary is then obtained after a small incremental time Δt .

Figure 1.3 The fossil shell of an ammonite of the genus *Promicroceras* [916]. Arrows denote the accretion vectors.



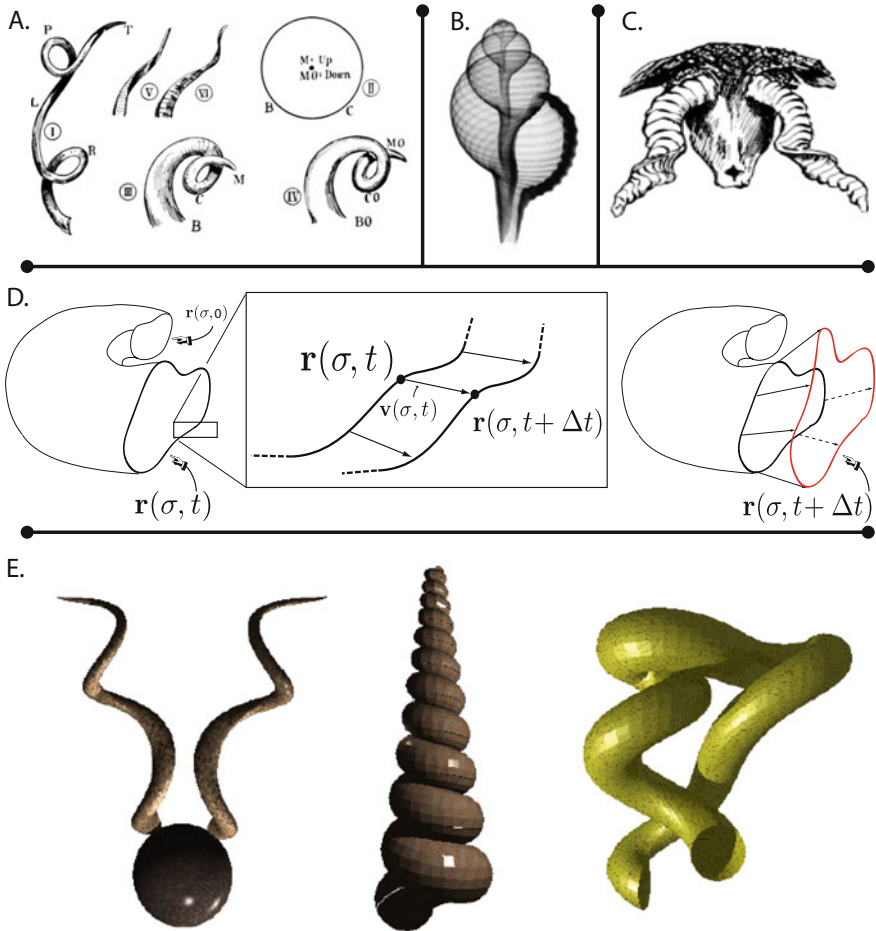


Figure 1.4 Accretive growth. ABC. Growth of horns and seashells as described by D'Arcy Thompson [1230]. D. The theoretical basis of accretive growth. For a given body at time t , a growth vector is defined at the active growth boundary. At time $t + \Delta t$ a new surface is created. E. Different body forms obtained by different choices for the growth vector (adapted from [914]).

The key question from a modeling point of view is to derive an accretion law based on the interaction between the soft part of the animal and the new hard accreted part. Mathematically, the main problem is to understand and classify the shapes and patterns that emerge through this process [202].

1.1.3 Volumetric Growth

Bulk, *volumetric* or *interstitial* growth all refer to processes in which local volume elements in the body change over time rather than on its boundary as in accretive or tip growth. Bulk growth is typical of many developmental, physiological, and pathological processes and has been particularly well documented in arteries, muscles, solid tumors, and the heart [242, 636, 1206].

Bulk growth encompasses *hyperplasia*, the increase of volume due to cell proliferation which is typical of many developmental systems; *hypertrophy*, the change of volume due to enlargement of its constituents, typical of many physiological processes; and *neoplasia*, the abnormal and often unregulated growth or division of cells found in cancer.

Mathematically, bulk growth offers many outstanding challenges. First, a local volume element may not remain isotropic during growth which implies that a tensorial description of the deformation is needed. Consider an infinitesimal spherical volume element extracted from a tissue, as shown in Figure 1.5. In volumetric growth, this sphere is transformed into an ellipsoid. This deformation is fully captured by the transformation of three orthogonal vectors into three new vectors along the principal directions of the ellipsoid. Mathematically, this local mapping is described by a tensor. Accordingly, the process of volumetric growth assigns a tensor, the *growth tensor* $\mathbf{G}$, at each point of the body, describing the change of a local volume element. A theory of growth is therefore intrinsically rooted in the theory of tensors.

A second challenge in bulk growth is that it is relevant for soft tissues that are elastic and can also be deformed by the application of loads. When observing the deformation of a body from an initial state, we must determine whether it is due to the growth or elastic response of the material, or even a combination of the two processes. This problem, which will be discussed at length in further chapters, was

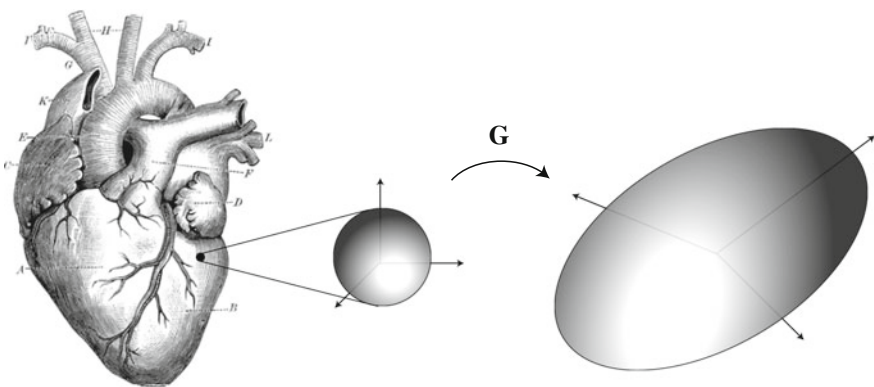


Figure 1.5 Volumetric growth. During growth, a local element inside the tissue can expand or shrink anisotropically. The description of such a process requires the definition of a growth tensor $\mathbf{G}$, locally transforming an infinitesimal sphere to an infinitesimal ellipsoid.

first formulated by Hsu in 1968, arguably the first work to address the fundamental problem of mechanical growth modeling: “*If the form to which a body grows under no applied loads is known, what will be the form of the body if some mechanical loads are applied during its growth?*” [627].

From a modeling perspective, bulk growth can also be used to describe the growth of filamentary objects, such as neurons or plant stems that have distributed growth, or surfaces, such as epidermal layers of cells that do not change their thickness.

The classification of growth as tip, accretive, or bulk is descriptive but not formal. It depends on the scale at which the problem is being studied. Indeed, both tip and accretive growth can be modeled as bulk growth processes where a thin soft layer, close to the boundary, expands and stiffens in time. Essentially, tip growth is a bulk process that is localized at the apical part of the filament. A detailed analysis of this process requires an understanding of areal growth due to the insertion of new material. Similarly, bone growth and wound healing can be modeled either as an accretive process or a localized bulk process where density evolves.

1.2 The Scaling of Growth

The first question about growth is one that is shared by most parents: How does the size of an organism change in time? The first historical records of growth were on the height of human beings. In 1759, Count Philibert Gueneau de Montbeillard started to record the height of his first son on his birth and he continued to do so every six months until his son reached the age of 18. This record, shown in Figure 1.6, was published in the fourth volume of the supplement to Buffon’s “Histoire

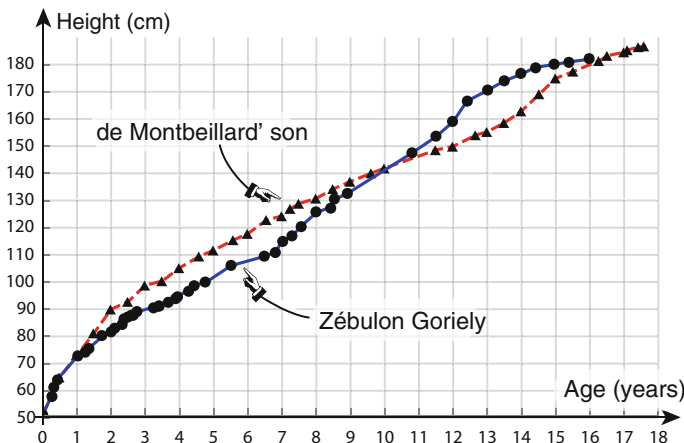


Figure 1.6 Record of longitudinal growth done by Count Montbeillard from 1759 (data from [1123]), compared to the height of Zébulon, the author’s first son.

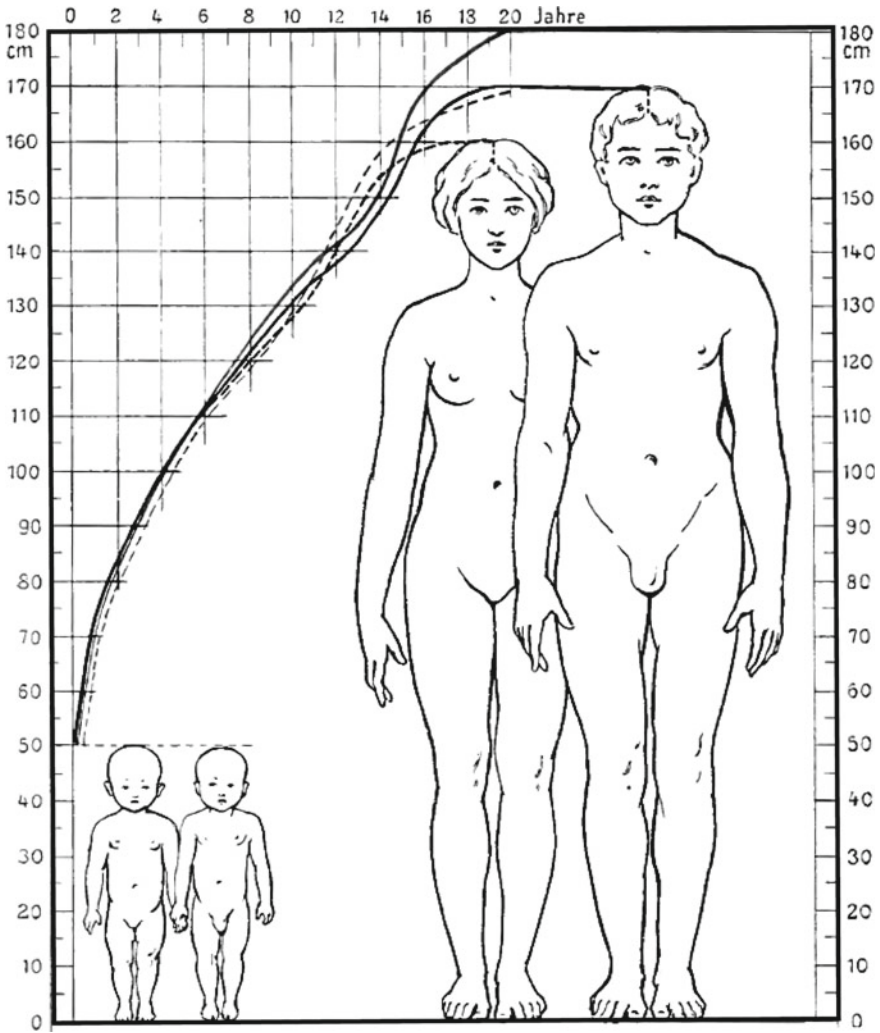


Figure 1.7 Growth curves obtained from statistical averages (from Stratz’s book published in 1904 [1200]).

Naturelle” [1123]. A quarter of a millennium later, it still captures the essence of human development from birth to adulthood. Its gross features are similar to the growth curve of the author’s first son as well as the curves found in modern medical growth charts, shown in Figure 1.7. These curves are the result of statistical averages over large populations and show variations over different geographic regions.

The first complete statistical study of the evolution of weight and height in human beings was conducted by the Belgian polymath, Adolphe Quetelet, and published in his “Treatise on Man” in 1835 [1053]. In this remarkable book, Quetelet pooled

and analyzed data from the Belgian population. He considered both general trends and deviations around the average using the Gaussian distribution. This work is considered to be the first application of the Gaussian distribution in a statistical study. Quetelet also suggested a law of growth by fitting the data of height $H(t)$ against time t

$$H(t) = at + \frac{b+t}{1 + \frac{4}{3}t}. \quad (1.1)$$

If both mass $M(t)$ and height $H(t)$ are known, one can speculate on how these two quantities might be related to each other. It was again Quetelet who proposed that, independent of time, weight is related to height by a scaling law of the form $M = cH^\alpha$, where $\alpha = 5/2$ during childhood and $\alpha = 2$ for adults. For $\alpha = 2$, the *Quetelet coefficient* c becomes the infamous *Body Mass Index* (BMI), which remains a critical estimate of fitness and obesity despite its obvious shortcomings and many criticisms [283]. Historically, Quetelet's proposal that height scales with respect to weight is the first case of an *allometric law*, that is, a power law between a given physical quantity and the total mass of the organism [649, 816, 1126, 1147] (see Section 1.3).

Quetelet's book prompted similar studies and, by the end of the nineteenth century, there was a flurry of activity dedicated to understanding growth in humans, animals, and plants [292]. The idea emerged that growth in different biological organisms could follow some universal laws that would determine sizes and forms. This research program was presented in the seminal book "On Growth and Form" by D'Arcy Thompson, first published in 1917 [1230]. This monumental book remains a reference and a source of inspiration for many researchers to this day.

Bogin reports that, by 1972, no less than 200 different models or fitting functions had been proposed to describe the evolution of human growth [110]. The modeling of growth as a slow continuous process is only valid on the long-time scale of months or years. A detailed daily recording and analysis of height in infants between the age of one and two shows that growth mostly occurs through discontinuous aperiodic *saltatory spurts* [759, 760] of about 0.5 to 2.5 centimeters separated by long intervals typically lasting between 2 to 63 days, where no growth takes place as shown in Figure 1.8. Jumps and oscillations during growth are also encountered in other biological systems including fungi [799], pollen tubes [188, 360, 590], plants [354, 728], and invertebrates [78].

The first attempt to model the evolution of the total mass from physical principles was based on an idea by Pütter, first published in 1920 [1048]. Pütter proposed that animal growth can be seen as a balance between addition and removal of building materials in the body. Growth proceeds as long as new material is added faster than it is removed, and stops when both processes are balanced.

Typically, in such models, the rate of material removal is assumed to be proportional to the mass $M(t)$ itself, as in a standard exponential decay problem, whereas the rate of addition of new material is proportional to a power of the mass. Combining these two effects leads to [1285]

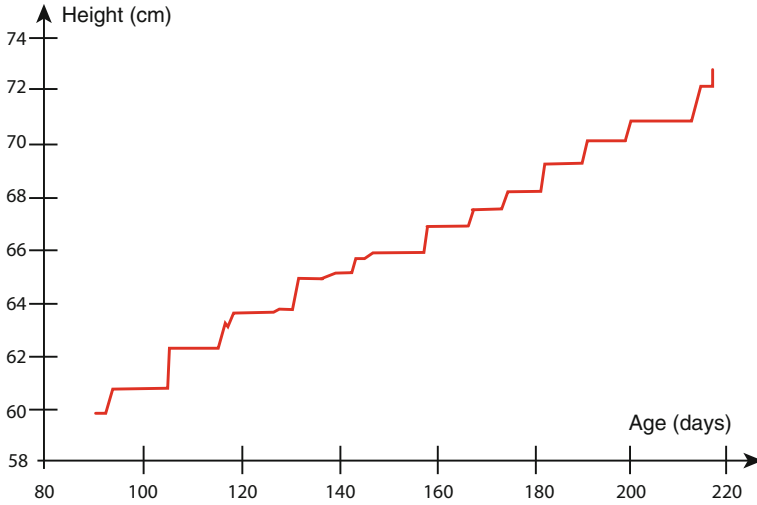


Figure 1.8 Daily measurements of the height in a boy between the age of 90 to 218 days show discontinuous growth spurts separated by periods of no growth (data from [760]).

$$\dot{M} = M(aM^{-p} - b), \quad (1.2)$$

where $\dot{M} \equiv dM/dt$ denotes the time derivative of $M(t)$ and $ab > 0$. The solution of this equation for $p = 0$ describes a simple exponential process

$$M(t) = M_0 e^{(a-b)t}, \quad (1.3)$$

where $M_0 = M(t = 0)$ is the mass at birth.

For $p \neq 0$, Equation (1.2) is a Bernoulli equation [460, p. 232] whose general solution is given by

$$\left(\frac{M(t)}{M_\infty}\right)^p = 1 - \left[1 - \left(\frac{M_0}{M_\infty}\right)^p\right] e^{-bpt}, \quad (1.4)$$

where $M_\infty = (a/b)^{1/p}$ is the asymptotic mass. Figure 1.9 shows examples of mass evolution as a function of time for various values of the parameters.

Equation (1.2) also contains the classic *logistic model* [1255] obtained for $p = -1$ with a and b negative, and the *Richards model* [1078], defined by $p < -1$, used to model the growth of plants.

While this general approach is appealing, the choice for the exponent p is problematic. A typical argument is to assume that the addition of new material is limited by energy input and metabolic rates. If the energy intake and growth rate are directly proportional to the weight itself, we have $\dot{M} = \alpha M$ for a certain $\alpha \neq 0$. This behavior is recovered with $a > b > 0$, $p = 0$, and exponential unlimited growth is observed.

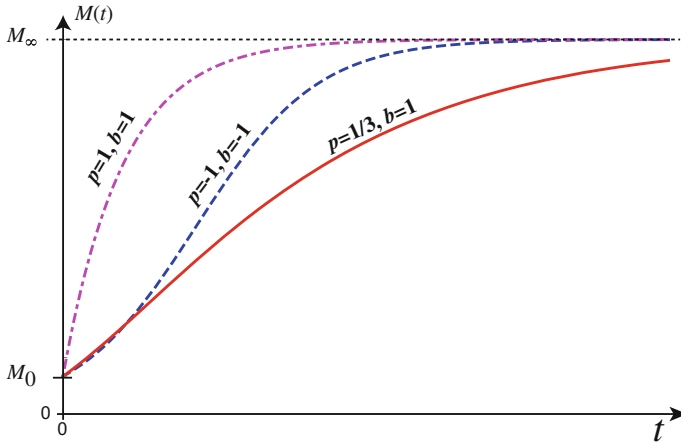
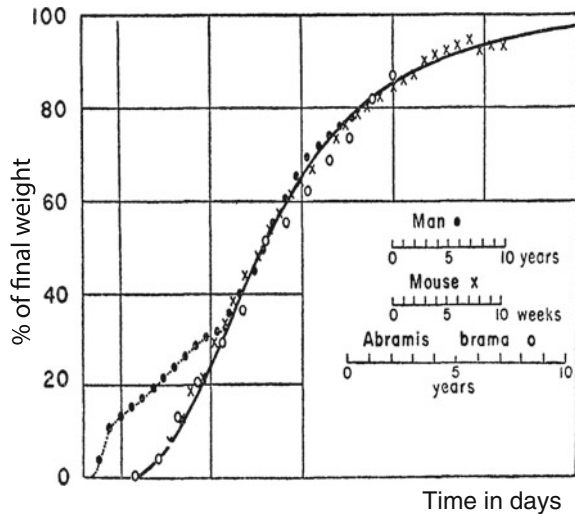


Figure 1.9 Examples of growth curves given by Equation (1.4) for various values of the exponent p .

Figure 1.10 Example of data fitting with $p = 1/4$ by von Bertalanffy [1285] (*Abramis brama* is the common bream).



This behavior, observed in the early developmental stages of insects, is only valid until a new phase of growth takes place.

If we assume that the metabolic rate follows a scaling law based on geometry by postulating that energy intake is proportional to surface area, we have $\dot{M} = \alpha M^{2/3}$, which corresponds to the choice $p = 1/3$. This power law was originally proposed in 1839 by Sarrus and Rameaux [1118]. Based on the same general ideas, Ludwig von Bertalanffy [1285] suggested that most biological systems grow in an intermediate regime with exponent $0 < p < 1/3$ and suggested $p = 1/4$ as suitable to fit different data sets, as shown in Figure 1.10.

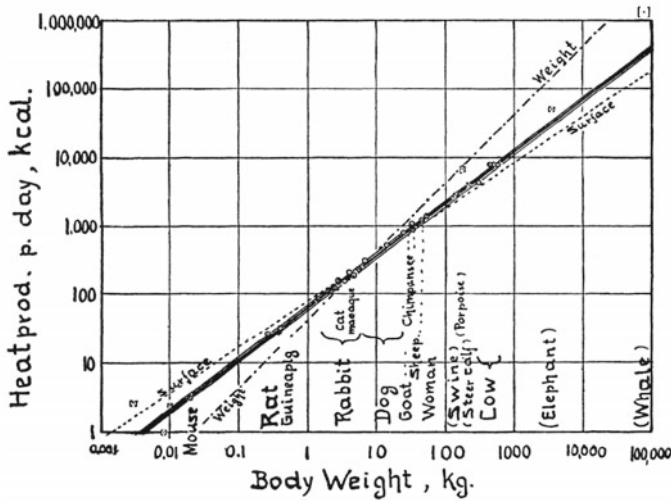


Figure 1.11 Kleiber's law: metabolic rate as a function of mass [704]. The experimental data for the variation shows a $3/4$ power law. It is compared with a scaling with respect to surface area ($2/3$) and weight (1).

More recently, it was proposed [1316] that the production of new material should be related to *Kleiber's law* [704], which states that the metabolic rate of an organism, defined as the energy expended by an organism per unit time, scales as the three-fourth power of the total mass as shown in Figures 1.11 and 1.12. This assumption also leads to von Bertalanffy's choice of $p = 1/4$.

It has been argued that this power law for the metabolic rate is widely applicable to biological systems from bacteria to whales and even plants and forests [957], spanning 27 orders of magnitude in mass. However, some authors have criticized the validity of this statistical analysis and have argued for exponents closer to two-third [572, 1126]. The problem is that the arguments used to derive such laws are inevitably vague and based on a number of simplifying assumptions that neglect many well-established physiological processes. Unfortunately, the absence of a theory for growth linking mass to size leaves room for endless discussions, controversies, and grandiose teleological theories with very little scientific content and no mathematical foundation. As a result, the general field of scaling laws for growth remains in its infancy [287, 1315].

For any choice of exponent $p \in (0, 1]$, the growth curves show a sigmoidal behavior observed in many organisms as shown in Figure 1.9. A slow initial phase is followed by quick maturation, that slows down after the reproductive age, eventually reaching an asymptotic limit.

Humans have evolved and adapted in such a way that they cannot be simply described by many of the power laws applicable to other species. However, these animal models can still be used to describe human growth if pre- and post-pubertal periods are considered independently [106].

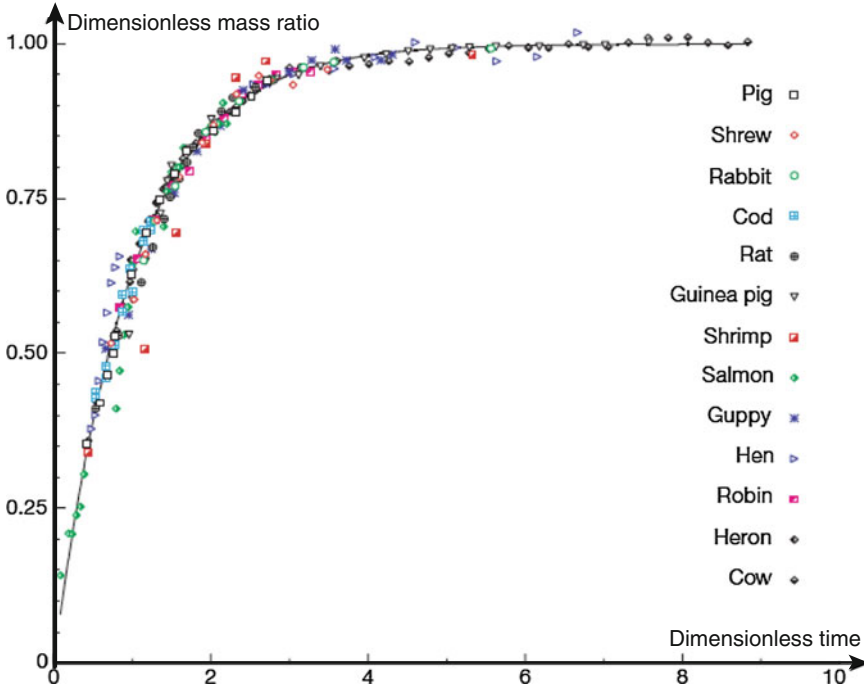


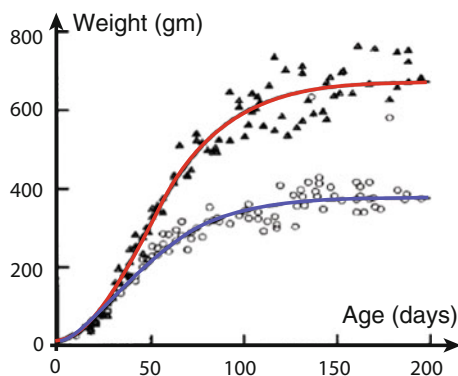
Figure 1.12 Scaling and data analysis based on Kleiber’s law [1316]. Here M/M_∞ is plotted against the dimensionless time $\tau = bpt - \ln(1 - (M_0/M_\infty)^p)$ as described by Equation (1.4) with $p = 1/4$.

The key feature of this simple power-law model is that it identifies the *specific growth rate*, defined as the growth rate per unit mass, $\dot{M}/M$, as a central quantity. The basic idea in all models showing a sigmoidal behavior is that a proportion of new tissue generated by growth is capable of growing itself, but as time goes by, this ability is reduced. These two typical trends were first presented as fundamental principles for growth by Peter Medawar in 1941 [856] when he wrote: “*What results from biological growth is itself, capable, of growing*” and “*Under the actual conditions of development, the specific acceleration of growth is always negative.*”

Another model that has been used in the context of growth is the so-called *Gompertz’ law*, first introduced in 1825 [455] for the evolution of human populations. It was subsequently used in actuarial sciences as a modified compound law, then rediscovered as a suitable growth law for organisms [244, 1329]. The Gompertz law is obtained as the solution of a Malthusian equation of growth, $\dot{M} = KM$, with a growth rate K decaying exponentially in time, following Medawar’s principles. Choosing $K = a \exp(-kt)$ with $a, k > 0$, we have

$$\dot{M} = ae^{-kt} M, \quad a = k \ln \left(\frac{M_\infty}{M_0} \right), \quad (1.5)$$

Figure 1.13 Gompertz' law. Growth curves for male (triangles) and female (circles) rats (*Rattus norvegicus*) fitted by a Gompertz law (adapted from [1195]).



which leads to

$$M(t) = M_{\infty} \left(\frac{M_{\infty}}{M_0} \right)^{-e^{-kt}}. \quad (1.6)$$

This equation, whose solution contains the exponential of an exponential and two characteristic time scales ($1/a$ and $1/k$), has been shown to be a particularly good fit for bacterial and tumor growth, among others [37, 965, 1090, 1341, 1369], and remains widely used for the purpose of fitting experimental growth data as illustrated in Figure 1.13.

1.3 Relative Growth

Extensive psychological studies have demonstrated that children and puppies are cute and lovable [20, 727]. It has been argued that this *cuteness factor*, a propensity or desire to cuddle or defend a person, is due in part to our perception of the relative size of body and facial features in children versus adults [110, 803]. As shown in Figure 1.14, the skull of babies is proportionally larger than those of adults [159]. Further, the relative dimensions of the skull, such as height versus diameter or roundness, are also different. Our ability to distinguish almost instantaneously children from adults independently of their size implies that no adult organism is simply a pure dilation of itself at birth.

The pure dilation of an organ or organism from birth to adult life, is referred to as *isometric growth*, as shown in Figure 1.15, whereas the relative growth of an organ with respect to the total weight of the organism is known as *allometric growth*. Therefore, the second fundamental problem of growth is to understand how organs, limbs, or tissues grow with respect to the total body mass. This is the general topic of the theory of *relative growth* [648, 649, 857].

The subject of relative growth was first discussed by Galileo in 1638 when he considered the relative size of bones in animals [414]. He writes: “*Nature cannot*

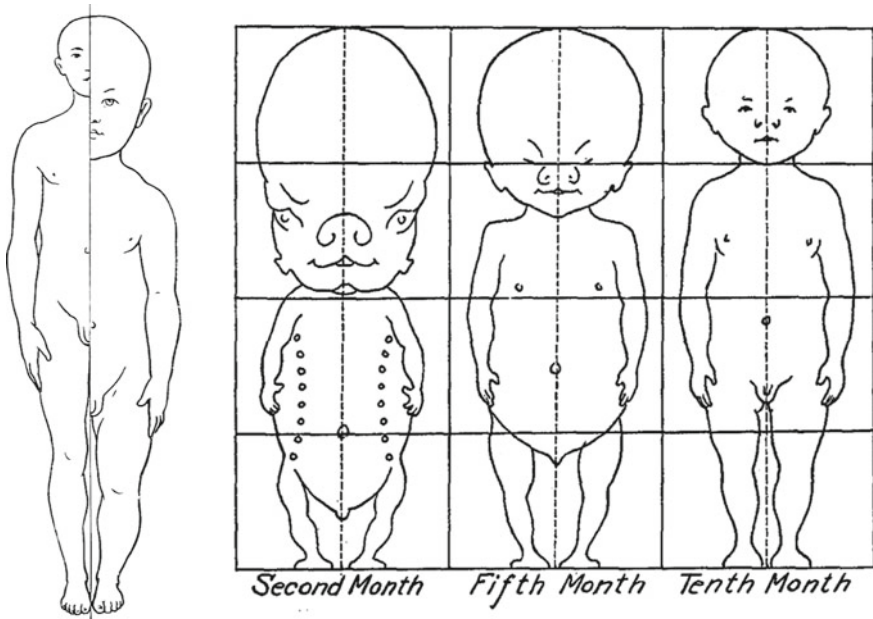
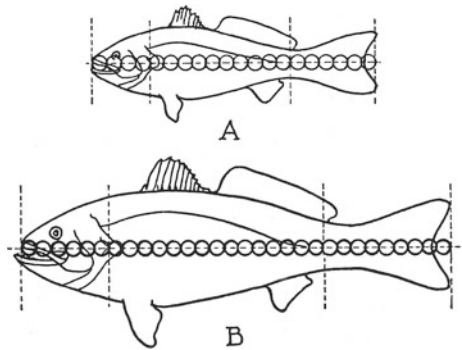


Figure 1.14 Relative proportion in the growth of man (adapted from Stratz [1200]).

Figure 1.15 Isometric growth. Hecht found in 1916 that the dogfish *Anchovia brownii* grows isometrically. Its adult form (B) is a uniform dilation of its infant form (A) [557].



produce a horse as large as twenty ordinary horses or a giant ten times taller than an ordinary man unless by miracle or by greatly altering the proportions of his limbs and especially of his bones.” That is, the same bones in larger animals are comparatively thicker than those in smaller animals, as illustrated in Figure 1.16B. The discussion on giants by Galileo is based on the common belief at the time that large fossil bones of dinosaurs or large mammals belonged to giants of the past. The biggest giant in Figure 1.16A, next to an “ordinary man”, is based on bones discovered in Sicily. Through simple scaling arguments, Galileo correctly concluded that if giants did exist they would not be a simple dilation of an ordinary man.

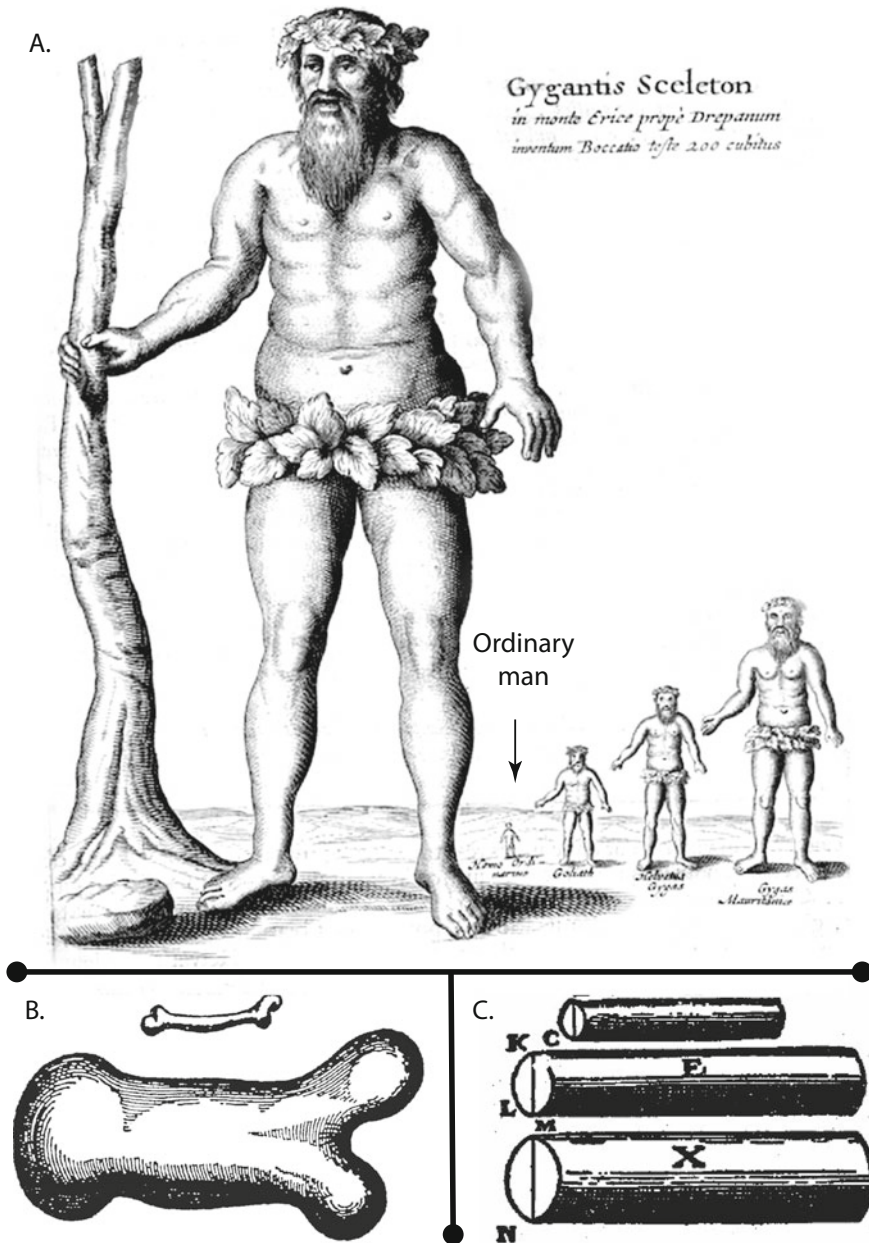


Figure 1.16 A. Improbable giants from “Mundus subterraneus” by Athanasius Kircher (1678) [697]. BC. In his “Discorsi”, published in 1638, Galileo noted that bones are subject to allometric growth and, therefore, giants could not have the same bones or proportions as ordinary humans. Galileo used the physical analogy that to support increasing loads, a column must grow thicker [414].

A systematic study of relative growth began at the end of the nineteenth century with the work of Dubois and Lapique, who compared brain sizes within and between species [308, 309, 770]. Their work follows an early observation from Cuvier that bigger mammals have relatively smaller brains [127, 141, 489]. Based on extensive research, D’Arcy Thompson reflected on the inevitability of differential growth in this passage [1230, p. 205]: “*An organism is so complex a thing, and growth so complex a phenomenon, that for growth to be so uniform and constant in all the parts as to keep the whole shape unchanged would indeed be an unlikely and an unusual circumstance. Rates vary, proportions change, and the whole configuration alters accordingly.*” The theory was further expanded on and applied to many different biological systems by Julian Huxley. In his book, “Problem of Relative Growth”, he coined the word *allometry* to describe relative growth that follows a power law with respect to mass [647].

The central idea in Huxley’s work is that the mass m or length l of an organ scales as a power of the total mass M of the organism, that is

$$m = kM^\alpha. \quad (1.7)$$

By expressing m as a function of M , the explicit dependence on time is removed enabling the comparison of the relative sizes of m and M at given points in development for different animals. The case $\alpha = 1$ corresponds to isometric growth, and any other value of α characterizes relative or allometric growth. If a fixed exponent α holds during growth (that is, when k and α are time-independent), allometry is equivalent to the statement that the specific growth rates of an organ and an organism are proportional:

$$m = kM^\alpha \iff \frac{\dot{m}}{m} = \alpha \frac{\dot{M}}{M}. \quad (1.8)$$

Starting in the 1920s, this simple, but fundamental, power law has played the role of an ordering principle in comparative biology and evolution [488–490, 1321]. The possibility for applications appears endless, as the size of any organ in a given species can be compared to any other species at any point in its development as illustrated in Figure 1.17. Generations after generations, students and researchers, ecologists and biologists, have combed the beaches, swept the forests, and fished the seas to gather data on size and weight in the hope of recovering existing laws or uncovering new ones. Depending on the data and the scientific question, one compares either the relative size of different organs in one species (*intraspecific allometry*), the relative sizes of one organ within different species (*interspecific allometry*), or the relative size of one organ to different organs, at different points in development for a given species (*dynamic allometry*).

A typical allometric study proceeds with the following steps [849, 958, 1037]:

- Gather experimental or bibliographic data on a given physical quantity q and the corresponding weight M of the animal. For instance, q can be the size or weight

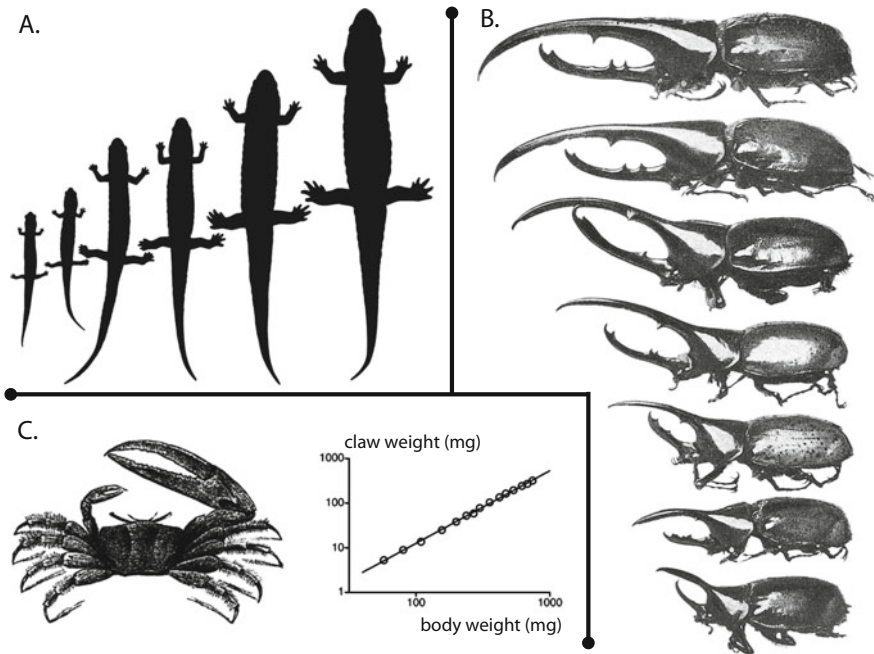


Figure 1.17 Isometric and allometric scaling. A. Six species of salamanders in the genus *Desmognathus* retain their proportions despite being of different sizes (reproduced from [681]). B. Different males in the beetles *Dynastes* showing the relative increase of horns as a function of size (1924 illustrations from Champy [182], reproduced from [427]). C. Allometric scaling for the claw of the fiddler crab in the genus *Uca* (adapted from [1192]).

of an organ, the metabolic rate of an organism, the growth rate, or the number of cells;

- Plot $\log(q)$ against $\log(M)$, so that a law of the form $q = kM^\beta$ would be represented as a line of slope β on this plot;
- From the plot, find the best linear fit and extract the slope β ;
- Find a rational number, α , preferably with a small denominator, close to β ;
- Justify, using arguments from geometry, physics, mechanics, or thermodynamics, that this exponent α can be obtained from first principles;
- Discuss the relevance of this law in the context of physiology, pathology, ecology, evolution, or optimal design;
- Discuss why some species or organs may not follow the expected law. This last step provides a falsidical justification of the law through its exceptions.

This approach is illustrated in Figure 1.18 which demonstrates allometric growth in plants. These studies, despite their obvious shortcomings from an epistemological point of view, have been extremely successful, as power laws have been shown to hold across diverse organisms [957, 1303]. As such, allometry remains a favorite tool and provides a methodological framework for comparative biology [136, 446,

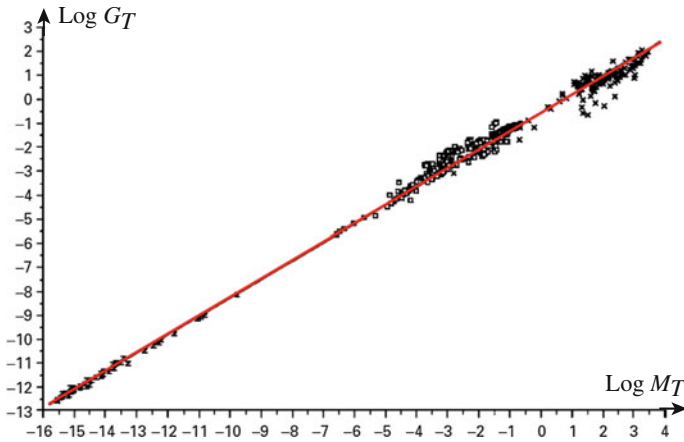


Figure 1.18 Allometry in plants. An interesting example of a possible allometric law for growth arises in plants when the growth rate G_T is plotted against the weight M_T in a log–log plot (adapted from [957]).

[956, 1320]. These studies clearly demonstrated that aspects of sizes, growth rates, or metabolic rates tend to cluster in a linear fashion against total weight when expressed in log–log coordinates. Therefore, the mere existence of observed scaling laws suggests that critical aspects of size and growth rate are governed or constrained by geometry, mechanics, and physics. This fundamental observation was already put forward by Medawar in 1941 [856]. However, Medawar believed that growth is dominated and limited by diffusion, which turns out to be relevant only at the microscopic scale.

At the organ or body level, relative growth can be tracked by simple external measurements. However, different regions of an organ may experience different growth rates. The skull of mammals elongates after birth, brains in humans fold onto themselves during development [466], and roots tend to lengthen by limiting their expansion in a small region at the tip. Typically, growth is neither isometric nor homogeneous. Therefore, different points on the growing body may expand at different rates creating, in the words of Huxley, *growth gradients* and *growth sources* [647], or in the terminology preferred by nineteenth century plant physiologists, *differential growth* [1107]. Differential growth is central to all aspects of growth mechanics; it is responsible not only for shaping an organism, but also for creating stresses through geometric incompatibility. However, to capture its key features, new experimental and mathematical methods are needed.

1.4 The Kinematics of Growth

The third fundamental problem in the modeling of growth is to track growth processes both spatially and temporally. It implies that the expansion and relative deformation of different points in an organ must be followed during growth.

This idea can be illustrated in one dimension. Initially at time $t = 0$, we paint a number of marker points, say A_0 and B_0 , on a filament as shown in Figure 1.19. During growth, we record the position of these marks as a and b , respectively. The problem is then to extract information from the dynamics of these material points, such as the growth rate or the region where expansion takes place. For instance, the stretch of the initial segment from A_0 and B_0 is the ratio of the lengths $\Delta x / \Delta X_0$. In general, we want to define the stretch at a single point by taking the limit $\Delta X_0 \rightarrow 0$. To do so, we denote by S_0 the initial position of a material point from one end, labeled $S_0 = 0$ at time $t = 0$. The position of this point at time t is denoted $s = s(S_0, t)$. Then, assuming that there is no other stretching process, the local stretch at the material point S_0 and time t due to growth is given by

$$\gamma(S_0, t) = \frac{\partial s}{\partial S_0}. \quad (1.9)$$

In particular, if growth is taking place independently of the position, we would have simply $\gamma = l/L_0$, the ratio of the two lengths.

Borrowing basic concepts from continuum mechanics, we define the *Lagrangian growth velocity* $V(S_0, t)$ as the velocity of a material point and the *Eulerian growth velocity*, $v(s, t)$ as the velocity at a spatial point s as

$$V(S_0, t) = \frac{\partial s}{\partial t}(S_0, t), \quad v(s, t) = V(S_0(s, t), t). \quad (1.10)$$

Then, the *Lagrangian growth rate* $\dot{\gamma}$ defines a local growth rate in terms of the initial material coordinate S_0 , which is given by

$$\dot{\gamma} \equiv \frac{\partial V}{\partial S_0}(S_0, t) = \frac{\partial^2 s}{\partial t \partial S_0}(S_0, t). \quad (1.11)$$

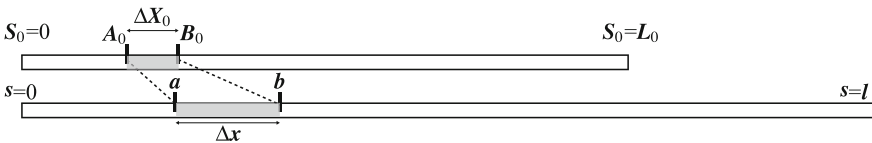


Figure 1.19 Kinematics of growth in one dimension. Two arbitrary points A_0 and B_0 are marked initially and tracked through growth. Of particular interest is the evolution of the relative distance between these points (the increments ΔX_0).

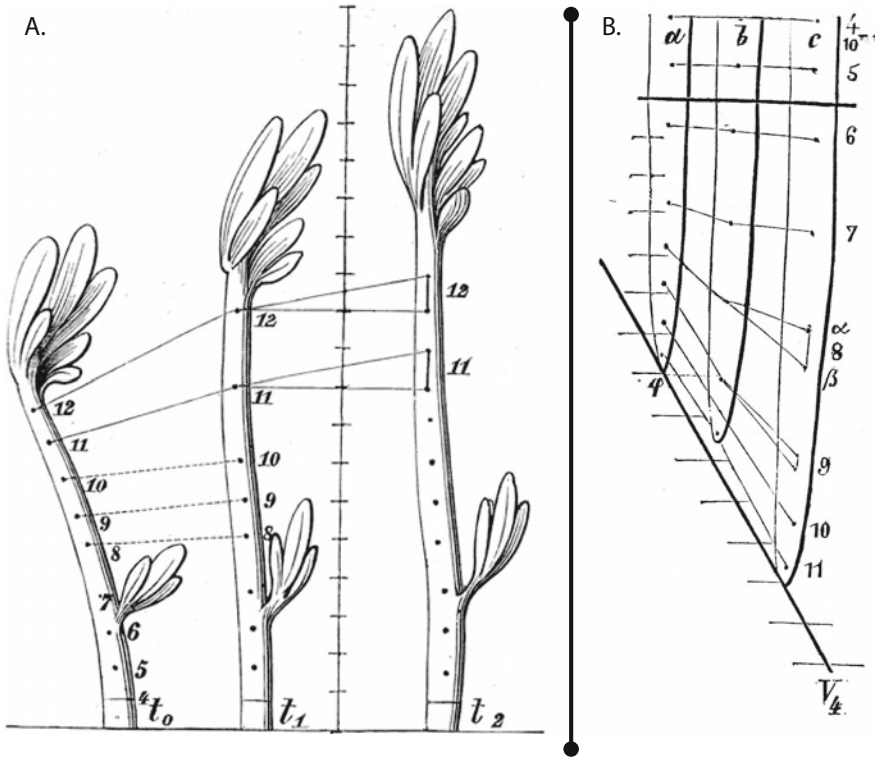


Figure 1.20 Tracking growth. Initial marker points are placed on the stem (A) and root (B) and are followed during growth (from Müller's textbook [924]).

In terms of Eulerian properties, one can define the *Eulerian growth rate* l_g as the spatial gradient of the Eulerian velocity, that is

$$l_g(s, t) = \frac{\partial}{\partial s} v(s, t). \quad (1.12)$$

This quantity expresses the rate of change of length of an infinitesimal element located at position s . By the chain rule, the Lagrangian and Eulerian growth rates are related by

$$\dot{\gamma} = l_g \gamma. \quad (1.13)$$

For problems where growth is localized in space, such as tip growth, an Eulerian description may be advantageous since the function $l_g(s, t)$ describes the growth experienced by a material point located in the growth region. If growth depends on the cells, and not on their spatial position, a Lagrangian description may be more appropriate. This description is particularly convenient in certain developmental stages when cell division dominates the growth process.

This approach was already used by plant physiologists of the nineteenth century to quantify the growth of stems [1159, 1182] and roots [187] and identify regions of active growth, as shown in Figure 1.20. The function γ is an important quantifier; it identifies spatial locations where growth takes place and is referred to as the *relative elemental growth rate* [193, 236, 444, 1158, 1181], a term coined by Erickson and Sax [344, 345]. To obtain this elemental growth rate in an experiment, the position of initial markers is followed over time and interpolated to obtain an estimate for both a discrete version of the Eulerian velocity and for its gradient [1157, 1302].

The analysis of growth kinematics in higher dimensions [1127, 1334] follows the same principle. In the case where growth is considered as the only possible deformation, we consider a body in an initial configuration $\mathcal{B}_0 \subset \mathbb{R}^3$ with coordinates $\mathbf{X}_0$ denoting the position of material points in the body. The same body at a later time t is in the current configuration, denoted $\mathcal{B}_t$. We will assume that the current configuration is related to the initial configuration by a smooth invertible map $\chi : \mathcal{B}_0 \rightarrow \mathcal{B}_t$ such that a material point located at $\mathbf{X}_0$ in $\mathcal{B}_0$ is mapped to a point $\mathbf{x}(t) = \chi(\mathbf{X}_0, t)$ in $\mathcal{B}_t$. In this case, the *Lagrangian* and *Eulerian growth vectors* are defined as

$$\mathbf{V}_g(\mathbf{X}_0, t) = \frac{\partial \chi(\mathbf{X}_0, t)}{\partial t}, \quad \mathbf{v}_g(\mathbf{x}, t) = \mathbf{V}_g(\mathbf{X}_0(\mathbf{x}, t), t). \quad (1.14)$$

The vector field defined by these growth vectors creates growth lines that indicate the direction in the body where expansion takes place, as shown in an experiment on rabbit ears in Figure 1.21.

Assuming that the density remains constant, the evolution of the mass density $\rho(\mathbf{X}, t)$ is governed by

$$\partial_t \rho + \rho \operatorname{div} \mathbf{v}_g(\mathbf{x}, t) = \rho \gamma, \quad (1.15)$$

where $\rho \gamma$ is the local growth rate (see Section 13.2 for a derivation). Therefore, once the growth vectors are known, the computation of the divergence provides information on the local growth rate through (1.15), as shown in Figure 1.22C.

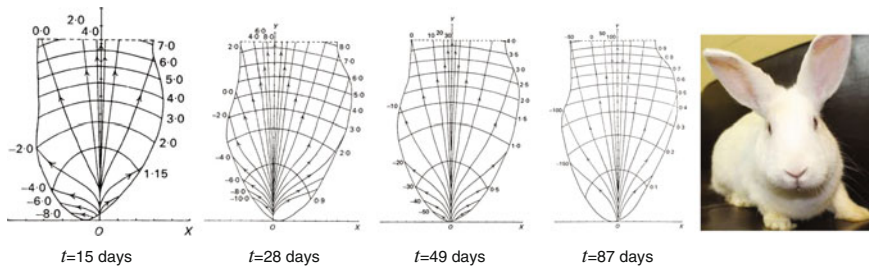


Figure 1.21 Tracking growth on rabbit ears. Streamlines and equipotential lines for the growth of a New Zealand white rabbit ear from day 15 to day 87 [249].

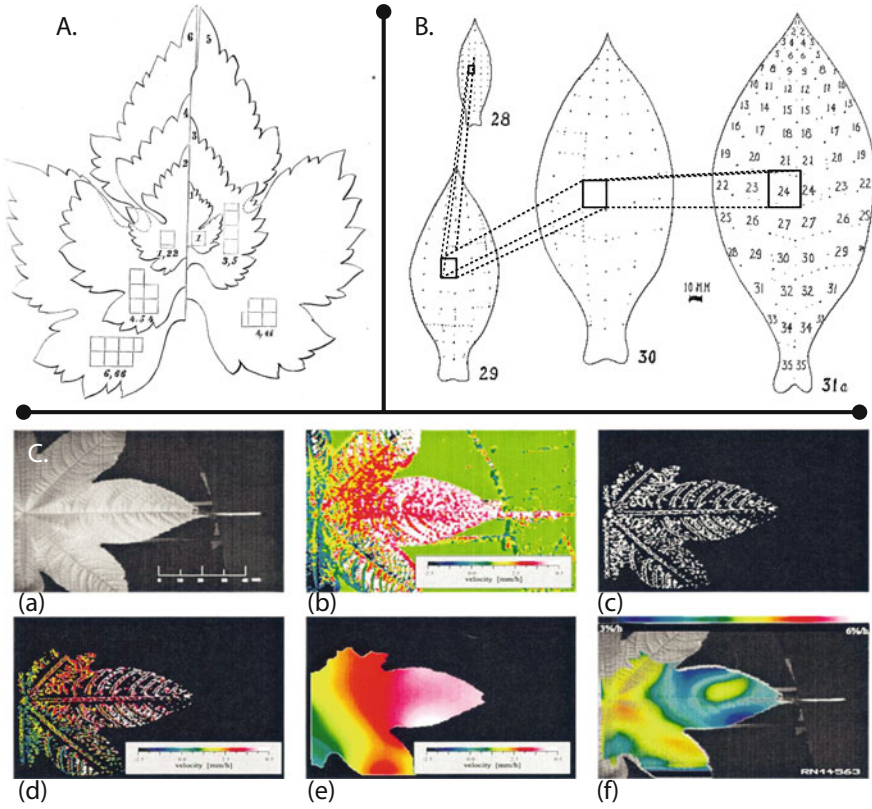
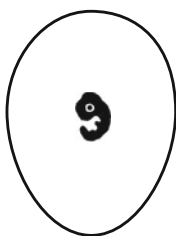


Figure 1.22 Tracking growth on leaves. A. Initial marker points are placed on the leaves and tracked through time (from Müller’s textbook [924]). B. Tobacco leaves from Avery [48]. C. Digital analysis of growth. Starting from an original time lapse sequence (a), the displacement vectors are calculated (b), a mask of nonmoving points is evaluated (c), and used to correct the displacement vector (d). A smooth interpolation of the displacements (e) provides a way to compute the divergence of the displacement giving the local rates of growth (f) (reproduced from Schmundt et al. [1127]).

The local mass density ρ is only related to the volumetric change of a volume element, without giving any information on the local direction of the deformation; that is, the anisotropy of growth. This information is contained in the gradient of the deformation and will be discussed in Chapter 12.

Chapter 2

Mechanics and Growth



2.1 Growth is Influenced by Stress

From a biologist's perspective, growth is mediated by gene activation and regulation. In a simplified view, different genes will trigger different growth responses. For instance, in the case of the leaf of the model plant *Arabidopsis thaliana* shown in Figure 2.1, a number of genes and microRNAs have been identified that regulate and control the shape of the plant's leaves during development. Exquisite details are known on the initial stage of leaf formation, including features such as adaxial–abaxial polarity, symmetry, and flat morphology, as well as the precise control of cell division, proliferation, and expansion. This genetic understanding of growth is fundamental as it identifies, at the smallest scale, the essential features that control cell division and expansion. It also provides information at the local level on the change in shape and volume of the growing components of a body. However, a leaf will only acquire its shape by developing physical forces between cells or within a cell. There are important physical, geometric, and mechanical constraints in the development of a tissue or an organ that need to be integrated with genetic and biochemical signals to obtain a full picture of growth.

The idea that mechanics shapes organisms and should play a fundamental role in the description of growth processes was first put forward by Wilhelm His in 1888,

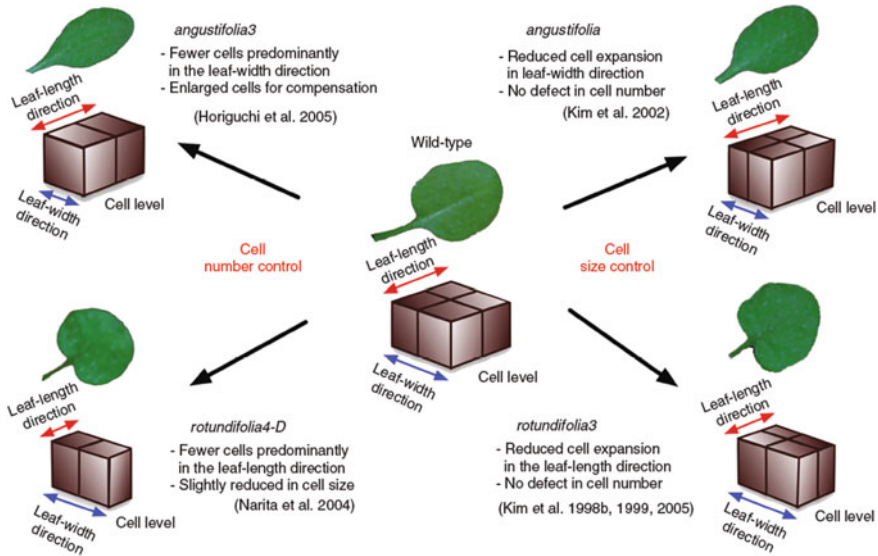


Figure 2.1 A genetic view of growth. The shape and size of a leaf is determined during development by a number of regulatory genes that have been identified by systematic genetic studies [693].

as shown in Figure 2.2 [578, 612]. In his treatise “On the Principles of Animal Morphology”, he writes: “*Embryology and morphology cannot proceed independently of all reference to the general laws of matter, to the laws of physics and of mechanics. This proposition would, perhaps, seem indisputable to every natural philosopher; but, in morphological schools, there are very few who are disposed to adopt it with all its consequences.*”

His’ comment was echoed by Le Gros Clark in 1945, in his quest to understand brain morphology [215]: “*Yet, whatever may be the primary cause which initiates a succession of growth processes leading ultimately to the differentiation of a specific form or pattern, the morphologist cannot but accept the thesis that the proximate factors, which immediately operate at the time when the form or pattern becomes manifest in embryological development, are capable of expression mathematically in terms of purely mechanical forces.*”

The fact that mechanical loading has an effect on growth is not surprising, given that there is much anecdotal evidence from our everyday lives. We know, for instance, that muscles will grow when repeatedly strained during exercise; the space program taught us that astronauts lose bone mass in space flights due to the effect of reduced gravity [1262]; and our obsession with competitive sports has led to the observation that tennis players have denser bones in their playing arms [1222]. We also know that trees will grow shorter and stubbier in windier areas [237], that the earlobe will stretch and grow under the action of heavy earrings (see Figure 2.3), and that the dreadful custom of foot-binding results in smaller foot size and permanent deformations [87].

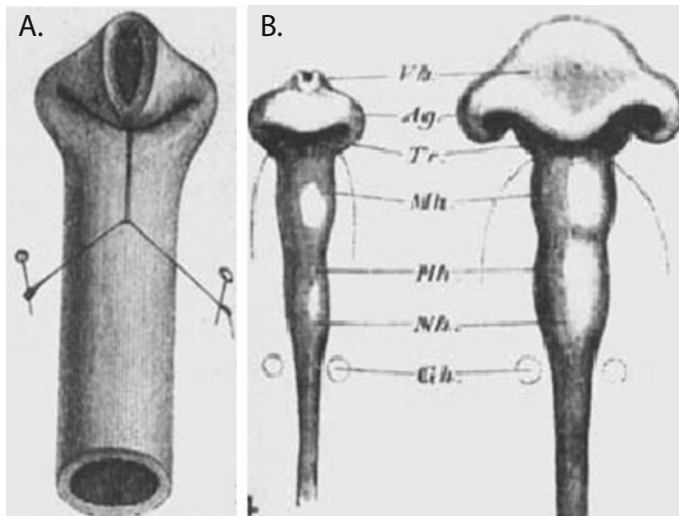


Figure 2.2 Wilhelm His' mechanical analogy between A. the folding of a rubber tube and B. the folding of a gut tube during morphogenesis (adapted from [445, 578]).

Figure 2.3 Ear gauging stretches the ear lobe and produces permanent deformations.



A change in mass or in material properties typically requires a cellular response. How is the information about forces and loadings carried through the cell? *Mechanotransduction* is the process by which mechanical signals, applied in the bulk or at the boundary of the body, are mediated down to the cellular level and then transferred to the nucleus. It is a complex process that is not yet fully understood. However, the effect of the mechanical environment on the regulation of growth is undeniable and it can be modeled mathematically, even in the absence of well-understood transduction mechanisms. Indeed, the precise influence of mechanical loading on growth and physiological regulation is well documented in many systems, some of which we briefly review next.

2.1.1 The Growth of Stems

Detailed experiments quantifying the relationship between growth and applied stress were performed by plant physiologists in the nineteenth century. The idea depicted in Figure 2.4 is simple and elegant: A string is attached to the tip of a growing stem and tied around a pulley. Weights can be placed at the other end of the string to apply a constant force to the growing stem. The length of the stem is then continuously recorded by an ingenious device, the *auxanometer*. It is therefore possible to record the length of the stem in different mechanical conditions by applying different weights. Once the length as a function of time is known, the growth rate can be extracted. Figure 2.4B presents the results of such an experiment on maize leaves. The evaluation of the growth rate shows that there is a positive correlation between growth rate and applied load. This type of experiments establishes the existence of a relationship between external loading and growth.

2.1.2 The Growth of Axons

Another interesting example of stress-mediated growth in a biological system is found in the development and branching of neurons. Most neurons have a very distinctive morphology with a large cell body and long protoplasmic protrusions extending from the cell body. These protrusions, called *neurites*, develop into either axons or dendrites that connect to those of other cells to create a connected network; the nervous system. The initiation, development, and growth of axons have been shown to depend on applied mechanical forces [126, 559]. *Initiation* refers to the early development of a neurite out of the cell body. It has been shown that the initiation of axons of chick sensory neurons can be manipulated experimentally by the proper application of tension on the surface of the cell body [1366]. Following initiation, the elongation of an axon can be induced by gluing a glass needle to the neuron and then towing it with constant force. These experiments clearly show that the growth rate depends crucially on the applied load as shown in Figure 2.5.

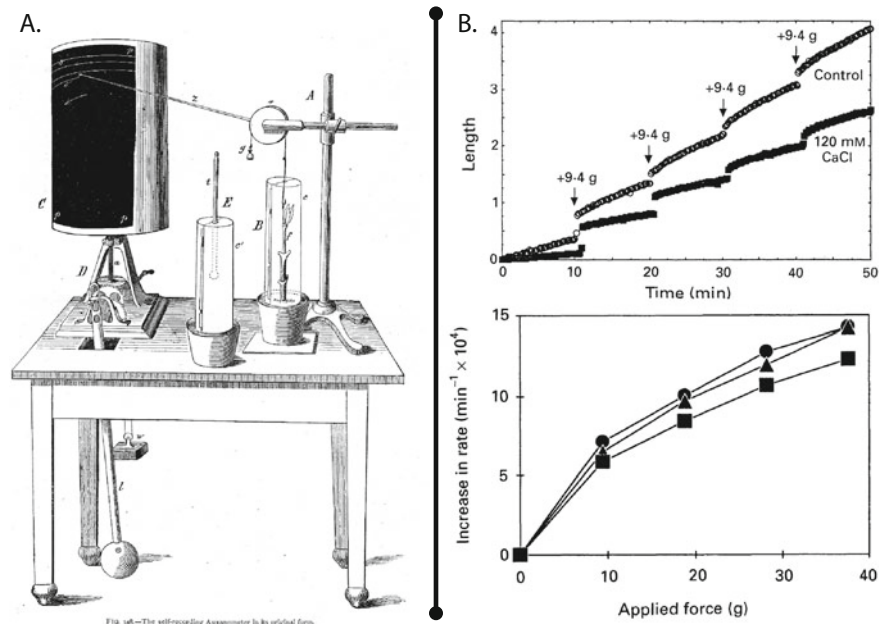


Figure 2.4 A mechanical view of growth. A. An auxanometer: The length of a growing stem is continuously recorded while the plant is being pulled by different weights (from Sachs’ “Text-book of Botany” [1107]). B. Results of similar modern experiments performed on maize leaves. Different weights are attached, leading to varied growth velocities and growth rates as a function of the applied force [251].

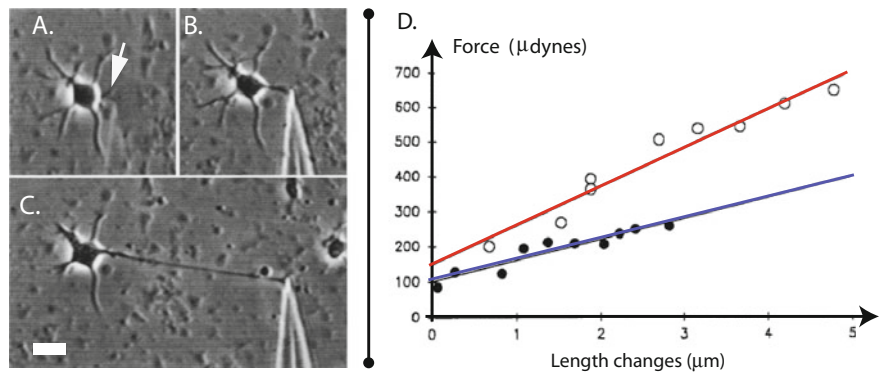


Figure 2.5 Experimental elongation of a neurite in a stage 2 hippocampal neuron induced by applied tension. A. Neuron immediately before needle application. The arrowhead marks the position where the needle was attached. B. Same neuron 30 min later during early stage of neurite towing. C. 5 hours and 40 min after panel B, at the end of towing. Bar, 20 μm [757]. D. Axonal elongation rate for chick sensory neurites as a function of experimentally applied tension (data and graphs adapted from [560]).

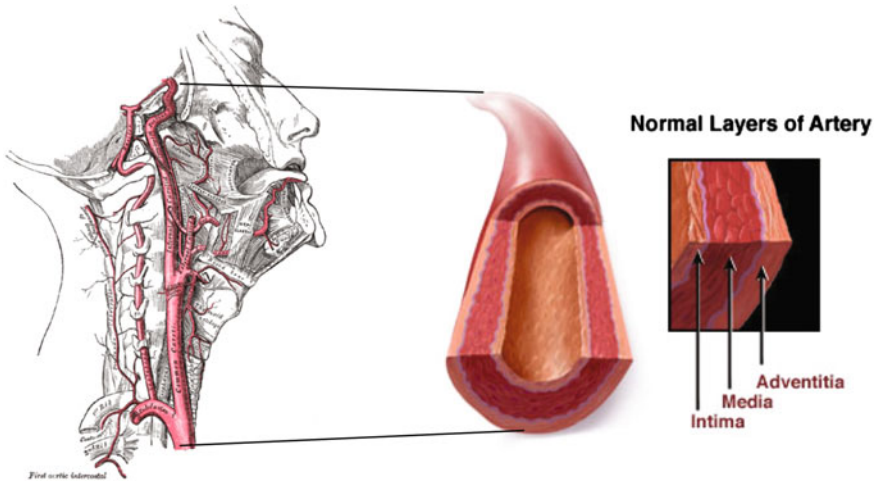


Figure 2.6 Arteries' thickness, diameter, and length are regulated by mechanical stimuli, among other processes.

2.1.3 Thoma's Law for Arteries

Arteries are the blood vessels that carry blood from the heart to organs and body tissues. Mechanically, they are cylindrical structures with a triple layer of viscoelastic material that can grow and remodel as shown in Figure 2.6. The arterial system is a highly complicated and regulated mechanical system sustaining varying pressures, axial loads, and shear stresses. It has been known since the early work of R. Thoma in 1893 ([1227], see also [91, 1207]) that the magnitude of blood flow in chick embryo blood vessels regulates the vessels' diameters and, furthermore, that this effect is mediated through shear stress on the inner arterial wall. Thoma also showed that the magnitude of pressure regulates the vessels' thicknesses. These observations on mechanical regulation of artery thickness and diameter have been reproduced and refined experimentally over the years [779, 1301]. Arteries also respond to changes in axial loading. A sustained increase in axial loading tends to lengthen arteries in culture [264] and in vivo [659], suggesting that axial stress (or strain) is also regulated toward a *homeostatic* value (that is, a level of stress considered to be the normal physiological regime) [448].

2.1.4 Woods' Law for the Heart

The heart is a complicated organ that pumps blood to the body by active muscular contractions. The size and thickness of the heart are regulated during homeostasis to maintain proper function. In 1892, R. H. Woods proposed that wall stress is a key factor in this regulation process [153, 1339, 1359]. The original idea of Woods is to look at the heart as an elastic membrane and use Laplace's law to obtain information

on wall stresses. Laplace's law (sometimes called Young's law [1360] or Laplace–Young's law [771, 1223]) relates the geometry of an elastic membrane of thickness h to the forces applied to it. In the simplest case of a sphere of radius R under pressure P , the law states that the force per unit area, σ , experienced by the material is simply given by

$$P = \sigma \frac{h}{R}. \quad (2.1)$$

The larger the pressure, the larger the force in the membrane. In general, the geometry of a membrane is locally characterized by its principal curvatures κ_1 and κ_2 , as defined in Chapter 10. Then, Laplace's law states that for an elastic membrane, the difference of pressure P across the membrane is related to the principal curvatures and the membrane thickness h , and the corresponding principal stresses σ_1, σ_2 , by

$$P = h (\sigma_1 \kappa_1 + \sigma_2 \kappa_2). \quad (2.2)$$

If we assume that the stresses are equal, $\sigma_1 = \sigma_2 = \sigma$, we obtain $P = h\sigma (\kappa_1 + \kappa_2)$. Therefore, we can obtain the stresses in the material from the pressure and the geometry of a membrane. This is precisely what Woods achieved. In his method, shown in Figure 2.7, Woods used a compass to measure the heart's curvatures. By evaluating the wall stresses at different points on the heart, he showed through direct geometric measurements that the *Woods' number*, defined as the ratio

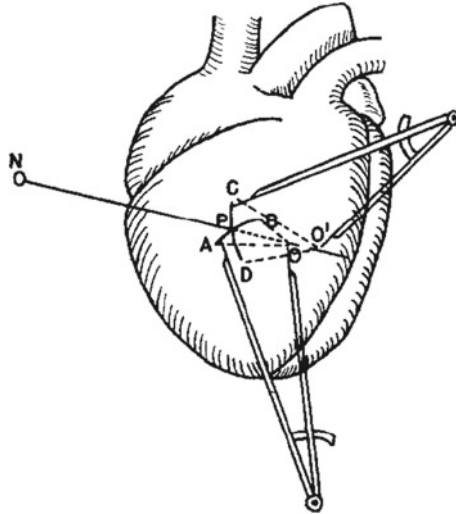


Figure 2.7 Principal radii of curvature on the heart surface. Woods used necropsy hearts. He picked several points on the surface and used a pin (N) to represent the normal direction to the surface. Assuming that the heart is close to a surface of revolution, the two directions of principal curvature are close to the horizontal and vertical directions (the arcs APB and CPD). Then, the problem is to find the center of curvature (O and O') such that a compass would trace the arcs. The opening of the compass is then related to the radius of curvature (from Burton [153]).

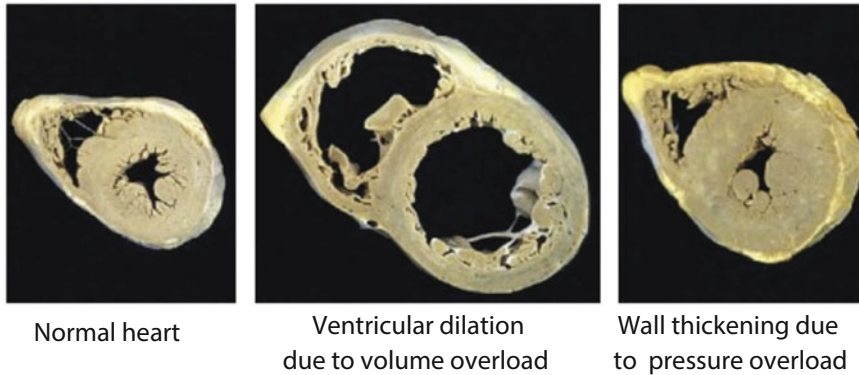


Figure 2.8 Growth and remodeling in the heart. Pathology of the heart leading to an increase in size. Left: normal heart, middle: ventricular dilation due to volume overload, right: increase in wall thickness due to pressure overload (adapted from [738]).

$$C_{\text{Woods}} = \frac{P}{\sigma} = h(\kappa_1 + \kappa_2), \quad (2.3)$$

is nearly constant across the heart.

More strikingly, Woods' number varies only by about 22% across different mammal and bird species [667, 834, 1206]. This observation suggests that wall stress could be the prime regulator of heart size and thickness. In simple terms, *Woods' law* states that the heart grows and remodels to keep the wall stress constant. This law is consistent with various pathologies and regulatory mechanisms [1206]. For instance, during long periods of high blood pressure P due to pathological conditions, the heart ventricles thicken by the addition of myofibrils which lower the wall stress over long periods, as shown in Figure 2.8 [450, 1063]. Similarly, athletic exercise leads to an increase in volume causing a decrease in the curvature κ . Subsequently, this change in curvature is compensated for by an increase in muscle fiber length which further causes an increase in the heart's thickness h [449].

2.1.5 Wolff's Law for Bones

The connection between mechanics and bone structure was noticed as early as 1832 when Bourguery [117, 124] first commented on the striking analogy between trabecular bone orientation and mechanical loading as shown Figure 2.9.

This observation was further developed by Culmann [254, 949] through the analogy between the tension and compression lines in the human proximal femur and those of the Fairbairn crane, which exhibits a similar shape. The analogy is based on the observation that the internal organization of the trabeculae is similar to the lines of principal stress obtained in an isotropic homogeneous material with the same geometry under mechanical loading. Wolff further suggested that this architecture is the result of the bone structure due to active processes, and that bones evolve accord-

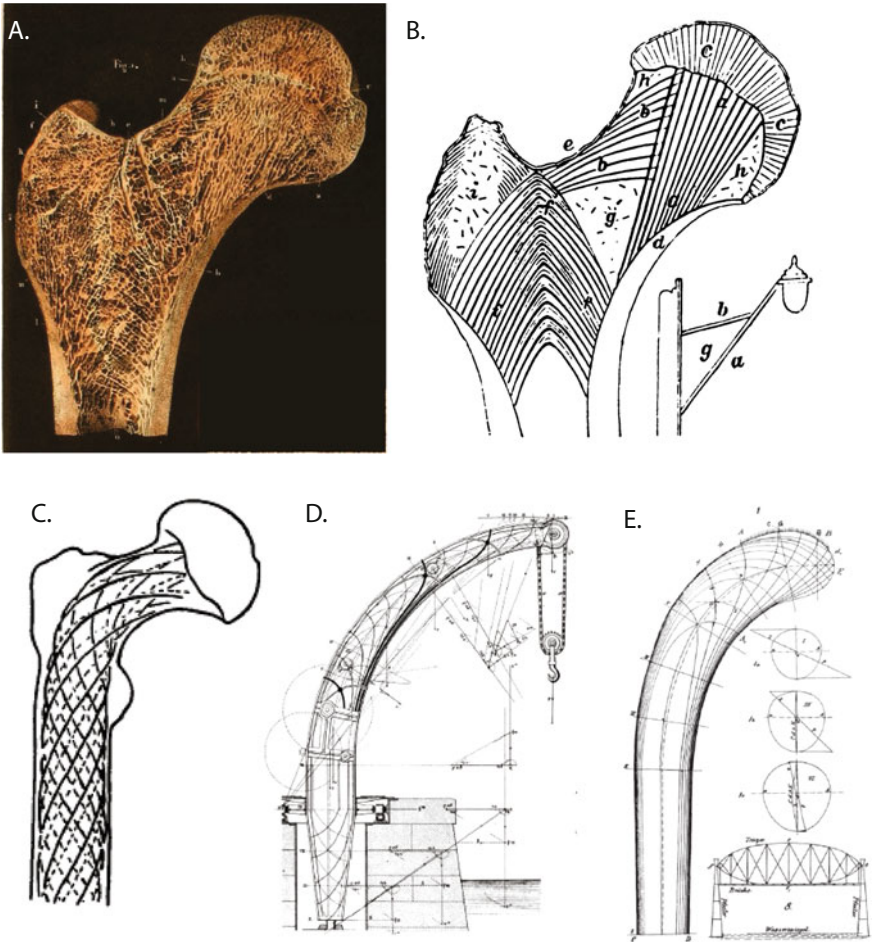


Figure 2.9 Wolff’s law for bones. A. Drawing of a Femur from Bourguery 1832 [117]. B. Drawing from Ward’s “Outlines of Human Osteology” [1298, p. 370]. C. A spiral model of bone due to Dixon [683]. D. Carl Culmann’s illustration of a Fairbairn crane [254, p. 622]. E. Wolff’s structural study of a bone [1335].

ing to some “mathematical laws” that were not given explicitly [1335]. Nowadays, *Wolff’s law for bone remodeling* is not understood as a scientific law *sensu stricto*, but is used instead to describe processes by which bones adapt by actively remodeling in order to best resist the applied load [1096]. This *functional adaptation principle* was first proposed by Wilhelm Roux in 1881 [1100]. Roux proposed that bone adaptation is the result of a “quantitative self-regulating mechanism” at the cellular level [633].

The mineralized cartilage that forms the bone is the result of a complicated process involving the interaction between many cell and tissue types. Early bone structure is built by the action of *osteoblasts*, bone forming cells, and *osteoclasts*, bone resorbing

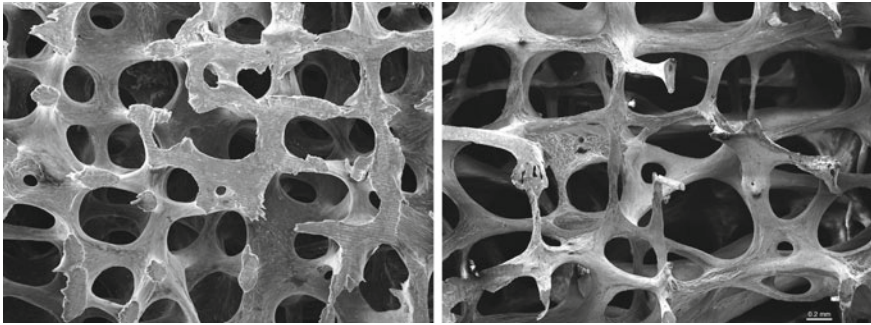


Figure 2.10 Bone growth. Normal (left) and osteoporotic (right) bone architecture (3rd lumbar vertebrae). Soft tissues and cells have been removed. The damage in the osteoporotic bone is caused by osteoclasts (picture courtesy of Tim Arnett).

cells. Osteoblasts continue to produce extracellular matrix that develop into mature bone cells called *osteocytes*. After ossification, osteoclasts and osteoblasts continue to build the typical microstructures of cortical or cancellous bone tissue. After maturation, the bone structure depends on the proper balance between new osteoclastic resorption and subsequent osteoblastic formation. For instance, the case of osteoporosis shown in Figure 2.10 is the result of a failure of this adaptive response to maintain the structure needed to withstand daily loading [39].

While the role of mechanics in bone remodeling is well established, the translation of different external forces into a cellular signal that controls the recruitment and activity of bone resorbing or producing cells is more delicate [441, 529]. Mechanotransduction provides the fundamental bridge between the mechanical and biological world. In the case of skeletal cells, the forces arising from mechanical loading can generate a number of mechanical stimuli, including strain in the bone tissue, stress in the central cavity and the outer cortex of bone shafts, microdamage or fracture, transient pressure waves, shear forces through the microscopic canals between the lacunae of ossified bone, and electric fields due to the motion of bone crystals [1206]. It is also known that remodeling is sensitive to changes in loading magnitude, the number of loading cycles, the distribution of loading, and the rate of strain among others [1102].

2.1.6 Davis' Law for Soft Tissues

In addition to Wolff's, Thoma's, and Woods' laws, the end of the nineteenth century provided us with yet another conceptual law for growth and remodeling. Around that time, the American surgeon Henry Gassett Davis developed innovative traction methods in orthopedic medicine. In his book, "Conservative surgery" [263], Davis studied the response of ligaments and tendons to the mechanical stresses imposed by

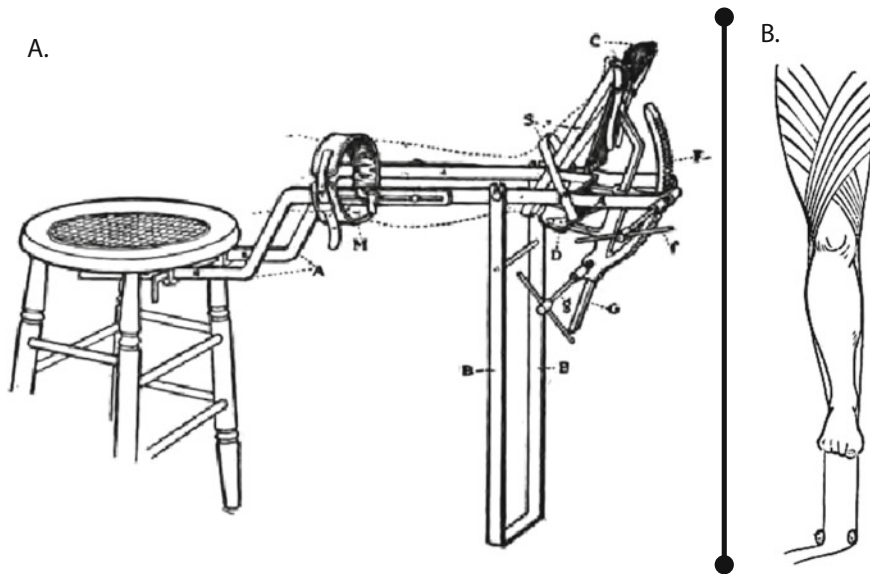


Figure 2.11 Davis and Nutt developed innovative techniques based on the idea that stresses influence growth. A. A traction shoe invented by Nutt to help elongate the gastrocnemius muscle [968]. B. Traction methods by Davis [263].

various mechanisms for straightening broken bones, as shown in Figure 2.11. Davis writes “*Ligaments, or any soft tissue, when put under even a moderate degree of tension, if that tension is unrelenting, will elongate by the addition of new material; on the contrary, when ligaments, or rather soft tissues, remain uninterruptedly in a loose or lax state, they will gradually shorten, as the effete material is removed, until they come to maintain the same relation to the bony structures with which they are united that they did before their shortening.*”

These ideas were later summed up by John Joseph Nutt in his 1913 book “*Diseases and Deformities of the Foot.*” When discussing the treatment of congenital club foot, Nutt refers to the influence of stress on soft tissues as *Davis’ law* and the effect of stress on bones as *Wolff’s law* [968, p. 157]. He writes “*These physiological laws are simply expressions of the influence of work, rest, and fatigue on metabolism and the resultant hypertrophy and atrophy.*”

Modern studies of tendons in simulated microgravity have confirmed that, in the absence of stress, tendons tend to lose their stiffness similarly to known skeletal muscle atrophy [1069].

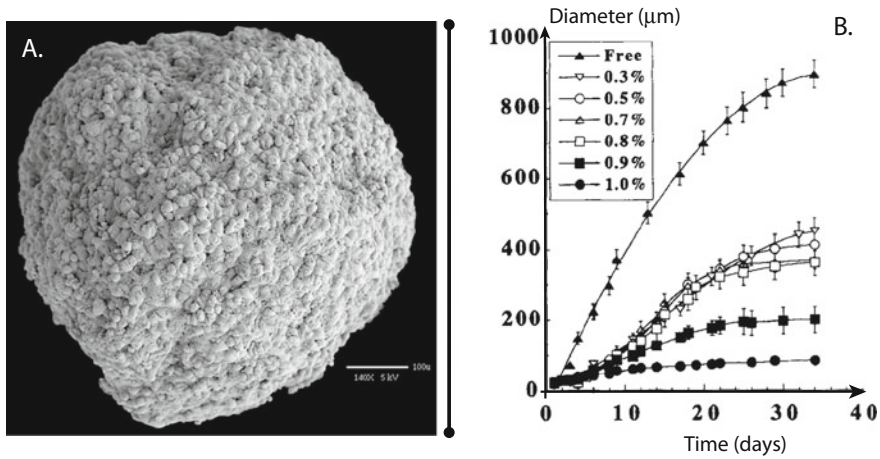


Figure 2.12 Multicellular tumor spheroids. A. Three-dimensional structure of a spheroid (bar is 250 μm) [920]. B. Growth kinetics of spheroids grown in agarose gels of different concentrations, showing that, as the gel becomes stiffer, the asymptotic size of the spheroid decreases. (adapted from [566])

2.1.7 Tumor Spheroid Growth

Cancer cells can be cultured *in vitro* to grow on a gel or in a pool of nutrients to form a sphere-like shape, called a *spheroid* [391, 1203], as shown in Figure 2.12. These spheroids are of great interest as they can be used in a variety of settings to understand the response of cancer cells under different physical, chemical, and genetic treatments [1116]. Mathematically, the delightful spherical symmetry of these aggregates simplifies the problem tremendously as the shape is fully characterized by its radius. It allows for a direct comparison to experiments and the analysis of the problem can be reduced by considering the evolution of the spheroid radius [5, 158, 384, 393, 1098].

The relationship between mechanical stimuli and tumor growth was demonstrated by Helmlinger et al. who showed that the final size of the spheroid depends on the concentration of the agarose gels in which it is cultured [566]. This study suggests that solid stress, among other factors such as nutrients and acidity, has a direct effect on growth, as high stress may limit the ability of cells to divide due to *contact inhibition* [530, 566].

2.2 Stress is Influenced by Growth

Wapas, Walapas, or Walabas are the generic names for trees belonging to the genus *Eperua*. They are found through the French and British Guyanas where they are the most abundant tree species. These trees, shown in Figure 2.13, grow rapidly and can be cut every 30 years, representing an important economic resource [238]. However,

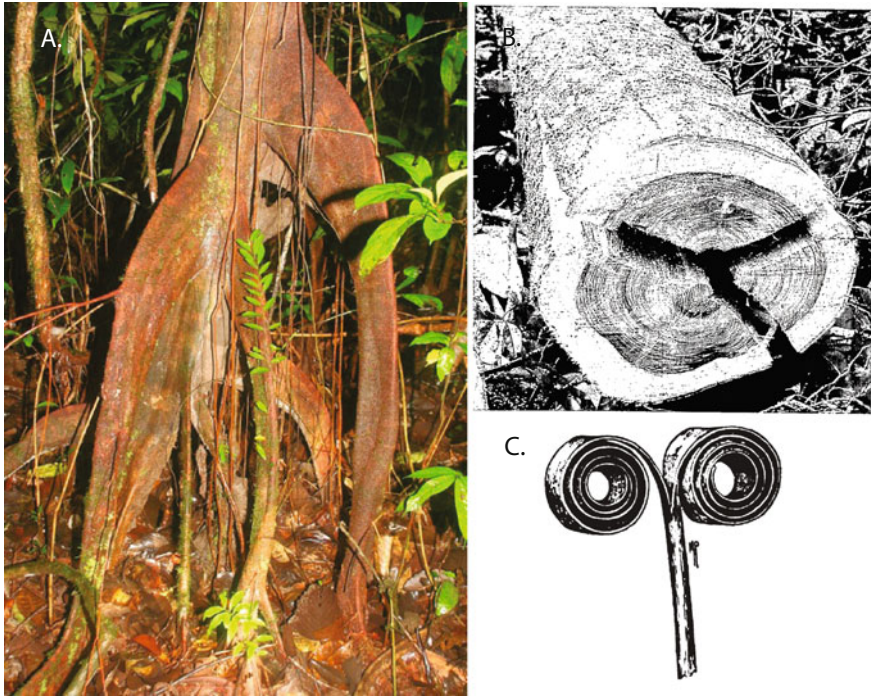


Figure 2.13 A. *Eperua venosa*. Wapas trees burst open when cut due to the residual stress caused by differential growth (picture by Jean Thiel, courtesy of Pierre D  tienne). B. When they are cut, they crack open [282]. C. Residual stress in plants can also be relieved by slicing them [412].

despite their abundance and rapid growth, Wapas are not widely exploited because of the dangers associated with harvesting them. Locally, wapas are known as “les arbres tueurs” (the killer trees) as they often burst open when they are cut, presenting a real threat for workers [282]. This tendency to burst is a perfect and extreme example of the release of residual stress in plants called *tissue tension* by plant physiologists [1031]. It is believed to be of prime importance in shaping plants [59]. In many biological tissues, due to a combination of cellular, chemical, and mechanical factors, different parts of the tissue experience distinct growth rates. The net result of this *differential growth* is that the tissue may be under stress even when unloaded. *Residual stress* is the stress field that may exist in a body when unloaded. The generation of residual stress through differential growth is a critical feature of any mechanical theory of growing bodies [1175]. Essentially, as growth takes place, parts of the body need to be stretched or compressed to ensure integrity (no cavitation) and compatibility (no overlap). In turn, the strains associated with these residual stresses are referred to as *residual strains* [584, 1171].



Figure 2.14 Residual stress in rhubarb. A. A rhubarb will naturally curve backward when cut. B. Cross section of a rhubarb showing clearly the two different tissues, the pith inside and the epidermis outside.

2.2.1 Tissue Tension in Plants

A smaller and simpler demonstration of the existence of residual stress in plants can be achieved in the kitchen by slicing a stalk of rhubarb (*Rheum rhabarbarum*), as shown in Figure 2.14A, and observing that it curls back to relieve some of its internal stresses [45, p. 47]. As shown in Figure 2.14B, a stalk of rhubarb is composed of an outer layer consisting of the epidermal tissue and the collenchyma layers, and an inner layer, the *pith*, consisting chiefly of parenchyma cells. This observation suggests that, in its natural state, the *pith* is in compression and the epidermis is in tension.

We can further quantify these two different states by peeling the epidermis with a kitchen peeler [1274]. If we carefully peel a strip of the stalk's outer layer and place next to its original position, we notice that the strip has shrunk in length by about 2%. If we remove completely the epidermis, as shown in Figure 2.15, we observe that the

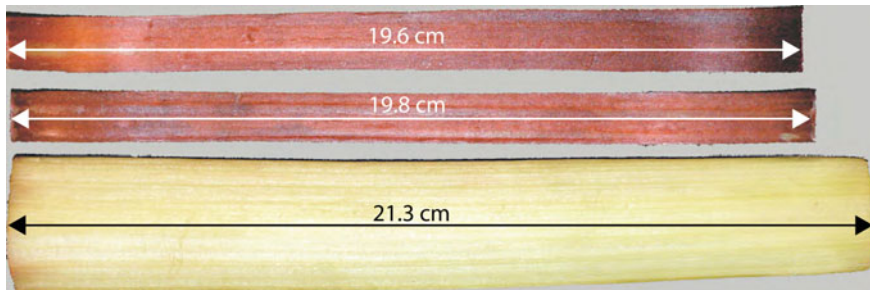
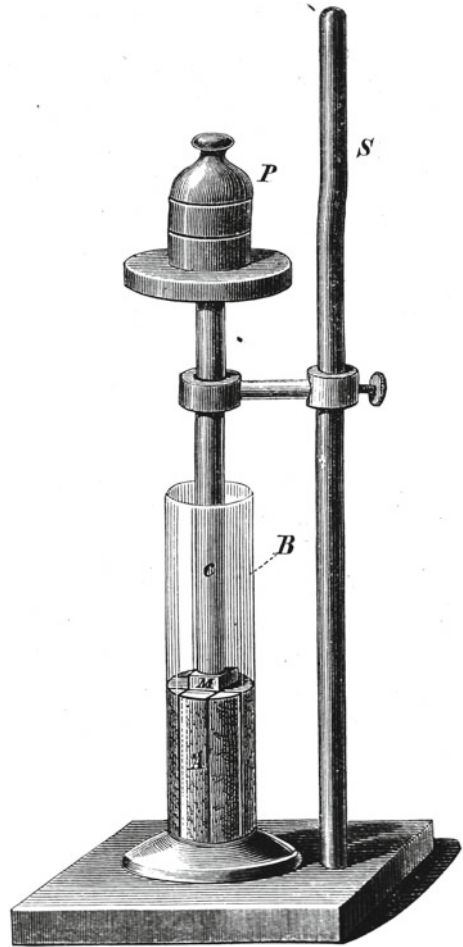


Figure 2.15 Residual stress in rhubarb. The middle segment of a long stalk of rhubarb was cut. This segment, of initial length 20 cm, was then peeled. The peeled strips are now shorter, by about 2–4%, and the pith is longer, by about 6%. The mutual tensions between inner and outer layers have been relieved.

Figure 2.16 Residual stress is measured by placing a peeled pith in a cylindrical tube and adding weight on it. The tube prevents the pith from buckling. Extra weight is added until the pith recovers its initial length. This weight is a direct measure of the overall residual stress developed in the stem before the epidermis is removed [924].



pith has increased in length by about 6%. This elementary experiment confirms that, before slicing, the outer wall is in a state of axial tension while the pith is in a state of axial compression. The actual force developed in the inner layer can be found by the ingenious experiment shown in Figure 2.16. The pith is placed in a cylinder to avoid buckling and a weight is added to the top so that it recovers its initial length. This weight is precisely the force exerted by the epidermis on the pith in its original state.

The possible mechanical role of this combination of tissues and their associated stresses can be appreciated by realizing that the peeled rhubarb has lost most of its rigidity; so much so that it now buckles under its own weight. Coming back to our first observation, if the rhubarb is cut along its axis, it will tend to bend outwards, as part of the elastic stress is relieved when the pith elongates and the outer tissues shorten by curving as shown in Figure 2.14A.

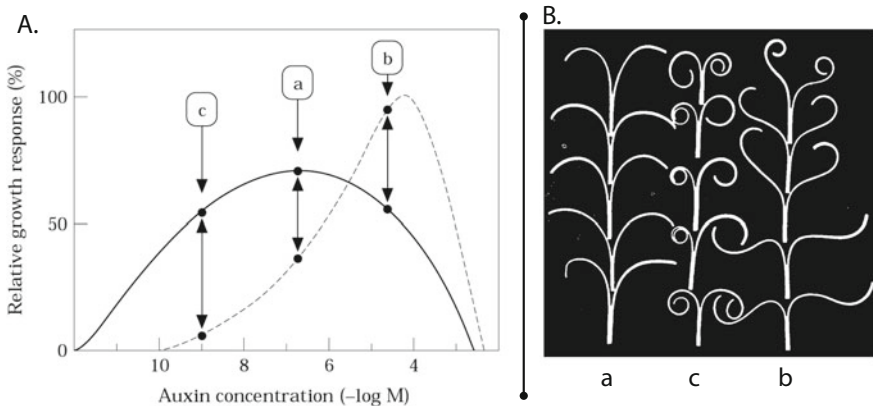


Figure 2.17 Curvature pea test to determine the role of plant growth hormones. A. Varying the concentrations of auxin induces different growth rates in the pith (solid line) and epidermis (dashed) [1031]. B. If the pith grows faster than the epidermis, the pea (*Pisum sativum*) hypocotyl will curve outwards (ac) or inwards (b) when cut (adapted from Thiman and Schneider [1226]).

The mutual tension between outer and inner tissues in rhubarb, and its possible role in plant mechanics, was mentioned as early as 1848 by Brücke, described by Sachs in 1857, and explored in detail by Hoffmeister in 1867, who noticed that the outer and inner tissues of common grape vine (*Vitis vinifera*) contract and extend elastically upon separation, respectively. The possible role of tissue tension in plant mechanics was well described by Sachs, who writes: “*We have here the case of an elastic stiff body consisting of two parts, each in a high degree flexible and by no means stiff; only in their natural connection do the epidermal tissue and internal tissues together form an elastic rigid body*” [1107, p. 216].

Following these early works, tissue tension became a central topic of interest in plant physiology: It was observed in many plants, including wheat roots, fennel leaves, rhubarb stalks, sweetgum trees, and hypocotyls of cucumber, sunflower, cantaloupe, and squash [134, 135, 152, 562–564, 739]. Mechanically, these stresses are attributed to the differential extension of the cell walls in outer and inner layers, creating an irreversible change in the resting lengths of both tissues [562, 739, 741].

Tissue tension also played a central role in the discovery of auxin as a growth hormone, through the so-called *curvature pea test* shown in Figure 2.17 [113, 837, 1030, 1128, 1226]. As auxin has a distinct effect on different tissues, the respective growth of the epidermis and pith of pea hypocotyl can be controlled by varying the auxin concentration, and explicitly tested, by slicing the pea along its axis and measuring the resulting stem curvature.

Despite the early success of mechanics in plant physiology, the advent of genetics and biochemistry changed the emphasis of plant research from physical to cellular mechanisms. However, by the end of the twentieth century, the study of tissue tension (sometimes called *growth stresses* in trees [55, 286, 379]) regained interest [365] and

the respective role of tissue tension, biochemical pathways, and genetic signaling in growth regulation became a controversial topic once again [742, 1031].

2.2.2 Residual Stress in Physiology

It is through the work of both Fung and coworkers, and the joint work of Vaishnav and Vossoughi in the 1980's [406, 407, 1269, 1270], that the importance of residual stress in physiology came to be fully appreciated. The classic experiment of Fung [407] exploits the fact that slicing a disk of artery will release residual stresses by opening as shown in Figure 2.18.

If we view the artery as a three-layer cylinder, the opening of the disk reveals that, in the closed position, the inner layer, shown in Figure 2.6, is in a state of compression whereas the outer layer is in tension. As shown in Figure 2.18B, residual strain can be quantified by the *opening angle* between the two open ends and the furthest point on the disk [408]. This angle has become a standard measure of residual strains in the study of arteries. The stresses associated with the opening angle are known to play a fundamental role in regulating the transmural stress gradient and lowering circumferential stress at the inner walls [184, 601, 635, 636, 1054]. Experimental observations [605, 607] also indicate that, not unlike the rhubarb, arteries exhibit axial residual stress due to the relative axial growth of the different layers, as first

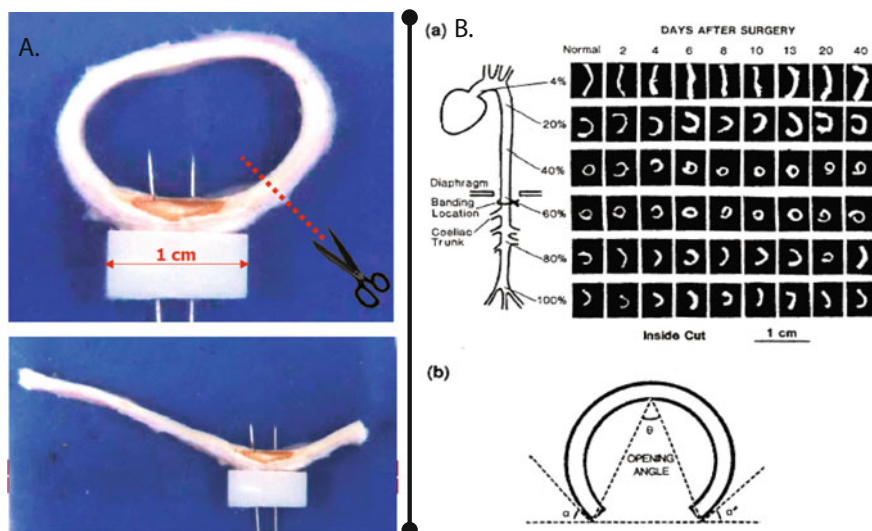


Figure 2.18 Residual stress in arteries. A. Slicing a disk of artery will result in the artery opening to relieve some of its residual stress (picture courtesy of Gerhard Holzapfel and Ray Ogden). B. Fung's classic experiments (a) and the definition of the opening angle (b) [408].

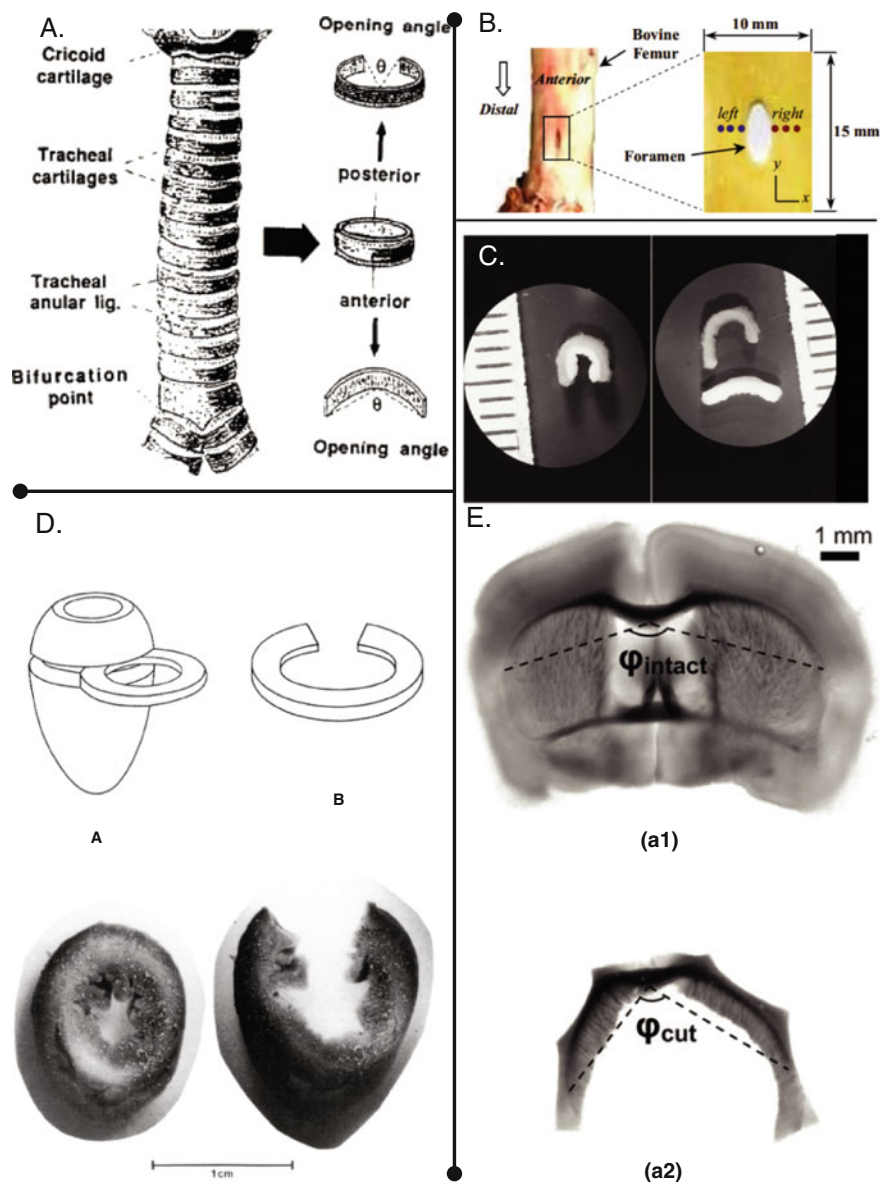


Figure 2.19 Evidence of residual stress in physiological systems. A. The trachea [534]. Notice how, after being cut, the disk relieves stress by opening. B. Bones [442]. Here, an incision creates an opening due to tension. C. The esophagus [510]. Different tissue layers have distinct opening angles due to varying residual stresses. D. The heart [986]. A slice of heart also opens when cut. E. Stress relief in the brain [1345].

noted by Bergel in the 1960s [89, 168, 426]. However, the role of axial residual stress in regular homeostasis still remains to be elucidated.

Once the importance of residual stress in arteries was established, it was not long before residual stress was observed in a number of other physiological systems, as shown in Figure 2.19. These systems include physiological tissues and organs such as the esophagus [510, 511, 513, 1365], the aorta [49], the heart [986], the trachea [534], the brain [140, 568, 1345], bones [443, 1214, 1347], cartilages [1138], and the developing embryo [77, 79]. It was also found in non-physiological systems such as solid tumors [26], sea urchins [902] and even in the drying of fruits [724] and in the aging of meat [784]. Residual stresses are a hallmark of living tissues and organs, but also play an important role in many classic elastic systems, as first noted by Ciley in 1901 [212], and in man-made structures [1256–1258]. The reviews [940, 941, 1330–1332] provide interesting discussions of the techniques used in engineering and bioengineering to measure residual stresses and their various effects on the properties and behaviors of different structures.

2.3 The Theory of Morphoelasticity

From a geometric point of view, residual stresses arise due to the incompatibility between a specification of the local change in a volume element and the continuity and integrity of the body. This incompatibility is easy to visualize in a one-dimensional thought experiment analog to the rhubarb experiment. Consider a sandwich of three identical elastic rods perfectly glued to each other. They are constrained so that they only deform along their lengths as shown in Figure 2.20. Now, we let the middle rod grow uniformly in length. To preserve the integrity of the composite body and prevent it from breaking apart, the middle rod must be in a state of compression and, accordingly, the outer two rods must be in a state of tension. As a result, this structure has developed residual stress. This stress could be relieved by simply removing the glue between the layers, hence allowing the three rods to return to their unstressed length after growth. It could also be partially relieved if the upper layer is removed and the two remaining layers are allowed to curve. Interestingly, the shape of the grown composite body depends not only on the geometry, but also on the elasticity of the three rods. If the outer rods are very stiff, negligible deformation will take place, but large stresses will be generated.

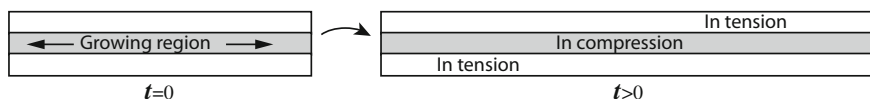


Figure 2.20 A simple system consisting of three elastic rods glued together. The middle rod grows in compression and places the outer rods in a state of tension, creating residual stress through the structure.

This elementary example outlines the interplay between the elasticity of the material, the local change in volume due to growth, and the overall geometry of the body. Furthermore, stresses also influence growth through evolution laws, creating further dynamical feedback in the development of stresses and geometry. Understanding this coupling, for given materials and growth evolution laws in a given geometry, is the central problem of the theory of *morphoelasticity* [464, 468]. The goal of such an approach is not only to obtain the new grown shape and the residual stress developed in the structure, but also to understand how such a new body evolves dynamically, how it responds to loading, how it reorganizes itself by remodeling, and how it fulfills key structural and biological functions. For example, the grown rhubarb is stiffer as a structure than its different tissues separately. What is the respective role of growth and elasticity in producing this final structure? Similarly, it is believed that arteries develop residual stress to counteract hoop stress gradients that may cause tissue separation. How is this structure obtained dynamically? How does its material response evolve during loading?

Yet another way that growth, geometry, and elasticity combine in biological materials is through the formation of new morphological patterns born as mechanical instabilities [80]. It is well known that, under external loads, elastic materials can develop instabilities such as buckling [486], wrinkling, or creasing [103] and a natural question is whether growth itself can generate sufficient stress so as to destabilize the body. It is not clear that such an instability can exist since the geometric effect of growth is to change the different length scales associated with the body, such as thickness, height, and width. It is also possible that growth may destabilize the body and trigger the development of new shapes. Examples of these growth-induced patterns can be found in bulk growth [80, 463] as well as in the growth of plates, shells, membranes [275, 277, 851, 852], and rods [917]. Growth may instead have a stabilizing effect as, typically, stubby bodies are more stable than slender ones under compression, and in the process support the function of the biological structure [485, 1274].

The general questions of interest in developing a mechanical theory of growth are in understanding the origins of the coupling and the interplay between growth and mechanics, as well as in determining possible consequences for biological functions and shapes:

- What is the role of mechanical cues in growing tissues?
- How does growth modify the structural properties of a tissue?
- What is the combined role of mechanics, geometry, and growth in morphological pattern formation?

2.4 A Short History of Growth Modeling

A brief summary of key discoveries connecting growth to mechanics and mathematics is given in Table 2.1.

On the modeling side, there have been many attempts to include the effects of growth and remodeling in biological materials [21]. The plant physiologists from the nineteenth century were interested in the coupling of mechanics and growth in plants. Among others, the textbooks of Sachs and Müller include growth data, elastic measurements such as Young's modulus, and the yield stress, as well as discussions on the role of physical stimuli in phenomena such as gravitropism, thigmotropism, circumnutation, aerenchyma, heliotropism, and tissue tension [45, 261, 412, 924, 1107]. However, no mathematical modeling was proposed, and the physical approach to plant physiology was replaced in the twentieth century by genetics and biomolecular considerations, as found in modern textbooks [1215].

Table 2.1 Early history of growth studies.

Year	Scientist	Study
1638	Galileo	First discussion of scaling
1758	du Monceau	First description of tip growth
1759	de Montbeillard	Record of height from birth to 18 years
1825	Gompertz	Population growth model
1832	Bourger	Connection between bone and mechanics
1835	Quetelet	Population study and power laws
1838	Moseley	Mathematical description of seashells
1839	Sarrus & Rameaux	Allometric law for energy with respect to area
1848	Brucke	First description of residual stress in plants
1867	Davis	Law for soft tissue remodeling
1870	Wolff	Mathematical law for bone design
1875	Sachs	"Textbook of Botany"
1875	Cohn	Tip growth in actinomycetes
1880	Roy	Nonlinear response, pre-stretch in arteries
1881	Roux	Functional adaptation principle applied to bone
1888	His	"On the Principles of Animal Morphology"
1892	Woods	Mechanical role of wall stress in heart
1892	Reinhardt	Description of tip growth in microorganisms
1893	Thoma	Remodeling of arteries
1897	Dubois & Lapicque	Brain mass with respect to total mass
1913	Nutt	"Diseases and Deformities of the Foot"
1917	D'Arcy Thompson	"On Growth and Form"
1920	Pütter	Growth viewed as an energy balance
1926	Cannon	Concept of homeostasis
1932	Huxley	"Problems of Relative Growth"
1941	Medawar	Principles of growth
1947	Kleiber	Metabolic rate scaling with mass
1957	von Bertalanffy	Growth model

One of the earliest attempts to develop a mathematical model taking into account the combined action of mechanics and growth, is found in the work of Lockhart on plant cell wall growth [798] and in the theoretical work of Hsu [627]. But the pioneer work in shaping a theory of growth was developed by Cowin and Hegedus, with a theory of adaptive elasticity for bones [239, 246, 247, 855], and, in the same period, by Murray, Maini, and coworkers in their models of wound healing and mechanical pattern formation [926, 929, 1243].

The general idea that growth can be modeled by considering the effect of both changes in mass and elastic deformations in a body can be traced to several theoretical works [307, 335, 627, 1190]. However, it was through the seminal work of Skalak, Hoger, and coworkers that a full theory of growth based on the foundations of continuum mechanics took shape [1171–1173, 1175, 1242]. They showed that by considering growth as a mapping from an initial configuration to a new reference configuration, the theoretical concepts of kinematics, such as velocity, velocity gradient, deformation gradient, and so forth, can be used to quantify both the evolution of a body and its response to mechanical loads. These lines of thought culminated in a general statement of growth [1091] in terms of the so-called *multiplicative decomposition of the deformation gradient*, a formulation that was previously confined to dislocation theory and elasto-plasticity [176, 179, 730, 777, 810, 933]. The fundamental idea of Rodriguez et al. [1091], which can also be found in [225], is that the deformation of a body can be decomposed into a growth step that describes the local addition of a material, and an elastic response, characterizing the reorganization of the body needed to ensure compatibility and integrity. Key to this approach is the fact that stresses generated through growth depend solely on the elastic step and can be computed by the theory of nonlinear elasticity. This early work on growth has since been amply discussed [242, 306, 636] and there have been a number of attempts to formalize it [284, 341, 811, 1350]. This kinematic theory is now the starting point for a large body of scientific literature and it will be explored in detail in this monograph [240, 422, 709].

Despite progress in this field, it has been commented by many authors [26, 1208] that one of the key remaining challenges is to develop a constitutive theory for the relationship between growth and mechanical variables such as stresses and strains. The criticism is that the kinematic approach of Rodriguez et al. is mostly a geometric modeling of growth that does not address the microscopic process by which growth occurs. Humphrey, Rajagopal, and coworkers [447, 635, 637, 639–641] have advocated that growth should be modeled within a mixture theory by following mass production, resorption, and remodeling of individual constituents. In this approach, growth is then represented by the evolution of separate natural configurations and the differences between these configurations lead to residual stress.

2.5 A Review of Reviews

There are a number of excellent reviews and introductory courses on the modeling of biological growth that are worth mentioning as a guide to the literature.

The first review of growth modeling is due to Larry Taber [1206]. This seminal review covers a great number of biological and physiological systems with detailed descriptions of the phenomena observed as well as a description of various models. Despite the fact that the field has expanded considerably since its initial publication, it remains a must-read for anybody interested in the subject.

Stephen Cowin has authored a number of interesting reviews focused mostly on aspects of adaptive elasticity, with a special emphasis on the response of cartilages and growth in bones, and the scaling of growth. It also includes fascinating historical perspectives not found in other reviews [241–244].

Krishna Garikipati gives a nice review of different aspects of the kinematics of growth, including both a thorough discussion of accretive growth and a critical discussion on the assumption of behind the multiplicative decomposition [421]. Garikipati is also the lead author of a multi-author review discussing and contrasting various aspects of a theory of growth [21].

Gareth Jones and Jon Chapman have coauthored an excellent review on growth containing comprehensive discussions on cell division, growth models, a comparison of different discrete computational models, and new ideas on how to combine these discrete models with their continuous counterparts [672].

Ellen Kuhl and Andreas Menzel, give in a number of reviews, a complete description of the theory of multiplicative decomposition and fiber anisotropy from a theoretical and computational perspective including many beautiful applications to bones, arteries, the heart, the brain, muscles, tendons, lungs, and skin based on their own modeling and computational work [349, 733, 873].

Jay Humphrey and colleagues, have discussed, in a series of reviews, the need for mixture models for growth and remodeling, with special emphasis and details on arteries and aneurysms [44, 635, 636, 638].

Finally, Marcelo Epstein authored an excellent chapter on the problem of growth in his book [339]. It includes an exhaustive discussion of the kinematics of multiplicative decomposition, widely used to describe growth and residual stress, and shows how such a decomposition naturally follows from basic kinematic assumptions and material symmetry.

Chapter 3

Discrete Computational Models



Since cells are responsible for most of growth in biological systems, it is natural, as a first step, to develop computational models of growth focused on the interaction of discrete entities, either representing the cell itself, or parameterizing the cells through its boundaries. These discrete computational models have been particularly helpful for biologists interested in developmental processes and pathology [895]. In particular, they have helped validate the differential adhesion hypothesis in cell sorting that states that two populations of cells will arrange themselves in separate phases based on their respective binding energy [128–130, 376, 1191]. We provide here a brief overview of different discrete approaches to model growth.

3.1 On-Lattice Models

3.1.1 Cellular Automata

The first attempts to develop computational models of growth were based on cellular automata. These models first introduced by von Neumann and Burks [945], and popularized by Conway's *Game of Life* [224], found their way in statistical mechanics [1336] and biology [347]. The basic idea of cellular automata for biological systems

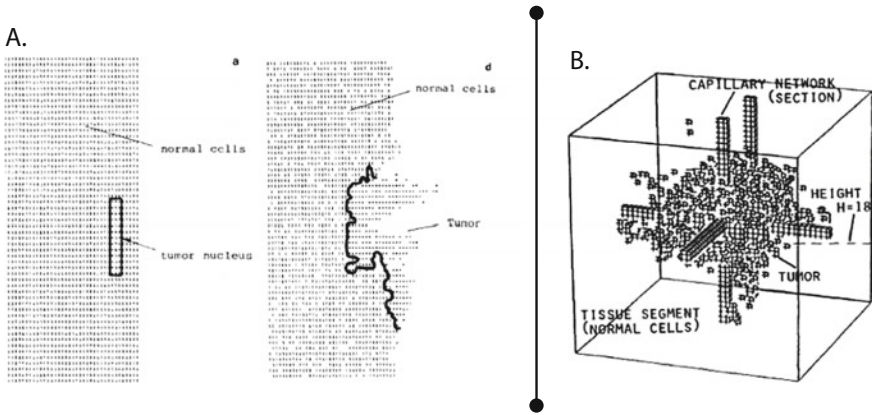


Figure 3.1 Cellular automata model of growth. A. In two dimensions, each square represents either a normal or a tumor cell. Cells change type following rules dependent on their neighbors. B. In three dimensions some of the lattice positions can be used to represent a capillary [310].

is that the domain of interest is divided into a number of lattice sites occupied by cells. At each discrete step in time, the lattice is updated based on rules of interaction between different cells.

For instance, the growth of cancer cells shown in Figure 3.1 is modeled by considering two types of cells: normal and tumor cells. Each cell occupies a position in a two-dimensional square or three-dimensional cubic lattice. Depending on the availability of free space, the nutrient, and other internal variables, each cell may change its internal state at each time step. Based on appropriate rules, cell growth and death are modeled by adding cells into a free space, removing a necrotic cell, or changing a normal cell to a tumor cell.

There are well-known problems with cellular automata: The symmetry emerging from these interaction rules typically follow the underlying symmetry of the lattice, and mechanical and diffusion effects cannot be easily taken into account. Attempts to overcome these problems include using irregular lattices [832], using density as a surrogate for pressure [1050], and computing underlying concentration fields separately [14].

3.1.2 Cellular Potts Models

An alternative method to use lattices to model cells is to assume that a cell occupies different lattice sites. In these *cellular Potts models*, a cell location is defined by several adjacent lattice sites. As the cell moves, grows, or deforms, the set of lattice coordinates that defines the cell evolves. This evolution is determined by a minimization process of a scalar function analogous to an effective energy in physical models. This pseudo-energy is a sum over the entire system and contains terms to

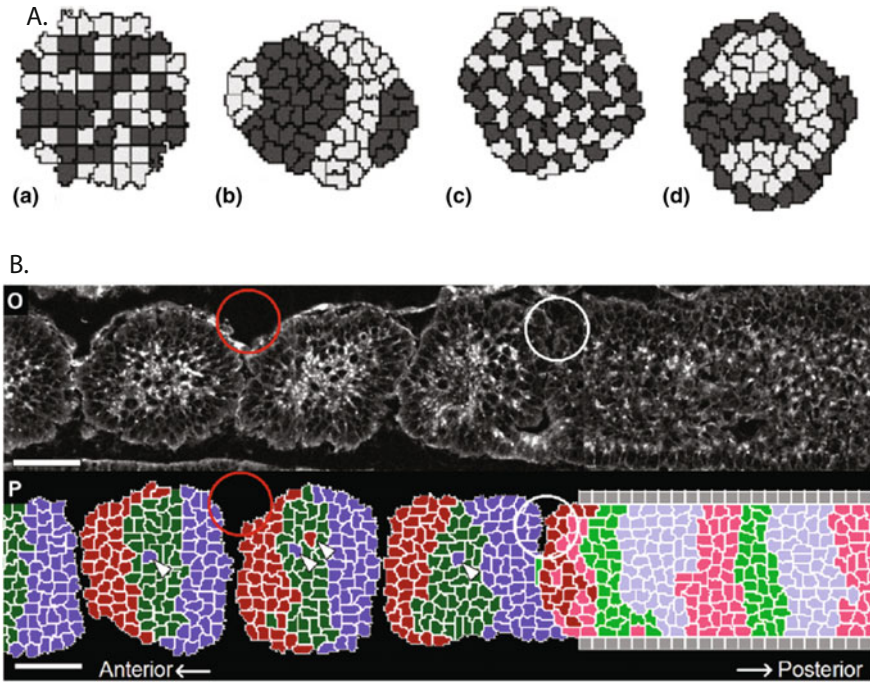


Figure 3.2 Cellular Potts models. A. Different types of cell patterning can be obtained by changing either cell–cell binding energy or cell–matrix binding energy. (a) Initial conditions, (b) cell sorting, (c) mosaic cell ordering, (d) engulfment. B. Application to vertebrate segmentation and somite formation. O: Confocal image of one half of the presomitic mesoderm in a live chick embryo (scale bar is 50 μm). P: corresponding cellular Potts simulation. The simulated morphology reproduces the basic features of the morphogenetic process (reproduced from [571, 876]).

penalize binding, volume changes, and boundary changes. The role of internal cell pressure is introduced by assigning a target volume to each cell. The volume term in the effective energy is minimized when the cell reaches its target volume.

The actual process by which cell dynamics is computed is performed by a stochastic modified Metropolis algorithm. It consists in randomly selecting two sites and accepting probabilistically a change of cell type based on the difference in energy that would result in this change. The change is automatically accepted if the energy after change is lower than a given energy threshold and accepted with a decaying exponential probability if it is higher.

Growth is implemented by changing the target volume, so that, over time, the energy is decreased if the volume is increased. Examples of cell dynamics modeled by such processes are given in Figure 3.2.

The introduction of cellular Potts models has resolved many issues of cellular automata and helped scientists to either validate basic hypotheses in cellular biology or explore the interaction of biological systems with multiple cell types [1134, 1205]. Yet, these methods require the introduction of many interaction rules and since the

pseudo-energy of the system is not a true energy, the exact form of different effects is somewhat arbitrary and cannot be derived from first principles. In particular, the correct application of loads and the inclusion of forces and stresses in these systems remain problematic.

3.2 Off-Lattice Models

3.2.1 Center Dynamics Models

An alternative description for the interactions between N discrete cells is to assume that cells are either spherical in three dimensions, or circular in two dimensions. Restricting our discussion to the planar case, the positions of the cell centers, $\{\mathbf{r}_i \in \mathbb{R}^2, i = 1, \dots, N\}$, fully characterize the entire system. The cell centers can either be seen as the center of overlapping circles or, equivalently, as the centers of Voronoi polygons in a tessellation of the system as shown in Figure 3.3. A two-dimensional *Voronoi tessellation* is a partitioning of a plane into polygonal regions based on distance to points in a given set. Each edge of a polygon is defined as the set of points closer to a particular point than to any other [608].

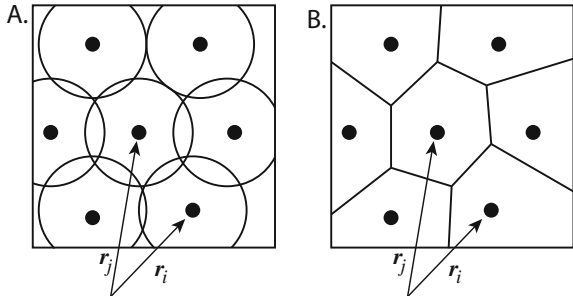
The dynamics of this model is produced by the interaction between cells following the equations of motion

$$m_i \ddot{\mathbf{r}}_i = \mathbf{F}_i - v_i \dot{\mathbf{r}}_i - \sum_{j=1, i \neq j}^N v_{ij} (\dot{\mathbf{r}}_i - \dot{\mathbf{r}}_j), \quad i = 1, \dots, N, \quad (3.1)$$

where m_i is the mass of the i -th cell, v_i the drag coefficient between cell and medium, v_{ij} the friction coefficients between cell i and cell j , and $\mathbf{F}_i$ the net force acting on the i -th cell (excluding drag). Here $\dot{\mathbf{r}}_i$ and $\ddot{\mathbf{r}}_i$ represent the first and second derivatives of the position with respect to time, respectively. Typically, biological systems are overdamped, in which case, the left-hand side terms can be neglected.

The key difficulty in modeling a system of interacting cells is to make the proper choice for the friction coefficients v_{ij} and the force $\mathbf{F}_i$ acting on each cell. Many

Figure 3.3 Configuration of cells represented either as A. overlapping spheres or B. a Voronoi tessellation (adapted from [672]).



different functional forms of forces have been proposed to capture the basic effects of repulsion when the cells are overlapping, adhesion at short range, and vanishing interaction at long range [299, 672, 1006]. Once the force is postulated, the dynamics is obtained by integrating forward the system of differential equations (3.1). If the forces derive from a potential, stochastic effects can be easily included using a Monte Carlo approach [298, 301].

Growth is implemented by assuming that certain cells undergo mitosis [107]. As the cell volume is increased, it will reach a critical size at which time it will be replaced by two smaller cells with the same volume. At this point in time, a new cell is added to the system [300, 1058]. This process can take place while keeping the spherical symmetry, or in small increments transforming a sphere into a dumb-bell shape as shown in Figure 3.4.

Center dynamics model have been used to model a number of multicellular systems such as intestinal epithelia [859], growing population of tumor cells [156], the regeneration of liver tissues [589], slime mold cells migration and response to loads

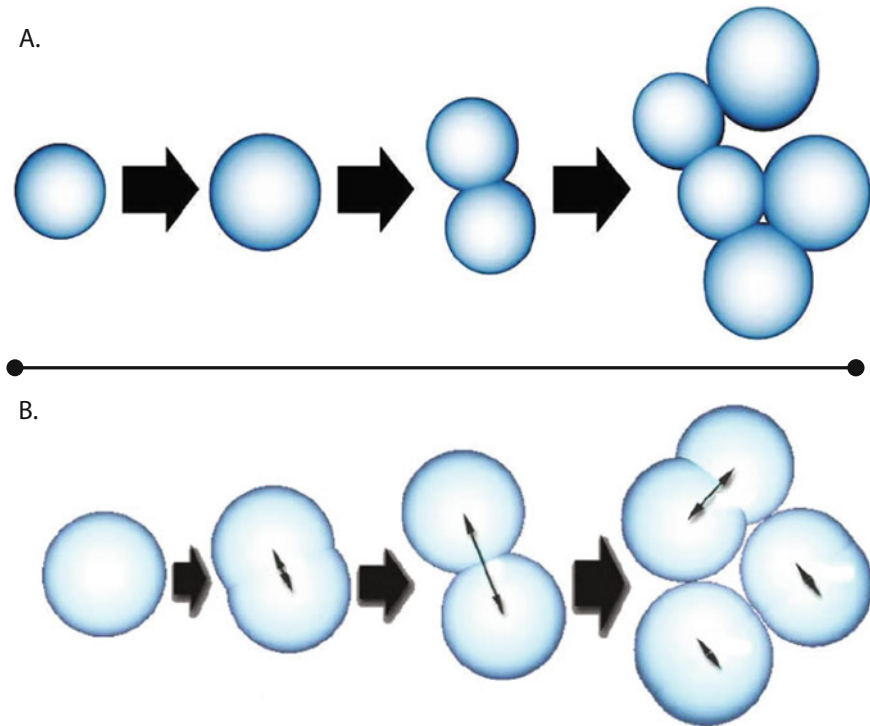


Figure 3.4 Growth in center dynamics models. A. The radius is first increased to mimic the doubling of the cell volume and a daughter cell is added to the system. B. During cell division, a cell deforms from a perfect sphere into a dumb-bell in small steps. When the dumb-bell reaches a certain size, it divides into two cells (adapted from [300]).

[258, 1005]. These methods remain an important part of cellular modeling and are continually refined and generalized.

One of the main drawbacks of these methods is the difficulty in choosing the correct interaction potential between cells. While many choices seem plausible at a microscopic scale, the overall macroscopic behavior can lead to unphysical effects. For instance, it was shown that if the attraction from next-nearest neighbors is too large, the repulsion of nearest neighbors may not be sufficiently large to overcome an overall attraction of the cells leading to massive cell overlap [1020]. In this last publication, the authors further demonstrate that the response under loads may show undesirable effects, especially under shear where the tissue may rupture. Nevertheless, these models are useful for exploring the behavior of cell population at the discrete level.

3.2.2 Vertex Dynamics Models

In center dynamics model, the cell wall or cell membrane is characterized by either a fixed distance from the center or by its Voronoi tessellation as shown in Figure 3.3. Since both the shape of a cell and its interactions with other cells depend on its interface, an alternative way to model packed cells is to follow their interfaces. In these *vertex dynamics models*, cells in two dimensions are defined as polygons and the positions of all vertices are the main dynamical variables in the model. These models assume that cells are tightly packed so that each vertex is either the boundary between two cells or part of the domain boundary. They are particularly suited to model the various forces acting on cell membranes.

Consider a system of N polygonal cells with a total of M vertices. Each cell has an area A_α and perimeter L_α where $\alpha \in \{1, \dots, N\}$. As shown in Figure 3.5, an edge joining vertex i to vertex j has length l_{ij} and line tension t_{ij} . We model the mechanical response of this system by introducing an energy function of the form

$$W = \sum_{\alpha=1}^N \frac{\mu_\alpha}{2} (A_\alpha - A_\alpha^0)^2 + \sum_{i=1}^{M-1} \sum_{j=i+1}^M t_{ij} l_{ij} + \sum_{\alpha=1}^N \frac{\nu_\alpha}{2} L_\alpha^2, \quad (3.2)$$

where A_α^0 is a target area and μ_α plays the role of an elastic area stiffness as it describes the work stored in a cell when the area is modified away from its preferred target area. The last term describes the boundary energy with a coefficient ν_α that describes the contractility of the cell boundaries. A change in adhesion between cells can be modeled by varying the tension t_{ij} . From the energy W , the forces acting at each nodes can be derived as

$$\mathbf{f}_i = - \frac{\partial W}{\partial \mathbf{r}_i}. \quad (3.3)$$

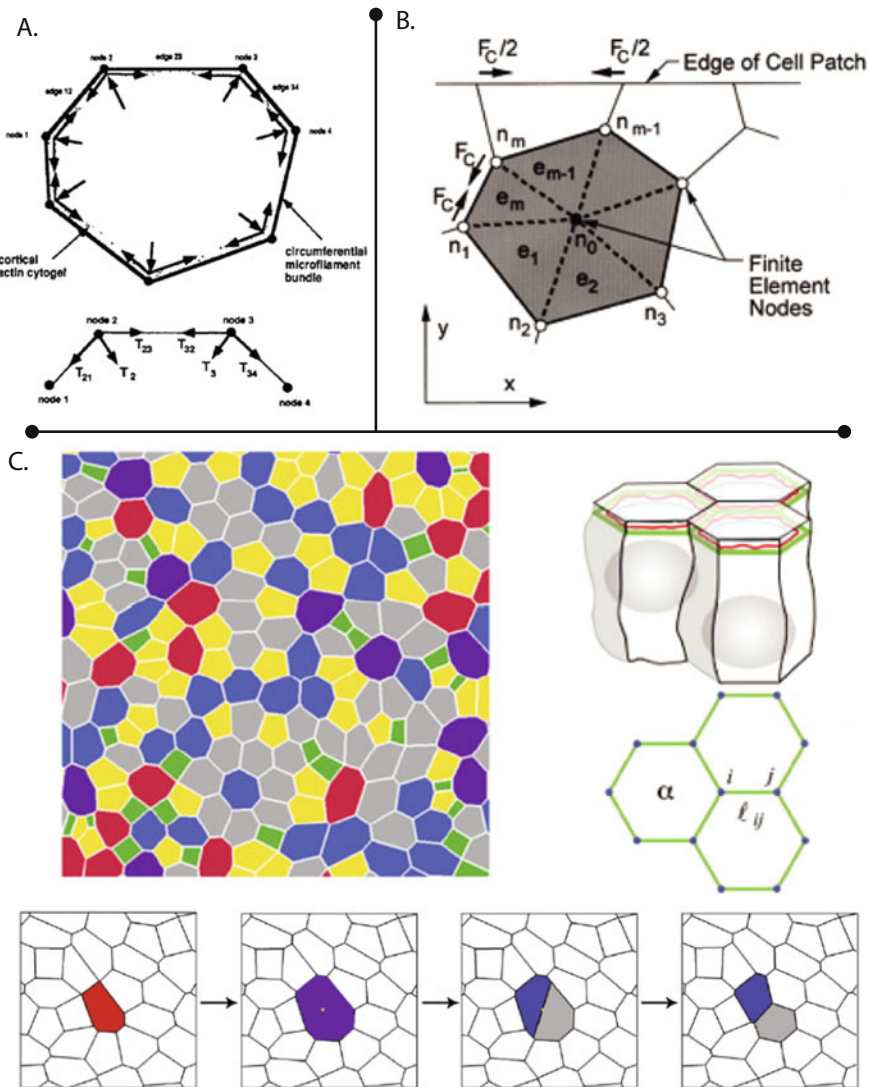


Figure 3.5 Vertex dynamics model. The cell is represented by its edges. On each vertex a force vector is defined and used for the global force balance. A. Original model of Weliky and Oster [1310]. B. Model developed by Chen and Brodland [192]. C. Epithelia are sheets of columnar cells connected via cell-cell adhesion [356]. Left. Example of a stationary network patterns generated by repeated cell division. Bottom: rules for cell division. A cell increases its volume up to a critical size, at which point, a new cell is created.

At equilibrium, these forces must vanish, which can be accomplished numerically by integrating the Newtonian equations for each vertices in the presence of strong damping. The dynamics of a set of cells can be simulated by either deterministic integration of Newton's equations or by stochastic Monte Carlo methods.

Growth in vertex dynamics models is implemented by two different processes. First, the target areas of individual cells can be changed to simulate the enlargement of cells. Second, when a cell is sufficiently large, cell mitosis is modeled by introducing new vertices and edges in order to create new cells divide [131, 609]. Special rules about how cells divide and where division occurs need to be implemented as shown in Figure 3.5C. After division, each new cell is assigned a new target area.

3.2.3 *Advantages and Drawbacks*

Discrete, cell-level, models have the advantage to use directly information about cells, their behavior and their interaction with other cells. Depending on the type of cell assemblies, different methods should be considered. In a tight packing assembly with well-defined boundaries, vertex dynamics models are suitable, whereas for dilute collection of cells, center dynamics models are preferred. In two dimensions, these models can be easily implemented leading to interesting emerging global behaviors from simple local interactions. This computational framework constitutes an ideal platform to test biological hypotheses, to explore the importance of different local effects, and to suggest new behaviors in different parameter ranges.

However, discrete models, are still in their infancy and suffer from a number of problems. While two-dimensional simulations can be readily implemented, as soon as the geometry of cells is not spherical, three-dimensional simulations represent a major computing challenge [896]. Keeping track of the correct geometry, the neighbors, and their interaction requires dedicated algorithms that robs the interested scientist of the original appeal of this approach. However, a number of authors have taken on the challenge and produced convenient software packages to help with the process [194, 580, 646, 1153].

Another issue is the observed macroscopic behavior. It is well understood that starting from a continuum formulation of a problem we can obtain systematically different discrete versions of the problem. However, starting from discrete systems, there is no systematic way to obtain a continuum version of the problem. It could be argued that biological systems do not have a continuum equivalent. Yet, assembly of cells and tissues can be tested mechanically as a continuum using classical means. We should expect that the characterization of tissues at the macro-scales could be informed by the discrete interactions of their components. This connection is still lacking and remains one of the main stumbling block in linking cellular properties to tissue properties.

The specification of interaction rules can also become an issue. While it is relatively easy to formulate plausible rules based on educated guesses, it is not clear that these rules can be easily validated and quantified at the microscopic level. Discrete

models rely not only on basic principles dictated by a pseudo-energy but they also rely on many evolution, geometric, and interaction rules. Each rule is typically encoded by several parameters and the total number of parameters quickly increases with the complexity and dimensionality of the problem. In many instances, it is tempting for the researcher to add new rules to obtain expected behaviors. The problem is then to decide whether discrete models can be reliably used as a predictive tool rather than a way to mimic known observations. Strict guidelines on how to set working hypotheses for these models do not exist as the final product is obtained iteratively by adding new components, new rules, new species, and new physical effects.

Nevertheless, since the main ingredients in discrete modeling can be directly related to biological experiments and the output is mostly visual, these computer models are a perfect discovery vehicle for multidisciplinary collaborations with biologists. As such they constitute an important toolbox to explore the dynamics of cells and tissues [895]. For these reasons, discrete models have been and will continue to be extremely successful, especially in developmental biology.

Part II

Filament Growth: A One-Dimensional Theory

*And then the lover,
Sighing like furnace, with a woeful ballad
Made to his mistress' eyebrow. Then a soldier,
Full of strange oaths, and bearded like the pard,
Jealous in honour, sudden, and quick in quarrel,
Seeking the bubble reputation
Even in the cannon's mouth. . .*

Chapter 4

Growing on a Line

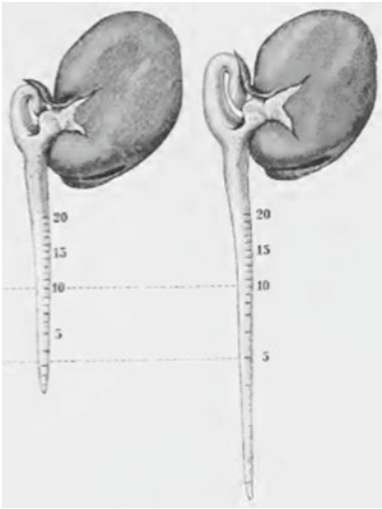


Filamentary structures can be observed in nature at all scales, from the microscopic chains of molecules, to the gigantic braided magnetic flux tubes in solar flares [83, 1185]. They are three-dimensional objects that are characterized by one length scale much larger than the other two scales. Due to their geometric similarities and despite their widely different length scales and microscopic structures, filaments of all sizes grow, move, and change shape and topology according to universal laws [682]. For example, a sufficiently twisted rope will coil on itself [1362]. The same change of configuration is observed to occur in bacterial fibers, DNA molecules [1228] and telephone cables [58, 478]. Understanding the dynamics and growth in these fundamental structures is not only of intrinsic theoretical interest, it also lies at the heart of a host of important processes in biology [84, 826], physics [1163], and engineering [561].

Here, we consider the modeling of growth as it applies to various biofilaments such as bacterial fibers [473], bacterial filaments [1139], fungi [90, 1088], root hairs [1095], stems [59, 910], roots [921, 980], tendrils [477, 684], neurons [758], umbilical cords [461, 890], tendons [1059], arteries [18], and the spine [335].

Filamentary growth can occur essentially in three different ways. First, filaments can extend axially as shown in Figure 4.1; that is by increasing the length of the

Figure 4.1 Axial growth of a root. Growth acts by extending the length of the filament. Adapted from [1035].



filament’s centerline. This change in length can be localized at the tip as discussed in Section 1.1.1 or distributed along the length, especially when the filamentary structure does not grow against a dense medium [756, 866, 1139].

A second type of growth occurs if the thickness or the density of the filament increases. In this case, the filament adds mass without changing its length, leading for instance to the formation of growth rings in trees [378–380]. This process, known as *secondary growth*, is typically found in plants where it takes place after an initial period of axial extension.

A third type of growth occurs when points in a cross section of a filament grow axially at different rates. Then, differential growth takes place and the structure may develop curvature and torsion [67]. A simple physical analog of growth-driven curvature is found in the thermal buckling of a bimetallic beam first studied by Timoshenko [1235] as shown in Figure 4.2. In that process, two straight metallic

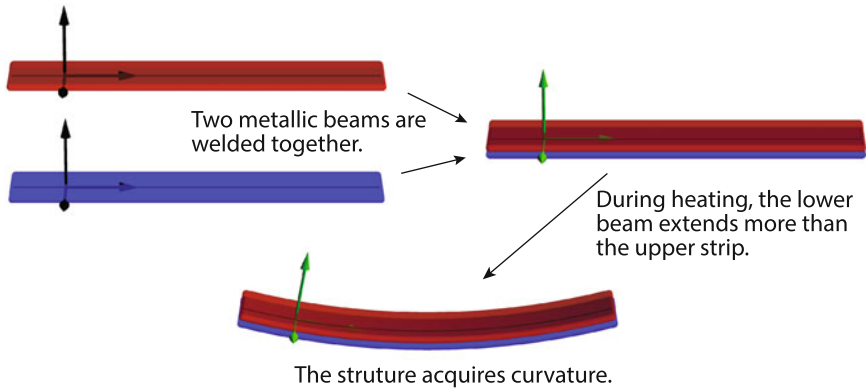


Figure 4.2 Bilayer metallic strips curve due to the difference in thermal expansion of the two materials.



Figure 4.3 Gravitropism. A plant turned on its side will change growth direction by developing curvature (adapted from [1035]).

beams with different thermal expansion coefficients are fastened together. Under a change of temperature, one beam expands faster than the other and induces curvature for the entire structure [149, 150]. In biological systems, differential growth acts mechanically in a similar fashion. For instance, in plants, variation of growth rates in the section of a stem, branch, or root is the main mechanism responsible for the *gravitropic response*; that is, the ability of plants to redirect their overall growth direction vertically [68, 69, 415, 562, 911]. If a stem of *Impatiens glandulifera* (policeman's helmet) is turned on its side as shown in Figure 4.3, it will react by growing faster on the lower side than the upper side until it is aligned with the direction of gravity [740].

In a three-dimensional setting, curvature is closely coupled to torsion. If differential growth does not occur symmetrically in a cross section, it will induce torsion and twist as well as curvature, resulting in *helical growth*. This phenomenon is observed in twining vines, [1156, 1161] but also in bacteria [866] as shown in Figure 4.4, fungi [483], and in plants [75, 155, 470].

At the mathematical level, the growth of biological filaments involves interesting aspects of curve dynamics [914]. A natural starting point for the modeling of

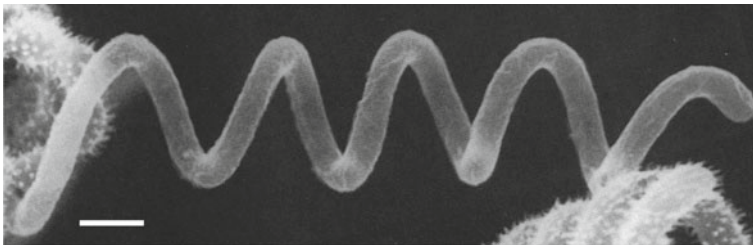


Figure 4.4 Helical growth. The aerial growth of *Streptomyces violascens* shows clear helical structure, Bar is 1.0 μm [1].

biofilaments is to consider them as slender elastic rods subjected to external constraints. The basic idea is to perform an average over a cross section of the forces acting on the filament and then define a resultant force acting on the centerline of the rod. This procedure leads to the Kirchhoff equations [33, 221, 285, 478, 1282], relating averaged forces and moments to the curve's strains characterized by the curvatures, shears, and axial extension. These equations provide the starting point for much theoretical analysis and numerical modeling and will be discussed at length in Chapter 5 and 6.

The theory of growing three-dimensional structures requires great care. Growth, through incompatibility, naturally changes the underlying geometry and induces local residual stress. A full mechanical and geometric theory is needed to capture these fundamental aspects of volumetric growth. This general theory will only be developed in Part IV.

If a one-dimensional structure is allowed to grow both axially and in girth, no residual stress can be created and the effect of growth can easily be captured by a slight generalization of the classic theory of elastic rods, taking into account variations in arc length and changes in material properties. Therefore a natural starting point is to develop a general framework for growing material in one dimension.

4.1 Example: A Growing Rod in One Dimension

Rods are elastic structures that can support bending, twisting, stretching, and shearing. However, when restricted to deformations in one dimension, rods support only stretching. When allowed to grow this stretch can be due to either elastic deformation or extension due to an increase of mass.

Figure 4.5 shows a rod where a material point is parameterized by S_0 , denoting its arc length in an initially unstressed configuration from one end at time $t = 0$. This rod can change its length in time and a point initially at a position S_0 is located in the current configuration at time t at a position $s = s(S_0, t)$. Accordingly, the total

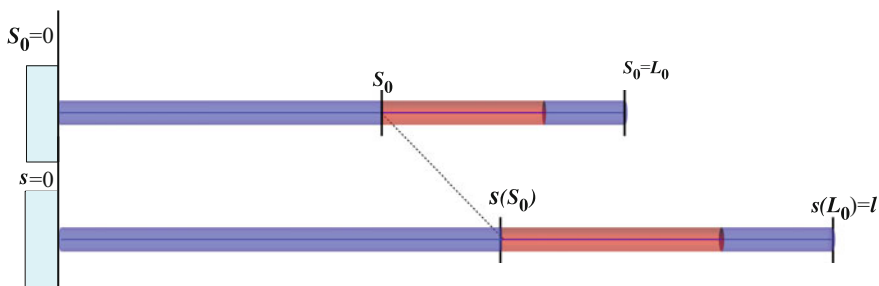


Figure 4.5 Extension of a filament constrained in one dimension. Initially of size L_0 , the filament changes its length due to growth, stretching, or a combination of the two to reach a new size l .

length at time t is $l = s(L_0, t)$, where L_0 is the initial length. Assuming that the change in length at all points is smooth enough, the local change of length is given by the *stretch*

$$\lambda(S_0, t) = \frac{\partial s}{\partial S_0}. \quad (4.1)$$

If all segments of the rod experience the same stretch so that the deformation is uniform, λ is constant, in which case $\lambda = l/L_0$. In general, wherever $\lambda > 1$, there is a local increase in length with respect to the initial configuration, whereas $\lambda < 1$ represents a local decrease in length.

In the context of growing elastic structures, a change in length can be due to either growth or elastic stretching due to tension or compression. These processes are very different and we first consider them separately.

4.2 Purely Elastic Deformations

In a purely elastic deformation, the elastic energy stored by stretching or compressing the rod can be recovered when the loads are removed. In such a case, we denote this *elastic stretch* by α and since it is the only type of deformations admitted, we have $\lambda = \alpha$. The value of α for a given load and a given material is specified by a *constitutive law* that relates stresses to strains. In general, a *stress* is a force per unit area. In our one-dimensional setting, the only relevant stress, σ , is the force acting on a cross section, along the axis, divided by the cross-section area. Here, we further assume that this area does not change during the deformation. A *strain* is a measure of the deformation. A simple choice for the strain is $\epsilon = \alpha - 1$ so that in the absence of deformations an unstretched rod, i.e., $\alpha = 1$, has no strain, i.e. $\epsilon = 0$.

For illustrative purposes, we start by assuming a spring-like Hookean behavior, that is, we assume that the stress is proportional to the displacement:

$$\sigma = E\epsilon = E(\alpha - 1). \quad (4.2)$$

The parameter E is the *Young's modulus*. In the general theory of elasticity, the Young's modulus is a measure of the stiffness of a material. It is defined as the ratio between a uniaxial stress and the corresponding uniaxial strain in small deformations. Assuming that E is constant along the rod, this relationship completely specifies the deformation as a function of the applied stress σ , that is, we have

$$\sigma = E \left(\frac{\partial s}{\partial S_0} - 1 \right) \implies s = \left(\frac{\sigma}{E} + 1 \right) S_0, \quad (4.3)$$

and the current length is $l = (\sigma/E + 1)L_0$.

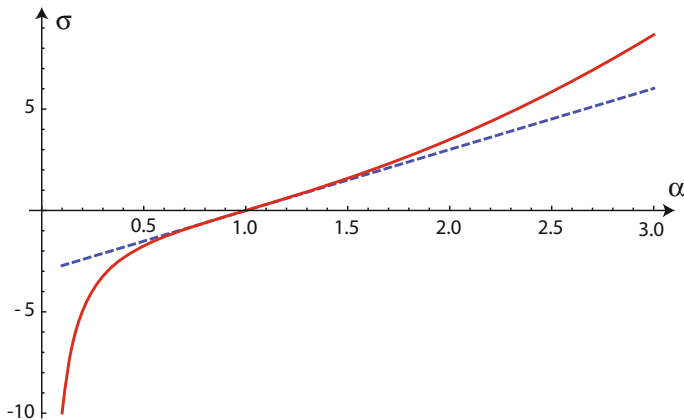


Figure 4.6 Stress–stretch curves. Comparison between the linear Hookean (dash) and nonlinear (solid) response of a filament for $\mu = 1$, $E = 3$ in arbitrary pressure units. Note how the nonlinear response captures the expected behavior of a solid in high compression for which increasingly large compressive stresses are needed to further compress the material.

It is important to realize that the Hookean law (4.2) is only valid for small deformations. In larger deformations, it predicts that a finite compressive stress of $\sigma = -E$ would shrink any line element to a point ($\lambda = 0$), a clearly unphysical behavior.

This law can be corrected for large deformations by using the theory of three-dimensional elasticity. We will show in Section 11.8.1 that the uniaxial extension of an incompressible rectangular *neo-Hookean* bar leads to the following nonlinear law for the extension of a filament:

$$\sigma = \mu(\alpha^2 - \alpha^{-1}), \quad (4.4)$$

where μ is the *shear modulus*. Close to $\alpha = 1$, we recover a linear behavior that justifies the use of the Hookean model. In that regime, we can also identify the relationship, $E = 3\mu$, between the shear modulus and Young’s modulus as shown in Figure 4.6. In general, materials that show strain stiffening, that is, an increase in stiffness for large deformations, or strain softening, a decrease in stiffness, can be modeled by various functions of the stretch, in which case the constitutive response in one dimension will be given by the general relationship

$$\sigma = f(\alpha), \quad (4.5)$$

with the requirement that $f(1) = 0$. For such systems, the Young’s modulus is defined as $E = f'(1)$ and represents the linearized behavior for small deformations around the stress-free state.

4.3 Growth Without Elastic Deformations

If a rod grows in the absence of applied loads and elastic response, it will increase in length. This change in length can be described by a local *growth stretch* analogous to the elastic stretch, that is, $\lambda = \gamma$. In a growth process that takes place in time, the function γ evolves with time, so that $\gamma = \gamma(t)$. It is often easier to describe such processes as an evolution law describing the addition of mass occurring in a small increment in time. Therefore, we postulate the existence of an *evolution law* of the following form:

$$\frac{\partial \gamma}{\partial t} = G(\gamma, s, S_0). \quad (4.6)$$

For example, *uniform linear growth* is achieved by taking $G = 1$, in which case $s(S_0, t) = tS_0$. If the rod is made of cells that reproduce at a constant rate and each new cell can reproduce again, the rate of growth is proportional to the local growth stretch:

$$\frac{\partial \gamma}{\partial t} = k\gamma, \quad (4.7)$$

which results in *exponential growth* of the rod

$$s(S_0, t) = S_0 e^{kt}, \quad l(t) = L_0 e^{kt}, \quad (4.8)$$

and we identify k as the relative growth rate introduced in Section 1.3.

4.3.1 Example: Tip Growth

Tip growth is a generic mechanism for many growing biofilaments as described in Section 1.1.1. A detailed description of the mechanisms underlying tip growth is given in Section 9.2.1. Here, we consider the kinematic description of an arbitrary growth process localized at the end of a one-dimensional structure. The universal feature of tip growth is that addition of mass occurs only at the end, which in the simplest case can be described by the function

$$G(\gamma, s) = \gamma k (1 - H(s - a)) = \begin{cases} \gamma k & 0 < s \leq a, \\ 0 & a < s < l, \end{cases} \quad (4.9)$$

where $H(\cdot)$ is the Heaviside function and $a > 0$ is the length of the growing zone. In many respects, this simple model contains some of the difficulties that we will encounter later. The main problem is that the position s of a material point S_0 changes as a function of time, so that $s = s(S_0, t)$ and the equation $\partial_t \gamma = G = g\gamma$ cannot be directly integrated. At $s = a$, we have a moving interface between a growing

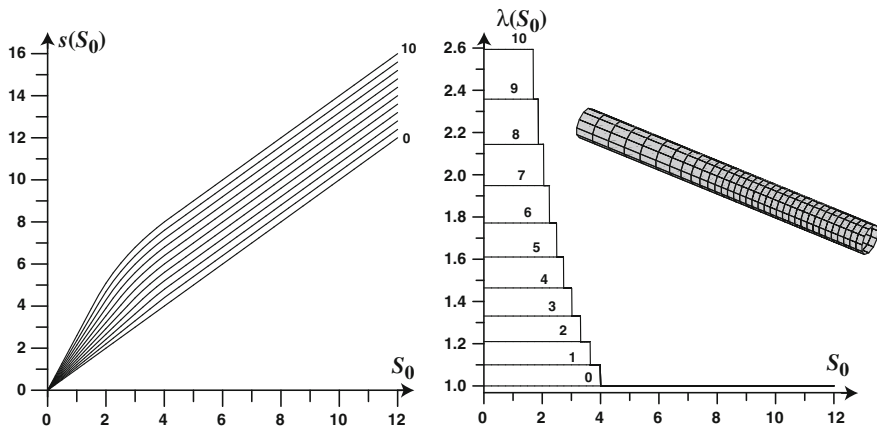


Figure 4.7 A simple kinetic model of tip growth obtained from the integration of Equation (4.13) with $\Delta t = 0.1$, $a = 4$, $k = 1$, and initial length $L_0 = 12$. Here, 10 successive iterations are shown. The grid on the filament corresponds to equidistant material points in the initial configuration.

and nongrowing material. An efficient way to solve the problem is to consider the coupled system

$$\frac{\partial \gamma}{\partial t} = g\gamma, \quad (4.10)$$

$$\frac{\partial s}{\partial S_0} = \gamma, \quad (4.11)$$

with initial conditions $\gamma(0) = 1$, $s(0) = S_0$.

Before deriving the exact solution, we can solve this system numerically in time by forward Euler integration

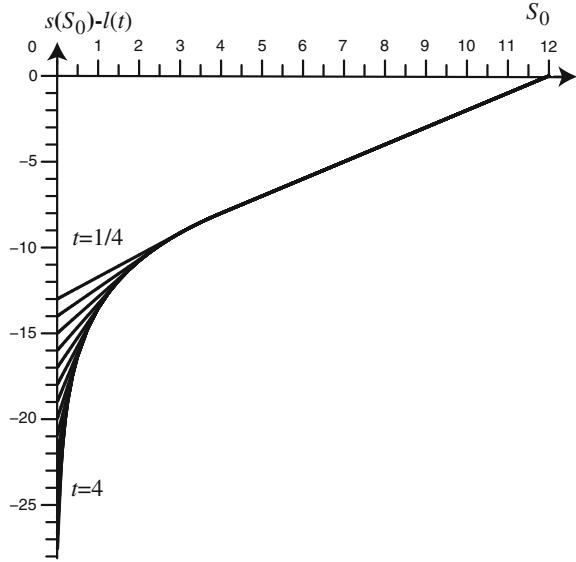
$$\gamma(t + \Delta t) = \gamma(t) (1 + \Delta t g(s(t))), \quad (4.12)$$

$$s(t + \Delta t) = \int_0^{S_0} \gamma(t + \Delta t) dS_0. \quad (4.13)$$

An example of a position profile is shown in Figure 4.7. At each iteration, the growing rod extends its total length by $a(e^{k\Delta t} - 1)$ which, after a time t , amounts to a total increase in length of $a(e^{k\Delta t} - 1)t/\Delta t$. In the limit $\Delta t \rightarrow 0$, this process leads to a linear law for the overall growth $l(t) = L_0 + akt$. Interestingly, despite the fact that the tip is growing exponentially, the overall length increases linearly since the expanding zone remains constant.

Now, consider an initial point at material position $S_0 = P$. If $P > a$, the point is not in the growing region and changing L_0 to P in the previous argument gives $s(P, t) = P + akt$. If $P \leq a$, this point is in the growing region and will move exponentially away from the origin until it reaches the position a , at a time t_c , so

Figure 4.8 The solution to the growth profile, viewed in a reference frame placed at the growing tip, shows convergence to a self-similar solution ($a = 4$, $k = 1$, and $L_0 = 12$). Here, 16 successive iterations are shown from $t = 1/4$ to $t = 4$.



that $s(P, t_c) = a = P \exp(kt_c)$, or equivalently, $t_c = k^{-1} \ln(a/P)$. For $t > t_c$, this point will not be in the growing region and its distance from the origin will increase linearly according to the previous computation. We combine the different position and time intervals together to obtain the general solution:

$$s(P, t) = (P + kat) H(P - a) + \{P e^{kt} [1 - H(t - t_c)] + [a + ka(t - t_c)] H(t - t_c)\} [1 - H(P - a)]. \quad (4.14)$$

With respect to a reference frame placed at the growing tip, we observe a rapid convergence to a self-similar profile as a function of the initial arc length as seen in Figure 4.8. This profile is self-similar in the sense that for large time the function $s(S_0) - l(t)$ viewed as a function of S_0 becomes independent of time.

4.3.2 Application: Spheroid Tumor Growth

4.3.2.1 Background

As an application of the idea of growth in a localized region, we consider a simple model for tumor growth where a spherically shaped tumor expands depending on the level of nutrients diffusing through its boundary. This model is an example of a large

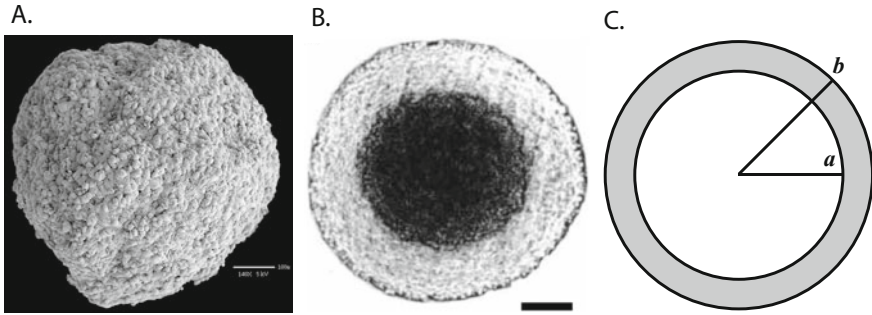


Figure 4.9 Multicellular tumor spheroids. A. Three-dimensional structure. B. Cross section. In a typical spheroid structure, the inner necrotic core is surrounded by a layer of quiescent cells. This layer is itself surrounded by a layer of active cells at the outermost boundary (reproduced from [920], bar is $250\ \mu\text{m}$). C. Simplified geometry of the problem, a core of inactive cells is surrounded by a single spherical shell of active growing material.

class of experimental and theoretical models used in oncology, known as *spheroid models* [385].

As shown in Figure 4.9, cancer cells can be cultured *in vitro* to grow on a gel or in a pool of nutrients to form a sphere-like shape, the spheroid [391, 1203]. These spheroids are of great interest as they can be used in a variety of settings to understand the response of cancer cells under different physical, chemical, and genetic treatments [566, 1116]. Mathematically, the spherical symmetry of these aggregates allows for a simplification of the problem by considering the evolution of the radius; in essence, reducing the problem to one dimension [5, 158, 384, 393, 1098].

4.3.2.2 A Model

We model a tumor spheroid as a time-dependent perfect sphere of radius $b(t)$. Initially, the radial position of a material point inside the tumor is R_0 with radius B_0 and we are interested in the evolution of each point as a function of time, $r = r(R_0, t)$. In particular, we look for the outer radius of the tumor as a function of time, that is, $b(t) = r(B_0, t)$. Since we assume radial symmetry, we can focus our attention on any line from the origin to the boundary of the sphere. We assume that growth is isotropic, that is, there is no preferred direction of growth; a volume element dV_0 initially located at a point R_0 will grow to a new volume element dv at the point $r = r(R_0, t)$ with a volumetric growth coefficient $\eta = \eta(r, R_0)$ dependent either on the type of cells (dependence on the original R_0) or its position r in the sphere:

$$dv = \eta(r, R_0)dV_0. \quad (4.15)$$

Expressing both volume elements in spherical coordinates (so that $dv = r^2 \sin \varphi dr d\theta d\varphi$) and assuming that the sphere remains spherical, the angles in the initial and current configurations are identical. Integrating over these two angles leads to

$$\frac{\partial r}{\partial R_0} = \eta R_0^2 r^{-2}. \quad (4.16)$$

By definition of the growth stretch, we have $\partial r / \partial R_0 = \gamma$, so that

$$\gamma = \eta R_0^2 r^{-2}. \quad (4.17)$$

In the absence of an elastic deformation, this problem is equivalent to the growth of a rod. We assume that at each point, growth is exponential and proportional to the nutrient concentration $u(r, t)$, so that

$$\frac{\partial \eta}{\partial t} = k \eta u(r, t), \quad (4.18)$$

$$\frac{\partial r}{\partial R_0} = \gamma, \quad (4.19)$$

where $u(r, t)$ satisfies the diffusion equation

$$\frac{\partial u}{\partial t} = \frac{D}{r^2} \frac{\partial}{\partial r} \left(r^2 \frac{\partial u}{\partial r} \right) - Q. \quad (4.20)$$

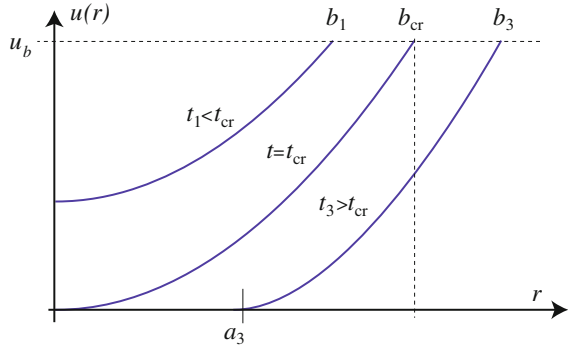
Here, D is the diffusion constant and Q is a constant nutrient uptake. The tumor is assumed to sit in a well-mixed bath of nutrients so that the concentration at the outer surface is $u(b, t) = u_b$. Since this partial differential equation is second order in space, we need a second boundary value. The second condition is $u_r(0, t) = 0$ if $u(0, t) > 0$ or $u(r, t) \geq 0 \forall r \in [0, b]$ if $u(0, t) = 0$. This condition expresses the constraint of no-flux if the concentration at the origin does not vanish and is everywhere positive if the concentration at the origin vanishes.

4.3.2.3 Analysis

Starting with a small size tumor, we expect the nutrients to penetrate all the way to the origin. However, as the tumor grows, it will reach a critical size b_{cr} at time t_{cr} so that the concentration at the origin vanishes $u(0, t_{\text{cr}}) = 0$. Since the concentration remains positive for all time, for $t > t_{\text{cr}}$ the concentration will vanish at a point a with $0 < a < b$ as illustrated in Figure 4.10.

Assuming that the typical diffusion time of nutrients is much faster than growth, it is reasonable to assume that the nutrient concentration has reached equilibrium so that the steady state of Equation (4.20) can be solved exactly. If $b \leq b_{\text{cr}}$, we have:

Figure 4.10 Nutrient concentration as a function of the radius. For $t < t_{cr}$, the nutrient penetrates throughout the entire spheroid. For $t = t_{cr}$, the concentration vanishes at the origin and for $t > t_{cr}$, the concentration vanishes in the region $r < a$ where a necrotic core develops.



$$u(r) = \frac{Q}{6D}(r^2 - b^2) + u_b. \quad (4.21)$$

The critical radius b_{cr} is then defined as the smallest radius for which $u(0) = 0$. This condition leads to

$$b_{cr} = \sqrt{\frac{6Du_b}{Q}}. \quad (4.22)$$

For $b \geq b_{cr}$, we impose the condition $u(a) = 0$ for a value of $a \in [0, b]$, and the solution is now

$$u(r) = \begin{cases} 0 & \text{if } r \leq a, \\ \frac{Qr^2}{6D} + \frac{Q(b^3 - a^3) - 6Dbu_b}{6(a-b)D} + \frac{abQ(a^2 - b^2) + 6abDu_b}{6(a-b)Dr} & \text{if } r \geq a. \end{cases} \quad (4.23)$$

The value of the inner radius a is determined by a no-flux condition at $r = a$, $\frac{\partial u}{\partial r}|_{r=a} = 0$. This condition implies that a is given as the first positive root of the polynomial

$$P(a, b) = Q(2a^3 - 3a^2b + b^3) - 6bDu_b. \quad (4.24)$$

In Figure 4.10, the nutrient profile is shown for different values of the external radius. The inner shell of radius a can be associated with the so-called *necrotic core*, a region inside the spheroid where the cells die due to lack of nutrients. As the radius increases, the proliferating zone $(b - a)$ tends rapidly to a constant determined by taking the limit of the solution of (4.24) for large b , that is,

$$\Delta = \lim_{b \rightarrow \infty} (b - a) = \sqrt{\frac{2Du_b}{Q}}. \quad (4.25)$$

Once the nutrient profile is known, the growth of the tumor can be computed by integrating (4.18). The position of a material point, labeled R_0 in the original configuration, is given by

$$r^3 = 3 \int_0^{R_0} \eta(r) R_0^2 dR_0. \quad (4.26)$$

Taking the derivative with respect to time and using (4.18), Equation (4.26) simplifies to

$$\frac{\partial(r^3)}{\partial t} = 3 \int_0^{R_0} u(r) k \eta R_0^2 dR_0, \quad (4.27)$$

and by changing variables in the integral using (4.16), we have

$$\frac{\partial r(R_0, t)}{\partial t} = k r^{-2} \int_0^r u(\rho) \rho^2 d\rho, \quad (4.28)$$

where $u(\rho, t) = 0$ for $\rho \leq a$. In particular, the radius of the sphere is given by

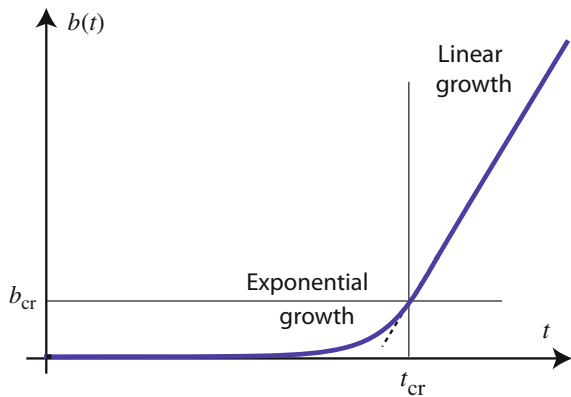
$$\frac{\partial b(t)}{\partial t} = k b^{-2} \int_0^b u(\rho, t) \rho^2 d\rho. \quad (4.29)$$

Initially, the entire spheroid is proliferating and exponential growth is observed as shown in Figure 4.11. As the necrotic core forms, growth is still exponential but in a region of constant width. Therefore, following the argument in the previous section on tip growth, we conclude that, for large b , the radius increases linearly in time as shown in Figure 4.11.

4.3.2.4 Discussion

We comment that this model is quite simplistic, since we expect a quiescent zone to form where the cells do not proliferate but remain alive and are in a state of dormancy [509, 694]. Nevertheless, this toy model captures the essence of the problem and gives

Figure 4.11 Evolution of the spheroid radius in time. For $t < t_{cr}$, the tumor grows exponentially. However, when $t > t_{cr}$, a necrotic core develops and only a spherical shell proliferates. For large time, linear growth is observed in much the same manner as systems exhibiting tip growth.



a basic understanding for the concepts of penetration length, proliferation zone, and necrotic core frequently used in the study of tumor growth [815].

Apart from the effect of nutrients, it is believed that mechanical stress also plays an important role as high stress may limit the ability of cells to divide through contact inhibition [530, 566]. However, in order to investigate the effect of mechanics on growth, an analysis of the full stress tensor at any point in the spheroid needs to be performed [25, 29, 1098].

4.4 Growth with Elastic Deformation

So far, we have considered growth and elastic deformations as two independent processes. In general, growth may induce stresses and stresses can depend on growth. For instance, if we let a filament grow between two rigid plates, the ends cannot move and resist extension, thereby generating an axial compressive stress in the rod. Therefore, growth and elasticity are coupled and we must integrate them within a single framework.

In the one-dimensional context, the fundamental assumption of *morphoelasticity* is that a change in length can be produced by both processes. Mathematically, it can be expressed by postulating that the full axial stretch is the product of a growth stretch γ , and an elastic stretch, α :

$$\lambda = \alpha\gamma. \quad (4.30)$$

This apparently simple multiplicative decomposition is rather subtle and will be further discussed and justified in the general context of nonlinear elasticity discussed in Chapter 12. Before discussing this problem in more detail, we explore the consequences of this decomposition by considering several examples.

4.4.1 Growth of a Rod Between Two Plates

As an example of the coupling between growth and stress, we first consider the simple problem of a rod growing between two immovable plates. Initially, the rod has a length L_0 equal to the distance between the plate. Since, the rod is constrained, the total length, $l(t) = L_0$, of the rod remains constant for all time. Therefore, we simply have $\lambda = l/L_0 = 1$ for all time.

We assume that the rod grows uniformly and linearly in time, so that

$$\gamma = 1 + t. \quad (4.31)$$

This growth creates a spatially homogeneous compressive stress. Indeed, since $\lambda = 1$, we have $\alpha = 1/\gamma = 1/(t + 1)$.

If we first assume a constitutive relationship of the form (4.2), the stress increases with time as

$$\sigma = -\frac{Et}{t+1}. \quad (4.32)$$

Paradoxically, as $t \rightarrow \infty$, the stress saturates asymptotically to $\sigma_\infty = -E$. Indeed, for a Hookean law (4.2), it takes a finite stress, namely σ_∞ , to compress a rod to zero length.

Clearly, real materials will not follow this behavior as a Hookean law is only valid for small displacements. Corrections to the Hookean law will enter the constitutive relation when compression or tension becomes sufficiently large. For instance, using the neo-Hookean law (4.4), we obtain

$$\sigma = \mu \left(\frac{1}{(1+t)^2} - t - 1 \right), \quad (4.33)$$

and an infinite compressive force ($\sigma \rightarrow -\infty$) is generated in the limit $t \rightarrow \infty$.

4.4.2 Three Different Configurations

A slightly different way to understand the coupling between growth and elasticity in the previous problem is to separate the response of the material into two distinct processes as shown in Figure 4.12. First, a growth deformation is applied; we let the rod grow without external constraints on the ends, so that at any given time t , it is in an unstressed state. In this configuration, the material point S_0 is at a position $S(S_0, t) = S_0(1+t)$ with total length $L(t) = L_0(1+t)$. Since this state

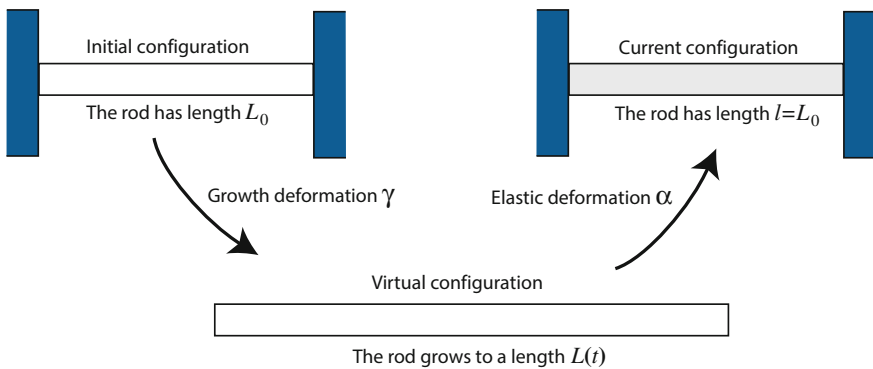


Figure 4.12 The growth of a constrained rod between two plates can be thought of as the composition of two distinct processes: A growth deformation which creates a stress-free virtual configuration, made of a rod of length $L(t)$, followed by an elastic deformation necessary to enforce the boundary conditions: a rod of length $l(t) = L_0$.

is not realized in the experiment, we refer to it as a *virtual configuration*; a useful mathematical construct needed to find the solution of the problem. Second, the grown rod is placed back in between the plates, and we find the elastic stretch necessary to satisfy this constraint to be $\alpha = 1/(t + 1)$.

This example also provides a simple illustration of one of the fundamental concept related to the modeling of growth; that is, the *evolution of the reference configuration*. In order to evaluate elastic deformations and stresses in a growing material, the strain must be defined. *Strain* is a measure of the deformation with respect to a reference configuration where the material is unstressed. As growth takes place, the reference configuration of the material evolves. In our example, the reference configuration is not the initial configuration but the virtual configuration obtained by removing stresses. The corresponding length of the growing filament in this virtual configuration is $L = L_0(t + 1)$.

We use the following notation throughout this monograph: Whenever possible most quantities in the current configuration are denoted by lowercase variables. The corresponding quantities in the initial stress-free configuration are written in uppercase with subscript 0. The same quantities in the virtual configuration are designated by the same variable in uppercase but without subscript, or with a subscript t . For instance, the length in the initial, virtual, and current configuration is denoted as L_0 , L , and l , respectively.

The standard picture of elasticity is to consider an initial reference configuration without stress and a current configuration where loads are applied and stresses can be computed from the mechanical balance and constitutive equations. We see in this simple example that an understanding of the stresses in a growing elastic medium requires another configuration, namely, the virtual configuration, where the material is grown in the absence of stress. In the case of one-dimensional extensions, the removal of stresses by unloading the material can always be carried out in an experiment. However, we will see that in many situations this configuration is not physically realizable, but can only be defined locally, hence the names *virtual configuration* or *virtual reference configuration*; a mathematically useful but often physically unattainable construct.

4.4.3 Homeostatic Growth

Next, we consider a situation where growth depends on stress. We assume that the filament has a natural *homeostatic stress* σ^* ; a stress that the filament, through the active process of growth, tends to recover when perturbed from its natural state. Here, for illustrative purposes, we assume that this process can be modeled by the evolution law

$$\frac{\partial \gamma}{\partial t} = \gamma(\sigma - \sigma^*). \quad (4.34)$$

This law implies that exponential growth or resorption will take place until the stress σ reaches homeostatic stress σ^* [1209, 1276]. Assuming again a Hookean stress–

strain relationship $\sigma = E(\alpha - 1)$, we see that there is a unique homeostatic strain $\alpha^* = 1 + \sigma^*/E$.

Next, we consider the following problem: We assume that at time $t = 0$ the filament is resting in a state of homeostatic stress with a length l_{init} . The filament is instantaneously extended to a constant length l . How will the filament evolve to reestablish its homeostatic stress?

The elastic stretch at any time t is $\alpha(t) = l/\gamma(t) = l/(L_0\gamma(t))$, and the initial length L_0 is

$$L_0 = \frac{l_{\text{init}}}{\alpha_{\text{init}}} = \frac{l_{\text{init}}}{\alpha^*} = \frac{l_{\text{init}}E}{\sigma^* + E}, \quad (4.35)$$

so that

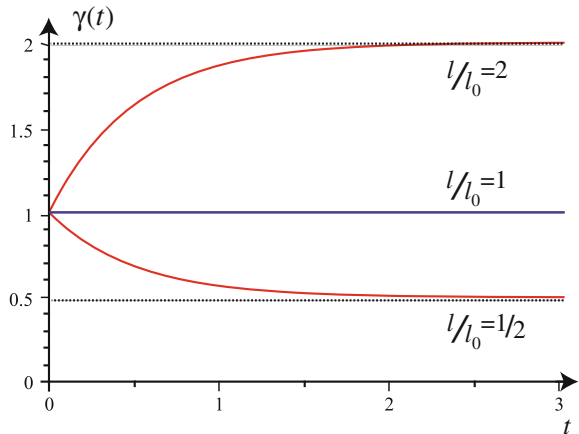
$$\sigma = E(\alpha - 1) = \frac{l(\sigma^* + E)}{l_{\text{init}}\gamma} - E, \quad (4.36)$$

which, upon substitution into Equation (4.34), leads to a single equation for γ which can be solved with the initial condition $\gamma(0) = 1$ to find

$$\gamma(t) = \frac{l}{l_{\text{init}}} + \left(1 - \frac{l}{l_{\text{init}}}\right) e^{-(E+\sigma^*)t}. \quad (4.37)$$

Examples of the dynamics of growth for stretching and compression are given in Figure 4.13. When the filament is instantaneously extended, it is in a state of tension. The system reestablishes its homeostatic stress by adding mass via growth which increases the internal compressive stress. Similarly, if the filament is compressed instantaneously, it is in a state of compression and the homeostatic stress will be recovered by shrinking the material. The notion of homeostatic stress is central in understanding normal maintenance and function of many tissues [1209] and will be considered again in Chapter 14.

Figure 4.13 Growth recovery of a filament with homeostatic stress σ^* of length l_{init} either extended to a filament of length $l = 2l_{\text{init}}$ or compressed to a filament of length $l = l_{\text{init}}/2$ ($\sigma^* = 1$ in both case).



4.4.4 Application: The Growth of Neurons

4.4.4.1 Background

An interesting example of stress-mediated growth in a biological system is found in the development and branching of neurons. Most neurons have a very distinctive morphology with a large cell body from which long protoplasmic protrusions, the *neurites*, extend. Neurites develop into either axons or dendrites that are intertwined to create a network, *the nervous system*. The axon carries the electrical signals to other neurons. Individual axons are about a micron in diameter but may extend across the entire body. The initial formation, development, and growth of axons have been shown to depend on applied mechanical forces [126, 559]. For instance, it has been shown that the initiation of axons in a chick's sensory neurons, chick's forebrain neurons, and rat's PC12 cells can be experimentally triggered by the proper application of tension on the surface of the cell body [1366]. Following initiation, the elongation of an axon can occur either spontaneously *in vivo* or it can be manipulated by external forces.

In the first case, tension is produced either by the motion of the *growth cone*, the specialized tip of the axon [755] or by the overall growth of the tissue in which it is embedded [1036]. The growth cone generates tension in the axon through an actin-based motor-clutch system [57].

In the second case, shown in Figure 4.14, a calibrated glass needle is glued to a neurite with the proper adhesive proteins and is towed [560], thereby controlling the elongation process. The applied tension at the end of the axon can be imposed by the deflection of the glass needle. This setup can be used to control either the velocity of the growing tip or to prescribe a pulling force with high accuracy [560, 1036].

Figure 4.14 Elongation of a neurite in a hippocampal neuron induced by pulling. A. Before needle application. Arrowhead marks attachment position. B. Same neuron towed 30 min. C. Same neuron 5:40 h/min after panel B (Bar is 20 μm , reproduced from [757]).

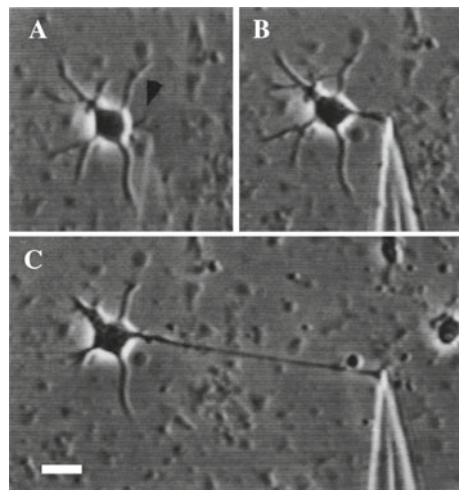
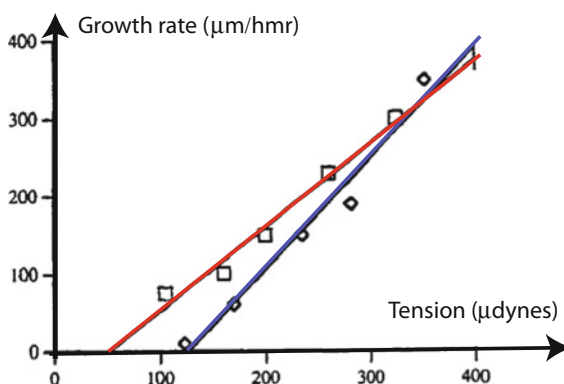


Figure 4.15 Axonal elongation rate for chick sensory neurites as a function of experimentally applied tension. Each line reflects the data of a single towed neurite (adapted from [560]).



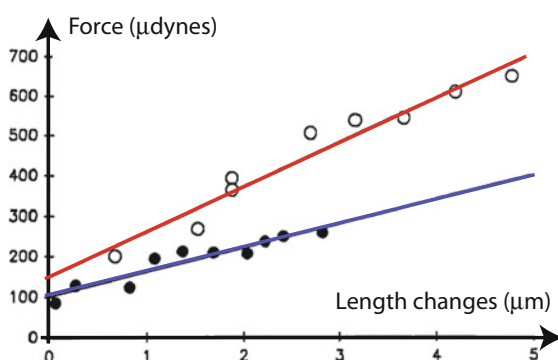
The typical range of applied forces is 1-8 nN (nano-Newtons) and the position of the axon tip can be measured by standard microscopy.

Remarkably, various analyses of the relationship between applied tension and tip velocity, as illustrated in Figure 4.15, reveal that, after a critical tension, below which no growth occurs, the growth rate is mostly linear with the applied tension [126, 181, 560, 755, 1366]. Note that both the slope and critical tension for these relationships differ from cell to cell [757]. This change in length results from stretching the neurons over long periods of time.

If the axon is suddenly plucked, its response will depend on its material property rather than on its growth response to external stimuli. On these small time scales, the axon shows a typical linear, spring-like, response past a critical rest tension that corresponds to the tension in axons in the absence of external loads. Experimental results are shown in Figure 4.16.

Most studies on axonal growth assume that growth occurs at the growth cone where most of the activity and microtubule assembly take place [807]. However, detailed observations of markers such as axonal branch points and docked mitochondria on the axon itself reveal that growth is neither restricted to the *distal end* (close to the growth cone) nor is it homogeneous along the axon. Instead, the growth rate varies

Figure 4.16 Axial tension of chick sensory neurites as a function of experimental stretching (obtained by “plucking” at their midpoint by a calibrated glass needle). Observe the Hookean behavior past a critical tension. This rest tension is the tension present in the neurite in the absence of external loads (adapted from [560]).



from the *proximal* (close to the body) to the distal site, accelerating closer to the growth cone and resulting in assembly and deposition of new material along the length of the axon [756].

4.4.4.2 A Model

From these basic observations, we model a growing axon as a one-dimensional elastic structure subject to growth as described above. The filament is of length $l = l(t)$ and is anchored at the point $s = 0$. Following the analysis and the ideas presented in [273, 1002], we assume that the tension in the axon, σ , is due to both the applied tension at the end, σ_L , and an adhesion force, f , between the substrate and the axon. At any given time, we assume that the axon is elastic and operates in small deformations, so that it is characterized by a Hookean relationship

$$\sigma = E(\alpha - 1), \quad (4.38)$$

where $\alpha = \partial s / \partial S$, and $s(S, t)$ is the current arc length of a material point $S(t)$, where $S(t)$ is the reference arc length corresponding to the distance from $s = 0$ at time t in the unstressed virtual configuration. Since there is an adhesion force f acting on the filament due to its interaction with the substrate, the tension along the filament is given by

$$\frac{\partial \sigma}{\partial S} + f = 0. \quad (4.39)$$

This relation can be obtained from the general Equations (5.79) for a growing Kirchhoff rod described in Section 6.2 by restricting the motion to a line and taking $\mathbf{n} = (0, 0, \sigma)$ and a body force $\mathbf{f} = (0, 0, f)$ in the tangential direction.

We further assume that the adhesion force can be modeled by a simple Hookean law

$$f = K(s(S) - S). \quad (4.40)$$

Taking an extra derivative of (4.39) and (4.40), and using the Hookean relationship (4.38), we obtain

$$\frac{\partial^2 \sigma}{\partial S^2} + \frac{\sigma}{a^2} = 0, \quad (4.41)$$

where $a = \sqrt{E/K}$ is a characteristic length for the problem. Since the proximal end of the filament ($s = 0$) remains fixed, $s(0, t) = 0$, which implies $f(0, t) = 0$ and $\partial \sigma / \partial S = 0$ at $S = 0$ for all time t . The other end is pulled with a tension $\sigma(S = L, t) = \sigma_L$.

To model the growth process, we need a law for the evolution of $S(t)$. At time $t = 0$, the filament is parameterized by its initial arc length S_0 and the change in reference configuration is described by $\gamma = \partial S / \partial S_0$ and a growth law of the form

$$\frac{\partial \gamma}{\partial t} = \gamma g(\sigma), \quad (4.42)$$

where growth takes place when the tension is larger than a critical homeostatic tension σ^* so that

$$g(\sigma) = k(\sigma - \sigma^*)H(\sigma - \sigma^*), \quad (4.43)$$

where $H(\cdot)$ is the Heaviside function and k is a constant.

4.4.4.3 Analysis

The solution of (4.41) with the given boundary conditions is

$$\sigma(S(t)) = \sigma_L \frac{\cosh(S(t)/a)}{\cosh(L(t)/a)}. \quad (4.44)$$

A large value of a corresponds to either a small adhesion force or a very stiff filament. In this case, the tension in the filament becomes uniform since we have

$$\lim_{a \rightarrow \infty} \sigma(S) = \sigma_L. \quad (4.45)$$

For large adhesion force or a very compliant filament, a is small and the tension is localized at the pulling side with an exponential decay of characteristic length a .

In an experiment where the end is pulled with a constant tension σ_L , the behavior of the filament would still appear Hookean since it will extend to a length $l = L + (a/E) \tanh(L/a) \sigma_L$, corresponding to an extension proportional to the applied tension.

Next, we consider the growth process for long times. If γ is known, the evolution of a material point, initially at position S_0 , is given by

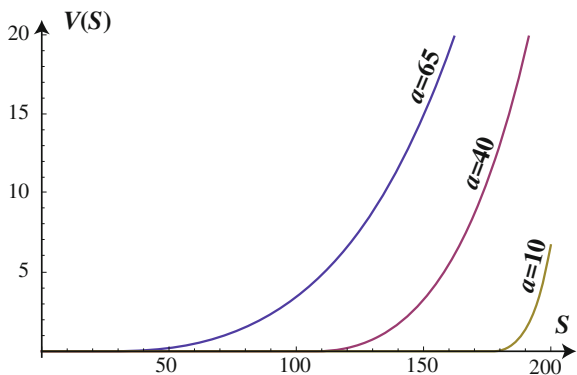
$$S(S_0, t) = \int_0^{S_0} \gamma \, dS_0. \quad (4.46)$$

Therefore, the velocity of this point is

$$\begin{aligned} \partial_t S(S_0, t) &= \int_0^{S_0} (\partial_t \gamma) \, dS_0 = \int_0^{S_0} \gamma g(\sigma) \, dS_0 \\ &= \int_0^S g(\sigma(S)) \, dS. \end{aligned} \quad (4.47)$$

Using both the explicit form (4.44) for the tension and the growth law (4.43), the equation for $S(t)$ is

Figure 4.17 Velocity of points along a growing axon ($L = 200$, $\sigma_L = 1$, $\sigma^* = 1/10$, $k = 1$).



$$\begin{aligned} \partial_t S &= kH(S - S^*) \int_{S^*}^S \left(\sigma_L \frac{\cosh(S/a)}{\cosh(L/a)} - \sigma^* \right) dS \\ &= kH(S - S^*) \left[\sigma^*(S^* - S) + a\sigma_L \frac{\sinh(S/a) - \sinh(S^*/a)}{\cosh(L/a)} \right], \end{aligned} \quad (4.48)$$

where

$$S^* = a \operatorname{arccosh}\left(\frac{\sigma^*}{\sigma_L} \cosh \frac{L}{a}\right). \quad (4.49)$$

This last equation gives, at any length L , the velocity of a material point S at time t , that is,

$$V(S, t) = kH(S - S^*) \left[\sigma^*(S^* - S) + a\sigma_L \frac{\sinh(S/a) - \sinh(S^*/a)}{\cosh(L/a)} \right]. \quad (4.50)$$

A typical velocity profile is shown in Figure 4.17.

Note that Equation (4.48) for $S(t)$ cannot be solved directly as both S and L depend on t . Therefore, to solve this free-boundary problem, we first consider this equation for the particular point $S(t) = L(t)$:

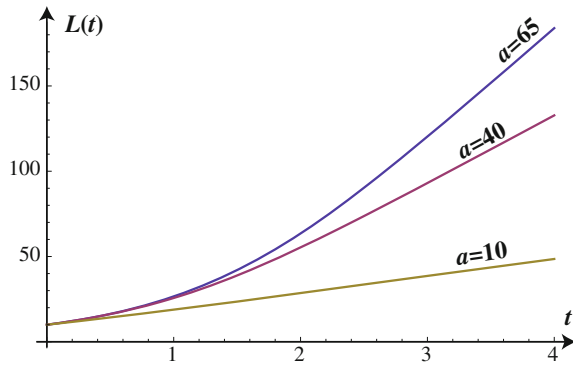
$$\partial_t L = k\sigma^*(S^* - L) + ka\sigma_L \frac{\sinh(L/a) - \sinh(S^*/a)}{\cosh(L/a)}, \quad (4.51)$$

with the initial condition $L(0) = L_0$. No useful closed-form solution exists for this equation. Instead, we consider the limit where $S^* \rightarrow 0$, which leads to $\partial_t L = ka\sigma_L \tanh(L/a)$, that is,

$$L(t) = a \operatorname{arcsinh} \left[e^{k\sigma_L t} \sinh(L_0/a) \right]. \quad (4.52)$$

Once the function $L(t)$ is known, it can be substituted into Equation (4.48) and an equation for the evolution of $S(t)$ can be found for all initial points of the form

Figure 4.18 Length as a function of time in the limit of $S^* \rightarrow 0$ ($L = 200$, $\sigma_L = 1$, $\sigma^* = 1/10$, $k = 1$).



$S(t = 0) = S_0$. After an initial exponential phase where the entire filament experiences growth, extension becomes limited to a finite zone close to the tip of characteristic size a which results in the length increasing linearly with time, as shown in Figure 4.18. This behavior is similar to the problem of growing spheroids seen previously.

4.4.4.4 Discussion

This simple model has focused on macroscopic aspects of axonal growth and its relationship to applied tension. Other mathematical models have focused on the tubulin production in the cell body, transport processes to the growth cone, and the assembly necessary to create new microtubules to extend the axon [494, 688, 847, 848, 988, 1272]. Furthermore, the extent and pattern formations of axons in three dimensions during development, rather than on the line, raise many fundamental questions about pattern formation and pathfinding [12, 494, 592, 1167, 1225].

4.4.5 Is This Just Plasticity?

For the reader familiar with the theory of plasticity, the discussion on the decomposition of deformations in elastic and growth processes may seem familiar. In a plastic deformation, the material flows irreversibly after a critical stress and we could argue that, superficially, the problem of growth is equivalent to the problem of plastic deformation. Many authors, especially in the plant literature, have argued along these lines and have adopted the view that elastic growth should be based on the theory of plasticity [514]. There are, however, many distinctions between the two theories and great care should be exercised before modeling growth processes as plastic processes. At the kinematics level, there are many similarities such as the decomposition between plastic and elastic deformations and the evolution of a reference configuration. However, plasticity has been developed chiefly to describe the properties of metals. The evolution laws for plastic strains are a direct consequence of the microstructure

of metals, with special emphasis on slip lines and shear stresses. There is no reason to believe that biological systems follow the same principles.

It is therefore important to be aware and to take advantage of the formal concepts and mathematical methods that have been developed for plasticity, but it can be misleading to restrict the deformations, due to growth, to plastic processes. Further, many of the relationships between growth and stresses observed in tissues and plants are different from the evolution rules given by the theory of metals.

The two theories, elasto-plasticity and morphoelasticity, are two instances of the theory of *anelasticity*: The general theory of continua that considers both conservative elastic and nonconservative anelastic deformations regardless of their origin. In our case, the anelastic deformations are due to growth, but other possibilities of physical theories involving anelastic deformations include elasto-plasticity, thermoelasticity, viscoelasticity, and dislocation theory [321, 843].

The deformations of a one-dimensional structure offer a good starting point for a discussion of the similarities and differences between growth and plasticity. A purely elastic material is one in which the response to applied stresses is instantaneous and reversible. Other materials which exhibit irreversible deformations can be modeled by the proper choice of constitutive relationships and multiplicative decomposition. Here, we postulate that a material can exhibit both an elastic deformations characterized by strain, $\epsilon_{el} = l/L - 1$, and an anelastic irreversible deformation characterized by the strain, $\epsilon_{an} = L/L_0 - 1$. Using the multiplicative decomposition, we have

$$\lambda = \lambda_{el}\lambda_{an} = 1 + \epsilon_{el} + \epsilon_{an} + \epsilon_{el}\epsilon_{an}. \quad (4.53)$$

If we further assume that these deformations are small, so that the product $\epsilon_{el}\epsilon_{an}$ can be neglected, we obtain that the total strain is decomposed additively into

$$\epsilon = \lambda - 1 = \epsilon_{el} + \epsilon_{an}. \quad (4.54)$$

Since we have two processes responsible for the deformation, we need to supply two separate constitutive relationships that characterize the material behavior.

- **An ideal fluid:** For an *ideal fluid*, we have no elastic response $\epsilon_{el} = 0$ and the rate of anelastic strain is proportional to the applied stress:

$$\frac{\partial \epsilon_{an}}{\partial t} = \frac{\partial \epsilon}{\partial t} = \frac{1}{\eta} \sigma, \quad (4.55)$$

where η is a viscosity. In this case, the material exhibits only irreversible flow.

- **A Maxwell fluid:** A *Maxwell fluid* combines both an elastic response of a Hookean material with an anelastic fluid-like response. That is:

$$\epsilon_{el} = \frac{1}{E} \sigma, \quad \frac{\partial \epsilon_{an}}{\partial t} = \frac{1}{\eta} \sigma. \quad (4.56)$$

Combining these two equations leads to a single relationship for the total strain

$$\frac{\partial \epsilon}{\partial t} = \frac{1}{\eta} \sigma + \frac{1}{E} \frac{\partial \sigma}{\partial t}. \quad (4.57)$$

Note that if the strain is turned off, the stress relaxes as $\sigma \sim e^{-t/\tau_r}$, where $\tau_r = \eta/E$.

- **A Kelvin solid:** A *Kelvin solid* (or *Kelvin–Voigt solid*) is an elastic material in which the response to the stress occurs over a finite time determined by the viscous nature of the material. Again, we assume a Hookean response for the elastic part, but the anelastic component decays both as a function of the stress and the anelastic strain itself:

$$\epsilon_{\text{el}} = \frac{1}{E} \sigma, \quad \frac{\partial \epsilon_{\text{an}}}{\partial t} = -\frac{E}{\eta} \epsilon_{\text{an}} - \frac{1}{E} \frac{\partial \sigma}{\partial t}. \quad (4.58)$$

These two relations can be written as a single equation

$$\sigma = E\epsilon + \eta \frac{\partial \epsilon}{\partial t}. \quad (4.59)$$

If $\eta \neq 0$, the material relaxes with a characteristic viscoelastic time $\tau_r = \eta/E$ as $\epsilon \sim e^{-t/\tau_r}$ describing the evolution of strains when the stress is turned off. This decay should be contrasted with the equivalent stress relaxation of a Maxwell fluid.

- **A Bingham material:** In a simple fluid there is irreversible flow in response to applied stress, however small. For non-Newtonian fluids such as paint, flow does not begin until a critical yield stress, σ^* , has been exceeded. This behavior is captured by the *Bingham model* which, in its simplest form, is expressed as

$$\epsilon_{\text{el}} = 0, \quad \frac{\partial \epsilon_{\text{an}}}{\partial t} = \frac{1}{\nu} (\sigma - \sigma^*) H(\sigma - \sigma^*), \quad (4.60)$$

where $H(\cdot)$ is the Heaviside function and ν/σ^* is a typical characteristic relaxation time. This behavior models an irreversible flow once a critical stress has been exceeded. It has been used as a paradigm for most plant growth models, as discussed in Section 4.5.

- **A Maxwell–Bingham material:** The Bingham model can be generalized to a *Maxwell–Bingham* type system by assuming an elastic response

$$\epsilon_{\text{el}} = \frac{1}{E} \sigma, \quad \frac{\partial \epsilon_{\text{an}}}{\partial t} = \frac{1}{\nu} (\sigma - \sigma^*) H(\sigma - \sigma^*), \quad (4.61)$$

which leads to

$$\frac{\partial \epsilon}{\partial t} = \frac{1}{\nu} (\sigma - \sigma^*) H(\sigma - \sigma^*) + \frac{1}{E} \frac{\partial \sigma}{\partial t}. \quad (4.62)$$

where ν/E is a characteristic relaxation time. Regarding terminology, the convention is to call a Maxwell fluid *viscoelastic*, reflecting the combination of irreversible

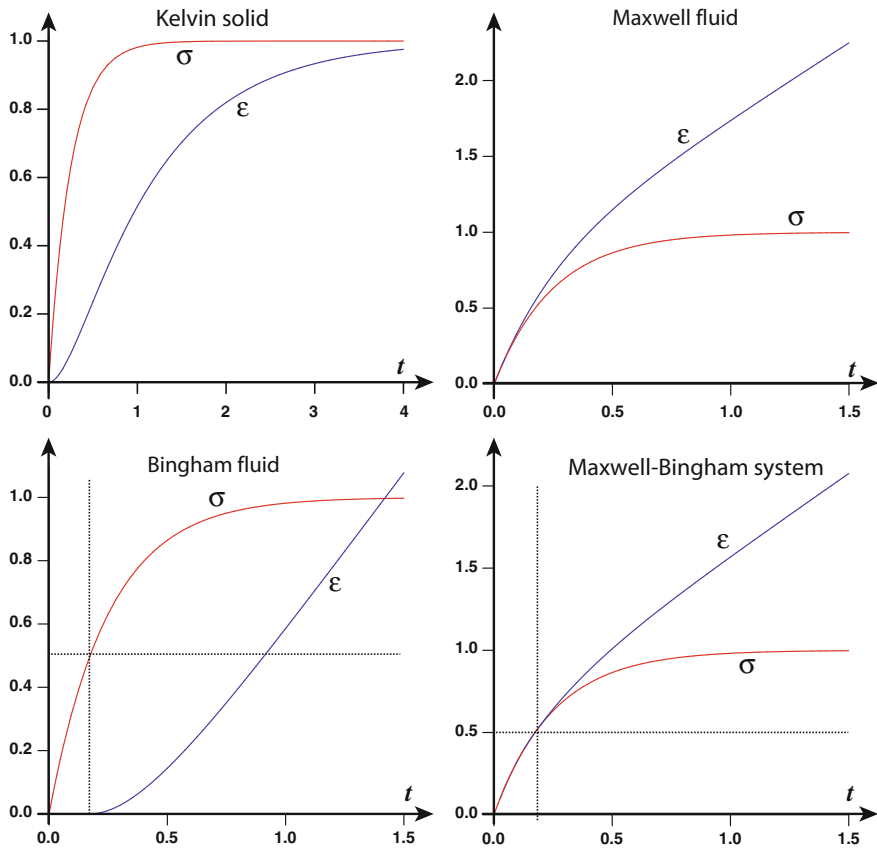


Figure 4.19 Comparison of strains produced by a ramping of the stress in time for four different materials, $\nu = 1/4$, $\sigma^* = 1/2$, $E = \sigma_0 = \eta = 1$.

flow generated by viscous stresses with an elastic component, and to term a Bingham fluid *plastic* to mean an irreversible deformation beyond a critical yield stress. A comparison of the strains produced by the different models, where stresses are ramped up linearly with respect to time, is given in Figure 4.19.

4.5 Application: The Growth of Plant Cells

The one-dimensional theory of elastic growth described in the previous section is elementary. Nevertheless, these ideas can be applied to simple models for the elongation of plant cells. The earliest quantitative model of plant cell growth is by Lockhart [798] and has been applied successfully to gain some insight into the role of plant growth hormones such as auxin.

4.5.1 Lockhart Model

4.5.1.1 Background

The axial organs of plants such as stems or coleoptiles are long filamentary structures that are generated mostly by cell expansion. The protoplasts of plant cells, consisting of the cytoplasm and nucleus, are surrounded by elastic cell walls, a composite structure formed by the complex interactions of a gel-like structure made of pectins, with a network of stiff fibers composed of cellulose microfibrils tethered by hemicelluloses, and glycoproteins [172, 741, 1016]. Due to the strongly anisotropic properties of the cell walls, axial organs grow almost exclusively in length. These cell walls are infiltrated by water as seen in Figure 4.20. Whereas the protoplast has large concentrations of solutes, the water in the cell walls has negligible amounts. This difference in solute concentrations creates an *osmotic pressure* P_{osm} on the order of 0.3 to 1 MPa [231, 1065, 1367]. This osmotic pressure is counteracted by the hydrostatic pressure inside the cell usually referred to as the *turgor pressure* P_{tur} . By analogy with hydraulic systems, the difference between these two pressures is called the *water potential*

$$\Delta P = P_{\text{osm}} - P_{\text{tur}}, \quad (4.63)$$

and, the cell can be thought of as a *membrane osmometer*. When the cell is fully turgid, that is, fully swollen, the osmotic pressure is completely balanced by the hydrostatic pressure and $\Delta P = 0$. In the absence of a growth mechanism, induced by cell wall loosening, the water potential drives reversible changes of cell wall volume which can be described by the basic laws of hydraulics.

4.5.1.2 A Model

We model the plant cell as an axisymmetric cylinder of constant radius, but varying length $l(t)$ with initial length L_0 and unstressed length $L(t)$, which corresponds to removing all pressure. Then, assuming that there is no change in the cross-section area, the relative rate of volume change is equal to the relative rate of length change. At equilibrium, the force acting on the cylinder cap is balanced by a constant elastic stretching $\alpha = l/L$ so that $d\alpha/dt = 0$ and the change in extension is proportional to the water potential. Hence, we have

$$\frac{1}{\lambda} \frac{d\lambda}{dt} = K \Delta P, \quad (4.64)$$

where $\lambda = l/L_0$ and K is the water conductance. Therefore, changes in osmotic concentration in the extracellular space drive reversible plant motion by changing the relative osmotic concentration. This process is, for instance, the mechanism by which *guard cells* on the surface of leaves regulate photosynthetic activity by opening

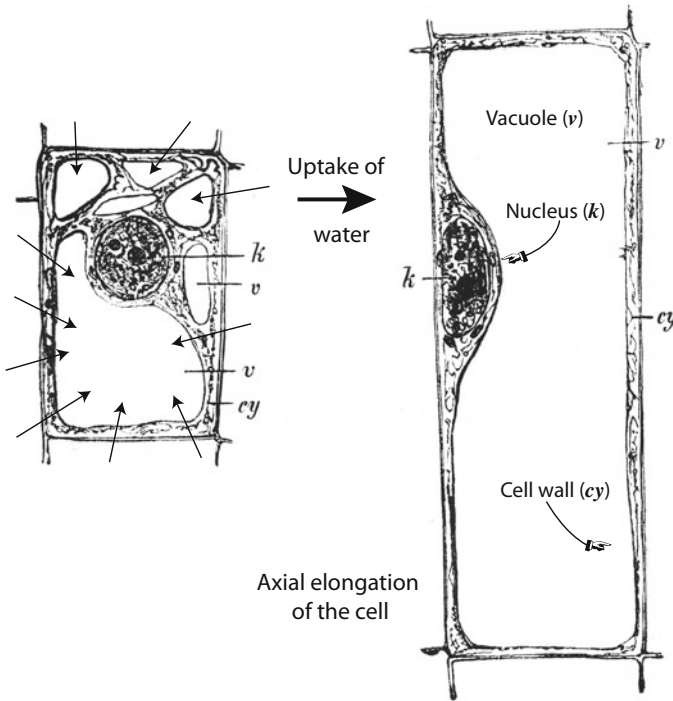


Figure 4.20 Elongation of plant cells. The vacuole increases in size due to uptake of water causing an axial elongation of the cell (adapted from [924]).

and closing pores due to varying physical conditions [1215]. Since the law for the change of volume due to change in water potential is of the form of a flow, the deformation is reversible but inelastic, in the sense that the work required to expand the cell during deformation cannot be recovered.

Plant cells also have the ability to increase their volume in an irreversible manner. This process of irreversible cell enlargement is referred to as the *growth of the plant cell*. The change in volume from the initial meristematic size to maturity can be up to a 1,000 fold for hair cells on the surface of young cotton seeds and 30,000 fold for xylem vessels [232]. After the initial cell division in the meristem region, growth is mostly achieved by *wall loosening*. This stress relaxation produces a decrease in the turgor pressure that drives water uptake. In order for this process to take place over long periods of time and to allow for steady growth, osmoregulation is necessary to balance the dilution of solutes with the addition of water. Furthermore, walls need to be constantly rebuilt to prevent thinning and turgor pressure needs to be maintained to keep the cell walls in a state of tension necessary for elongation [1066]. The cell wall extension created by loosening is usually referred to as a creep or plastic process and has been modeled as a Bingham-like response.

Let $\gamma(t) = L(t)/L_0$ be the growth stretch associated with this growth process. Assuming that the material response of cylindrical walls is isotropic and the cell can only be deformed in the axial direction, the axial stress is given by the pressure exerted on the caps of the cylinder. Then, the creep-response can be written directly in terms of the turgor pressure rather than the axial stress, that is,

$$\frac{1}{\gamma} \frac{d\gamma}{dt} = \Phi(P_{\text{tur}} - P^*)H(P_{\text{tur}} - P^*), \quad (4.65)$$

where P^* is the yield pressure threshold above which irreversible extension takes place with extensibility coefficient Φ , the amount of extension above threshold. Since both water uptake and enlargement take place at the same time, we model the extension as a morphoelastic process where $\lambda = \alpha\gamma$, which implies

$$\frac{1}{\lambda} \frac{d\lambda}{dt} = \frac{1}{\alpha} \frac{d\alpha}{dt} + \frac{1}{\gamma} \frac{d\gamma}{dt} = \frac{1}{\gamma} \frac{d\gamma}{dt}, \quad (4.66)$$

where we have used $d\alpha/dt = 0$. Therefore, the relative rate of volume changes given by (4.64) and (4.65) must be equal and, for $P_{\text{tur}} > P^*$, we can eliminate P_{tur} . After simplification, we recover *Lockhart's equation*,

$$\frac{1}{\lambda} \frac{d\lambda}{dt} = \frac{\Phi K}{\Phi + K} (P_{\text{osm}} - P^*)H(P_{\text{osm}} - P^*). \quad (4.67)$$

4.5.1.3 Analysis

We first note that we can recover, from Lockhart's equation, both Equations (4.65) and (4.64) as limit cases when either $K \gg \Phi$ or $\Phi \gg K$, respectively. In the first case, growth is limited by the microscopic processes that allow for cell wall extensibility. While in the second case, growth is limited by water conductance.

How do we use such an equation? Note that the left-hand side of this equation is the relative elemental growth rate $g = (1/\lambda) (d\lambda/dt)$ used by plant physiologists to describe the growth of stems as defined in Section 1.4. It can be obtained experimentally for steady growth by tracking the evolution of material markers in time. Similarly, the water conductance can be measured independently and the osmotic pressure can be controlled experimentally. Therefore, Lockhart's equation provides a way to obtain the cell extensibility parameter Φ and the yield threshold P^* by measuring the sensitivity of growth with respect to changes in the turgor pressure [231].

Different techniques to control the turgor pressure have been used such as:

- the incubation of excised tissues in solutions of varying concentrations of osmoticum [505, 506, 586];
- the water-stressed treatment obtained by letting the plants dry down, resulting in lower water potential [319];

- the control of pressure by enclosing the growing plant in a pressure controlled chamber [230];
- the injection of silicone oils into the vacuoles of cells [998];
- the use of a pressure probe to inject or remove cell solution [1367].

According to Lockhart's model, the growth rate g varies linearly with the turgor pressure, up to a critical pressure P^* , where the growth rate vanishes. So by plotting g as a function of P_{osm} or P_{turg} , the parameters Φ and P^* can be obtained from the slope and the horizontal intercept, respectively.

4.5.1.4 Discussion

As is often the case in biology, this simple idealized linear model is relevant for many different systems such as the growth of soybean leaf [147], but many other plants have relative growth curves which are not linear with changes of turgor pressure. For instance, the growth rate in *Nitella* measured in [505] is best fitted by a nonlinear function whereas *Chara corallina* exhibits linear rather than exponential growth. In this case, the relative growth rate is best modeled by taking g to be constant [1045].

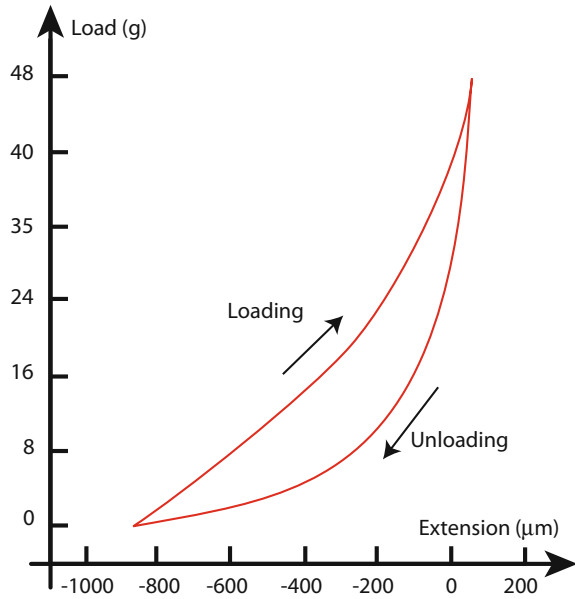
The study of the variations of the coefficient Φ , under growth induced by various concentrations of the plant hormone auxin, has revealed that cell wall extensibility is greatly affected by auxin while the turgor pressure remains essentially unchanged [587]. This basic result together with the measure of Φ through stress relaxation experiments [231] and the inhibition of growth by abscisic acid have demonstrated the importance of cell wall loosening or stiffening as factors controlling plant cell growth [1131].

Despite the wide use of the word “plasticity” to describe the irreversible deformation of plant cell walls, the actual rheological properties of cell walls greatly differ from those of a plastic material. In particular, growth stops after a few minutes following inhibition of respiration, despite possible changes in turgor pressure [1131]. Therefore, irreversible wall elongation is an active process mediated by biochemical regulators that depend on cellular mechanisms. It is not a purely physical property of the wall. Furthermore, experiments on segments of maize coleoptiles that have been frozen then thawed [588] have shown that these cells did not exhibit plastic flow under a loading–unloading cycle, but only reversible viscoelastic properties, as demonstrated in Figure 4.21.

4.5.2 Extending Lockhart's Model

Lockhart's model assumes both a state of constant elastic equilibrium, as a consequence of the assumed constancy of the stresses, and the absence of external loads applied to the tissue. If either the turgor pressure is changed rapidly or extra tensile loads are applied to the growing tissues, the growing walls simply follow the con-

Figure 4.21 Load-extension curve for a frozen-thawed segment of maize (*Zea mays* L.) coleoptile obtained by a sequence of loading steps followed by a sequence of unloading steps in a time frame of 90 minutes. Note that despite the fact that the loading and unloading curves are different, the segment returns completely to its original length after unloading. This closed hysteresis loop indicates a viscoelastic response of the walls rather than an irreversible plastic deformation (data from [588]).



stitutive relation given by (4.67). If external tensile loads are applied to a growing tissue, there is a temporary increase in the growth rate which is later modulated by an auto-regulatory mechanism. This response of growth to stresses was observed by Heyn [573, 574] who observed elastic and irreversible deformations in 1936 by loading and unloading a growing stem with weights. As illustrated in Figure 4.22, later experiments to distinguish between elastic and irreversible responses of growing tissues are based on the same idea; that is, a temporary application of an external loading force on the tissue [743, 744] or a sudden increase of turgor pressure [1045].

The influence of an elastic response on the rate of growth can be modeled by assuming that the total deformation is decomposed into an elastic and growth component [229, 994] so that we now have

$$\frac{1}{\lambda} \frac{d\lambda}{dt} = \frac{1}{\alpha} \frac{d\alpha}{dt} + \frac{1}{\gamma} \frac{d\gamma}{dt}. \quad (4.68)$$

Assuming that the water conductance is much greater than the extensibility of the cell wall, we can restrict our attention to the irreversible component of the extension rate given by (4.65). The elastic component is taken to be a simple Hookean law $\sigma = E(\alpha - 1)$ which leads to

$$\frac{1}{\alpha} \frac{d\alpha}{dt} = \frac{1}{E} \frac{dP}{dt}. \quad (4.69)$$

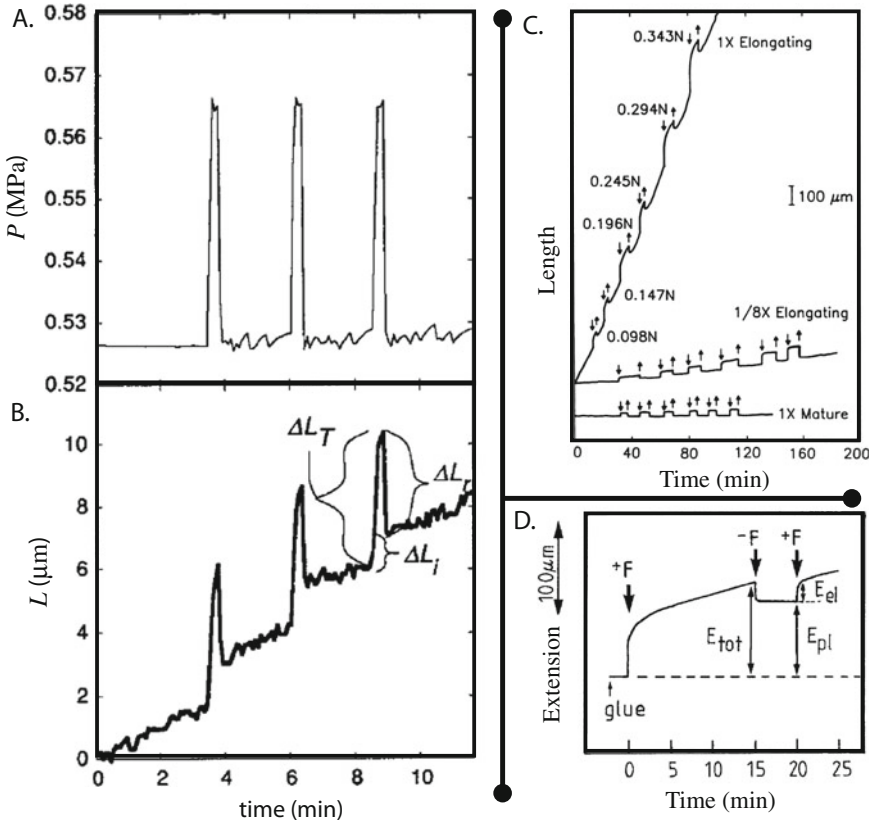


Figure 4.22 Elastic and growth deformations in plants. AB. Change in length of *Chara corallina* internode cells under a rapid change of pressure P (adapted from [1045]). C. Change in length following a change of applied forces in soybean hypocotyls in a well-watered (1× Elongating), water-stressed (1/8 × Elongating), and mature state (adapted from [964]). D. Length of a coleoptile segment of *Zea mays* during the measurement of in vivo extensibility in the extensometer (adapted from [744]). An intact segment was extended by applying a load of 20 g, (+F). After 15 min, the force was removed (-F) and reapplied after further 5 min (+F). E_{tot} , E_{el} , E_{pl} denote total, elastic, and plastic extensibilities.

The two effects combined together give

$$\frac{1}{\lambda} \frac{d\lambda}{dt} = \Phi(P_{tur} - P^*)H(P_{tur} - P^*) + \frac{1}{E} \frac{dP}{dt}. \quad (4.70)$$

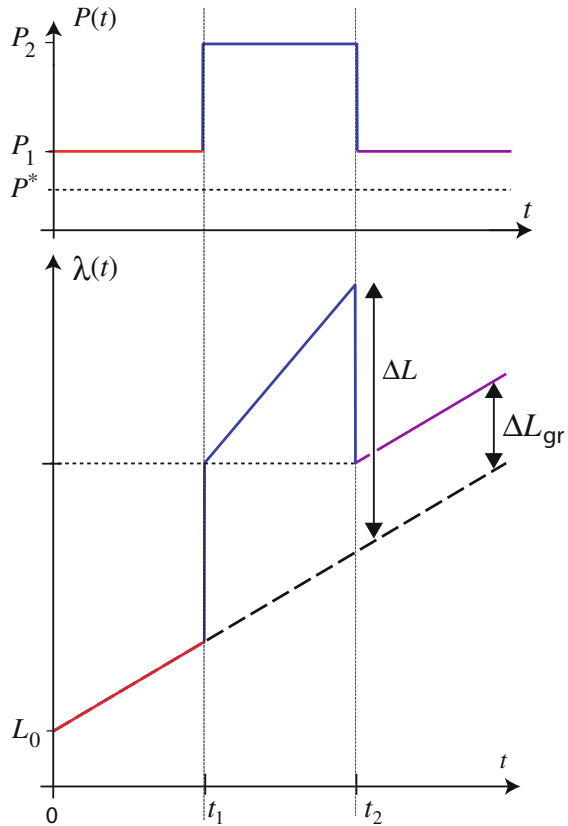
Note that this equation assumes that under fixed turgor, the steady state of growth increases exponentially in time. For plants whose length increases linearly in time [1045], this equation can be replaced by

$$\frac{d\lambda}{dt} = \Phi(P_{\text{tur}} - P^*)H(P_{\text{tur}} - P^*) + \frac{L_0}{E} \frac{dP}{dt}, \quad (4.71)$$

where L_0 is the initial cell length. Interestingly, this form of growth response is formally equivalent to a Maxwell–Bingham material (see Equation (4.61)) and it is therefore tempting to associate the plant behavior with the behavior of an elastoplastic material.

In order to isolate the growth contribution from the elastic contribution, one can subject the growing stem to changes in pressure. As long as the pressure remains constant, there is no contribution from the elastic part since the last term in Equation (4.70) vanishes identically. The elasticity of plant tissues can be tested by traditional methods in mature tissues ($\Phi = 0$), but mature cells tend to be more rigid than growing cells. Therefore, in order to probe the elasticity of a growing tissue, a variation of the pressure must be applied. In the thought experiment shown in Figure 4.23, we apply a constant pressure P_1 from $t = 0$ to $t = t_1$, then suddenly increase the pressure to P_2 for a time $\Delta t = t_2 - t_1$. The change in length after that time $\Delta L = \lambda(t_2^-) - \lambda(t_2^+)$ depends both on A and Φ as follows

Figure 4.23 Theoretical change in length of a growing morphoelastic filament under rapid changes of the pressure P .



$$\Delta L = (P_2 - P_1) \left(\Phi(t_2 - t_1) + \frac{L_0}{E} \right), \quad (4.72)$$

from which the Young's modulus can be found. In particular, if the duration of the pressure pulse is small enough, we have

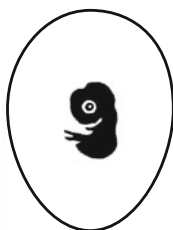
$$E = \frac{L_0}{\Delta L} (P_2 - P_1). \quad (4.73)$$

The Lockhart model has been used for the study of the impact of various chemical effects such as salinity, acidity, nitrogen supply [845]; biochemical factors such as growth hormones [121, 744]; and physical quantities, such as water potential, [840, 1317], and light action [233]. It has also been used as a basis for further modeling including elasticity [994], biochemical pathways [187], and spatial variation of Young's modulus [874]. It has become a starting point for many plant physiological studies and has been obtained as a continuum limit of microscopic processes by modeling the cell wall as a viscous fluid with reinforced fibers [67, 317, 318].

In later chapters, we will further study the mechanics and growth of fiber-reinforced plant cells viewed as three-dimensional structures.

Chapter 5

Elastic Rods



We now consider the general problem of growing elastic filaments in space. A natural starting point is to model growing filaments as thin elastic rods subject to external constraints. The basic idea behind the theory of elastic rods is to replace the stresses acting inside a three-dimensional tubular structure by a resultant force and moment vectors attached to a curve. This procedure leads to the Kirchhoff equations [33, 221, 285, 478, 1282], relating averaged forces and moments to the curve's strains, which are characterized by its curvatures, shears, and extension. These equations provide the starting point for much theoretical analysis and numerical modeling and have been successfully used to model one-dimensional structures as varied as DNA, proteins, neurons, springs, tree branches, and underwater telecommunication cables.

The extension from elastic rods to morphoelastic rods is performed by taking into account possible axial extension as well as changes in material properties such as density, cross-sectional area, and intrinsic curvature, due to growth and remodeling. Various aspects of a theory of growing elastic Kirchhoff rods were discussed in [451, 470, 473, 477, 478] mostly in biological contexts, and by O'Reilly and co-workers who developed a theory of planar growing plants with special emphasis on tip growth, branching, and constitutive laws [357, 991, 992] (see also [521] for

a three-dimensional extension of these ideas). Other related works include elastic growth in a fluid environment [1075, 1337] and thermo-elastic rods [213, 499, 500].

In this chapter, we first summarize the theory of Kirchhoff elastic rods by deriving balance laws for relevant mechanical quantities attached to a space curve. In the next chapter, using various examples, we develop a theory of growing elastic rods following [786, 917]. We show that a growing filament can develop stresses due either to its global geometry or boundary conditions. In turn, these stresses can be sufficient to cause buckling and, in the case of biological systems, initiate morphogenesis.

5.1 The Kinematics of Curves and Rods

5.1.1 Curves and Frenet Frames

We define a dynamical *space curve* $\mathbf{r}(S, T)$ as a function of a material parameter S and time T , i.e., $\mathbf{r} : [0, L] \times [T_0, T_1] \rightarrow \mathbb{R}^3$. We assume that the curve is of class C^3 in S and C^2 in T . If the first two S -derivatives of the position vector are linearly independent at each $S \in [0, L]$ and for all time T , the curve is said to be *regular*.

At any time t , the *arc length* s of a point S , measuring the Euclidean distance along the curve, is defined as

$$s(S, t) = \int_0^S d\sigma \left| \frac{\partial \mathbf{r}(\sigma, T)}{\partial \sigma} \right|, \quad (5.1)$$

where $|\mathbf{r}| = \sqrt{\mathbf{r} \cdot \mathbf{r}}$ is the usual Euclidean norm.

The arc length is a convenient parameterization of the curve to extract basic geometric properties and we view, interchangeably, the space curve as either a function of the material parameter S or the arc length s unless otherwise specified. The unit tangent vector $\boldsymbol{\tau}$ to the space curve, $\mathbf{r}$, is

$$\boldsymbol{\tau} = \frac{\partial \mathbf{r}}{\partial s} \equiv \mathbf{r}'. \quad (5.2)$$

We use the tangent vector and its derivatives to construct the standard *Frenet–Serret frame* referred to here simply as the *Frenet frame*. The Frenet frame, $\{\boldsymbol{\tau}, \boldsymbol{\nu}, \boldsymbol{\beta}\}$ is a set of three orthonormal vectors consisting of the tangent, $\boldsymbol{\tau}$, normal, $\boldsymbol{\nu}$, and binormal, $\boldsymbol{\beta}$, vectors at each point of the curve $\mathbf{r}$. The normal vector is the unit vector along the derivative of the tangent vector with respect to the arc length

$$\frac{\partial \boldsymbol{\tau}}{\partial s} = \kappa \boldsymbol{\nu}, \quad (5.3)$$

where the *curvature*

$$\kappa = \left| \frac{\partial \boldsymbol{\tau}}{\partial s} \right| = |\mathbf{r}''|, \quad (5.4)$$

measures the turning rate of the tangent along the curve and is geometrically given by the inverse of the radius of the best fitting circle at a given point.

The binormal vector is obtained as the vector product of the tangent and normal vectors: that is,

$$\beta = \tau \times \nu. \quad (5.5)$$

Since $\beta' = \tau' \times \nu + \tau \times \nu' = \tau \times \nu'$, β' is parallel to ν and we can write

$$\beta' = -\tau \nu, \quad (5.6)$$

for a certain function τ , the *torsion*, that measures the rotation of the Frenet frame around the tangent τ as a function of arc length. The torsion is a measure of the curve nonplanarity. For a regular curve, we have

$$\tau = -\nu \cdot \frac{\partial \beta}{\partial s} = \frac{(\mathbf{r}' \times \mathbf{r}'') \cdot \mathbf{r}'''}{|\mathbf{r}' \times \mathbf{r}''|^2}. \quad (5.7)$$

Along the curve, the Frenet frame moves as a function of arc length according to a closed system of first-order differential equations, the *Frenet equations*:

$$\frac{\partial \tau}{\partial s} = \kappa \nu, \quad (5.8)$$

$$\frac{\partial \nu}{\partial s} = \tau \beta - \kappa \tau, \quad (5.9)$$

$$\frac{\partial \beta}{\partial s} = -\tau \nu. \quad (5.10)$$

Given a regular curve $\mathbf{r} = \mathbf{r}(s)$, a unique curvature $\kappa(s)$ and torsion $\tau(s)$ can be obtained through (5.4) and (5.7). The converse statement is the *fundamental theorem of curves in space*: Given differentiable functions $\kappa(s) > 0$ and $\tau(s)$, $s \in [0, L]$, there exists a unique curve with $\tau \neq 0$, such that s is its arc length, $\kappa(s)$ is its curvature, and $\tau(s)$ its torsion, up to a global rotation, translation, and orientation of the curve [169]. This result is a direct consequence of the existence and uniqueness of solutions for the initial value problem consisting of the system of 12 linear ordinary differential equations (5.2) and (5.8)–(5.10) with initial conditions on the position $\mathbf{r}(0)$ and frame $\{\tau(0), \nu(0), \beta(0)\}$.

5.1.2 Rods and General Frames

In order to study the motion of elastic filamentary structures, we extend the notion of space curves to rods. Geometrically, a *rod* is a space curve $\mathbf{r}(S, T)$, known as the *centerline*, equipped with two additional unit orthonormal vector fields $(\mathbf{d}_1(S, T), \mathbf{d}_2(S, T))$ of class C^2 , neither of which are along the tangent. These two

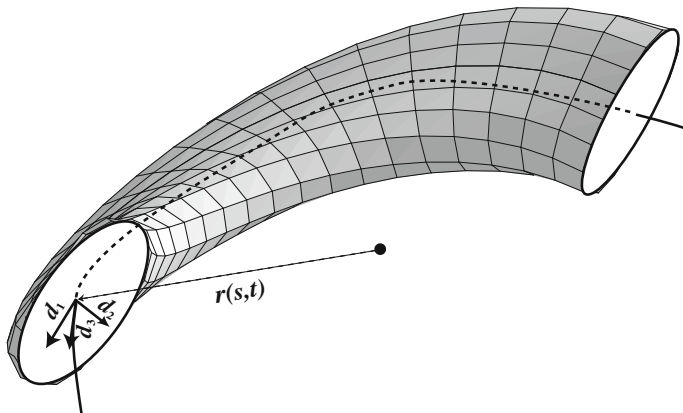


Figure 5.1 A rod consists of a centerline and a pair of unit orthonormal vectors. For a given point on the centerline, the vectors $\mathbf{d}_1$ and $\mathbf{d}_2$ are chosen to lie in the principal directions of the cross section. The vector $\mathbf{d}_3$ is a unit vector normal to the cross section.

unit vectors represent the orientation of a material cross section at S as illustrated in Figure 5.1. As before, $T \in [T_0, T_1]$ is time and $S \in [0, L]$ is a material parameter. A *configuration* is the shape of a rod. The *current configuration* is the shape of the rod at a given time t , whereas the *reference configuration* is a distinguished configuration used to evaluate strains. Here, we choose the material parameter S to be the arc length in a distinguished reference configuration, $\hat{\mathbf{r}}$, of the space curve. Hence, in this configuration, $\partial_S \hat{\mathbf{r}}$ is a unit vector. We will later identify this reference configuration with a stress-free configuration [205]. In the current configuration, we have

$$\frac{\partial \mathbf{r}}{\partial S} = \mathbf{v}, \quad (5.11)$$

where $\mathbf{v}$ is the *stretch vector*, with $|\mathbf{v}| > 0$ not necessarily equal to one.

The *general frame*, sketched in Figure 5.2, consists of the three orthonormal vectors $\{\mathbf{d}_1, \mathbf{d}_2, \mathbf{d}_3\}$ obtained by defining $\mathbf{d}_3(S, T) = \mathbf{d}_1(S, T) \times \mathbf{d}_2(S, T)$. We note that, by construction, $\{\mathbf{d}_1, \mathbf{d}_2, \mathbf{d}_3\}$ forms a right-handed orthonormal basis.

A complete kinematic description of the frame is given by

$$\frac{\partial \mathbf{d}_i}{\partial S} = \mathbf{u} \times \mathbf{d}_i, \quad i = 1, 2, 3, \quad (5.12)$$

$$\frac{\partial \mathbf{d}_i}{\partial T} = \mathbf{w} \times \mathbf{d}_i \quad i = 1, 2, 3, \quad (5.13)$$

where $\mathbf{u}$ is the *Darboux vector* and $\mathbf{w}$ is the *spin vector*. A rod is therefore characterized by six kinematic quantities. The Frenet frame is a particular case of the general frame obtained by choosing the vector $\mathbf{d}_3$ as the tangent and either $\mathbf{d}_1$ or $\mathbf{d}_2$ along the normal.

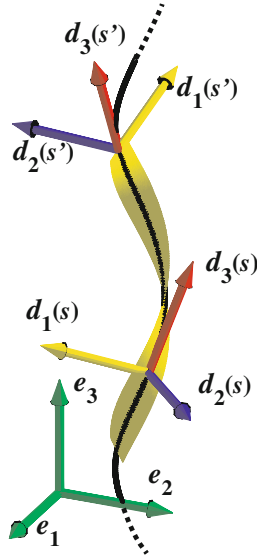


Figure 5.2 The general frame represents the evolution of a local basis along the rod. At two different material points s and s' , the general frame has different orientations. A vector attached on the centerline of the space curve can be expanded locally in these bases.

Since the general frame is a local basis, any vector $\mathbf{a}$ attached to the centerline can be expressed as a linear combination of the basis vector. Explicitly, we write

$$\mathbf{a} = a_1 \mathbf{d}_1 + a_2 \mathbf{d}_2 + a_3 \mathbf{d}_3, \quad (5.14)$$

where the components in the local basis are denoted by $\mathbf{a} = (a_1, a_2, a_3)$. We note that $|\mathbf{a}| = |\mathbf{a}|$. Here, we follow Antman's notation [33] and use **sans-serif** fonts to denote the components of a vector in the local basis. The first two components v_1, v_2 of the *stretch vector* $\mathbf{v}$ represent transverse shearing of the cross sections while $v_3 \neq 0$ is associated with stretching and compression. Since the vectors $\mathbf{d}_i$ are normalized, the norm of $\mathbf{v}$ gives the stretch of the rod during deformation away from the reference configuration: $\alpha = |\mathbf{v}| = |\mathbf{v}|$. Equivalently, we can write $\alpha = \partial s / \partial S$, where s is the current arc length.

The first two components (u_1, u_2) of the Darboux vector are associated with bending while u_3 represents twisting, that is, the rotation of the basis, but not the curve, around the $\mathbf{d}_3$ vector. It contains information on both the torsion of the centerline and on the rotation of the cross section for increasing values of S .

To understand the mathematical structure of the system, it is convenient to introduce an orthonormal matrix $\mathbf{D}$ describing the basis:

$$\mathbf{D} = [\mathbf{d}_1 \ \mathbf{d}_2 \ \mathbf{d}_3]. \quad (5.15)$$

This matrix can be used to extract the local components of a vector:

$$\mathbf{a} = \mathbf{D}\mathbf{a}. \quad (5.16)$$

An alternative representation of the kinematics is obtained in terms of matrices by introducing the *Darboux matrix* $\mathbf{U}(s, t)$ and the *spin matrix* $\mathbf{W}(s, t)$ as follows:

$$\frac{\partial \mathbf{D}}{\partial S} \equiv \begin{bmatrix} \frac{\partial \mathbf{d}_1}{\partial S} & \frac{\partial \mathbf{d}_2}{\partial S} & \frac{\partial \mathbf{d}_3}{\partial S} \end{bmatrix} = \mathbf{D}\mathbf{U}, \quad (5.17)$$

$$\frac{\partial \mathbf{D}}{\partial T} \equiv \begin{bmatrix} \frac{\partial \mathbf{d}_1}{\partial T} & \frac{\partial \mathbf{d}_2}{\partial T} & \frac{\partial \mathbf{d}_3}{\partial T} \end{bmatrix} = \mathbf{D}\mathbf{W}. \quad (5.18)$$

These two new matrices are the skew-symmetric matrices associated with the axial vectors $\mathbf{u}$ and $\mathbf{w}$, respectively,

$$\mathbf{U} = \begin{bmatrix} 0 & -u_3 & u_2 \\ u_3 & 0 & -u_1 \\ -u_2 & u_1 & 0 \end{bmatrix}, \quad \mathbf{W} = \begin{bmatrix} 0 & -w_3 & w_2 \\ w_3 & 0 & -w_1 \\ -w_2 & w_1 & 0 \end{bmatrix}. \quad (5.19)$$

The entries of $\mathbf{U}$ and $\mathbf{W}$ are not independent. By differentiating (5.17) with respect to time and (5.18) with respect to arc length and then equating their cross-derivatives, we obtain a compatibility relation for $\mathbf{U}$ and $\mathbf{W}$:

$$\frac{\partial \mathbf{U}}{\partial T} - \frac{\partial \mathbf{W}}{\partial S} = \mathbf{U}\mathbf{W} - \mathbf{W}\mathbf{U}. \quad (5.20)$$

We note that the two systems of linear partial differential equations (5.17) and (5.18) can be interpreted as a Lax pair for the nonlinear partial differential equations for the elements of the Darboux and spin vectors generated by the compatibility condition (5.20). Indeed, the natural kinematic structures of evolving rods have led to a large and beautiful body of work connecting the motion of curves to integrable systems [289, 453, 750, 752, 935]. However, this construction is purely geometric and has little to do with the evolution of elastic rods as governed by mechanical principles.

5.1.3 Inextensible, Unshearable Rods

A particularly important class of rods is obtained by choosing $\mathbf{v}_1 = \mathbf{v}_2 = 0$, and $\mathbf{v}_3 = 1$. In this case, $\alpha = 1$, and since we have $s = S$, there is no stretch and we can choose S to be the arc length in any configuration. The vector $\mathbf{d}_3$ is the tangent vector and there is no shear: The possible deformations of the rod are restricted so that the vectors spanning the cross sections remain perpendicular to the axis.

This geometric constraint is used to model rods which are both unshearable and inextensible (for simplicity, we refer to rods that are both inextensible and unshearable as *inextensible rods*). Geometrically, the vectors $\mathbf{d}_1$ and $\mathbf{d}_2$ lie in a plane normal to the axis and are related to the normal and binormal vectors by a rotation through the *register angle* φ ,

$$\mathbf{d}_1 = \nu \cos \varphi + \beta \sin \varphi, \quad (5.21)$$

$$\mathbf{d}_2 = -\nu \sin \varphi + \beta \cos \varphi. \quad (5.22)$$

This rotation implies that

$$\mathbf{u} = (\kappa \sin \varphi, \kappa \cos \varphi, \tau + \frac{\partial \varphi}{\partial S}), \quad (5.23)$$

where κ and τ are the usual Frenet curvature and torsion. These relations can also be inverted to yield φ , κ , and τ as functions of the Darboux vector components:

$$\cot \varphi = \frac{u_2}{u_1}, \quad (5.24)$$

$$\kappa = \sqrt{u_1^2 + u_2^2}, \quad (5.25)$$

$$\tau = u_3 + \frac{u'_2 u_1 - u'_1 u_2}{u_1^2 + u_2^2}. \quad (5.26)$$

The quantities τ , $\partial \varphi / \partial S$, and u_3 play related but distinct roles. The torsion τ is a property of the centerline alone and is a measure of its nonplanarity. Hence, a curve with null torsion is a plane curve. The quantity $\partial \varphi / \partial S$, the *excess twist*, is a property of the rod only. It represents the rotation of the local basis with respect to the Frenet frame as the arc length increases. An untwisted rod, characterized by $\partial \varphi / \partial S = 0$ is called a *Frenet rod*. In a Frenet rod, the angle φ between the binormal $\mathbf{b}$ and the vector field $\mathbf{d}_2$ is constant. Hence, the binormal is representative of the orientation of the local basis $\{\mathbf{d}_1, \mathbf{d}_2, \mathbf{d}_3\}$. The twist density, u_3 , is a property of both the space curve and the rod: It measures the rotation of the local basis around the space curve, defined by the Frenet equations, as the arc length increases. A rod with a straight centerline, $\tau = 0$, but with a twisted frame, $\partial \varphi / \partial S \neq 0$, may have the same twist density as a Frenet rod with helical centerline for which $\tau \neq 0$ and $\partial \varphi / \partial S = 0$.

Note that in the general case of an extensible and shearable rod, the components of the Darboux vector cannot be described purely by geometric parameters such as curvature, twist, and torsion since the material parameter S is not the arc length.

5.2 The Mechanics of Elastic Rods

Before considering the case of a growing rod, we review the fundamental equations for the dynamics of Kirchhoff rods. The dynamics of elastic rods can be derived from *Euler's laws* that are based on fundamental physical principles, namely the conservation of linear and angular momenta. Euler's first law states that the rate of change of linear momentum is equal to the total force acting on a body. Euler's second law postulates that the rate of change of angular momentum with respect to a given point is equal to the total couple acting on the body with respect to the same point.

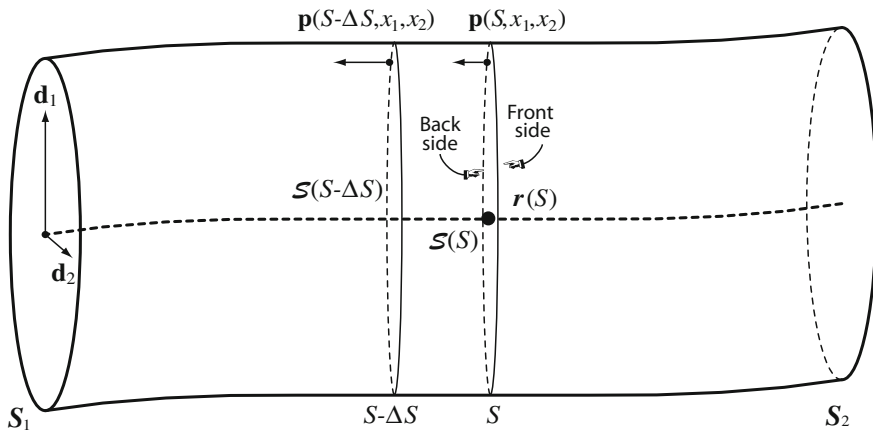


Figure 5.3 Forces and stresses acting on a given cross section with arc-length coordinate S due to neighboring sections at $S' < S - \Delta S$ and at $S' > S$.

5.2.1 Balance of Linear Momentum

The balance of linear momentum applied to a rod, as depicted in Figure 5.3, states that the rate of change of linear momentum of any segment of the rod is equal to the total force acting on the segment. We assume that the density is constant in time and only varies along the arc length. The shape of a cross section is also assumed invariant with respect to time.

We consider a segment of arbitrary length ΔS lying between the cross section $S(S)$ and the cross section $S(S - \Delta S)$. The linear momentum of that segment is

$$\int_{S-\Delta S}^S dS \left[\int_S dx_1 dx_2 \rho \frac{\partial}{\partial T} (\mathbf{r} + x_1 \mathbf{d}_1 + x_2 \mathbf{d}_2) \right], \quad (5.27)$$

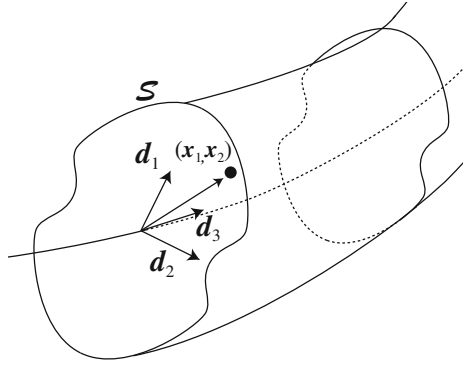
where ρ is the mass density defined as mass per unit reference volume, and x_1 and x_2 are the coordinates of a material point in the section along the directions $\mathbf{d}_1$ and $\mathbf{d}_2$, respectively. By the definition of the centerline, the point $x_1 = 0$, $x_2 = 0$ in (5.27) is the *centroid* of the cross section (see Figure 5.4). Hence, the terms linear in x_1 and x_2 vanish identically and the rate of linear momentum is

$$\int_{S-\Delta S}^S (\rho A) \frac{\partial^2 \mathbf{r}}{\partial T^2} dS, \quad (5.28)$$

where A is the cross-sectional area and (ρA) defines a *lineal density*, that is, the mass per unit reference length.

The total force acting on the same segment is the sum of the internal contact forces and the external body forces. We define $\mathbf{p}(S, x_1, x_2)$ as the *contact force* per unit area

Figure 5.4 Cross section of a rod and local coordinates.



exerted at the point (x_1, x_2) on the back side, in the sense of increasing S of $S(S)$, by the sections $S(S')$ with $S' > S$. The contact force $\mathbf{n}(S)$ exerted on the back side of $S(S)$ by the previous sections is called the *resultant force* at S , and is given by

$$\mathbf{n}(S, T) = \int_S dx_1 dx_2 \mathbf{p}(S, x_1, x_2, T). \quad (5.29)$$

The component n_3 of the force $\mathbf{n}$ along $\mathbf{d}_3$, in the sense of increasing S , is negative if the rod is subject to compressive forces, and positive in the case of tensile forces.

Note that by the action–reaction principle, the contact force per unit area exerted at the point (x_1, x_2) on the front side, in the sense of decreasing S , of $S(S)$ by the segment $S(S - \Delta S)$ is just $-\mathbf{p}(S - \Delta S, x_1, x_2, T)$. As a consequence, the resultant force exerted on the segment, including the contributions from both sides,

$$\mathbf{n}(S, T) - \mathbf{n}(S - \Delta S, T) = \int_{S-\Delta S}^S \frac{\partial \mathbf{n}(S, T)}{\partial S} dS. \quad (5.30)$$

Therefore, the total forces acting on the segment are the sum of the above contact force and the total body force acting on the segment, that is,

$$\mathbf{n}(S, T) - \mathbf{n}(S - \Delta S, T) + \int_{S-\Delta S}^S dS \mathbf{f}(S, T) = \int_{S-\Delta S}^S dS \left[\mathbf{f}(S, T) + \frac{\partial \mathbf{n}(S, T)}{\partial S} \right], \quad (5.31)$$

where $\mathbf{f}(S)$ is the *body force* per unit reference length applied on the cross section at S . The balance of linear momentum dictates that

$$\int_{S-\Delta S}^S (\rho A) \frac{\partial^2 \mathbf{r}}{\partial T^2} dS = \int_{S-\Delta S}^S dS \left[\mathbf{f}(S, T) + \frac{\partial \mathbf{n}(S, T)}{\partial S} \right], \quad (5.32)$$

that we rewrite as

$$\int_{S-\Delta S}^S dS \left[\mathbf{f}(S, T) + \frac{\partial \mathbf{n}(S, T)}{\partial S} - (\rho A) \frac{\partial^2 \mathbf{r}}{\partial T^2} \right] = \mathbf{0}. \quad (5.33)$$

Assuming that the integrand is continuous in S and given the fact that this balance law is valid for arbitrary ΔS , the integrand must vanish identically and we obtain

$$\frac{\partial \mathbf{n}}{\partial S} + \mathbf{f} = \rho A \frac{\partial^2 \mathbf{r}}{\partial T^2}. \quad (5.34)$$

The process of obtaining a partial differential equation from an integral relationship expressed over an arbitrary domain such as (5.33) is a central tool of continuum mechanics called a *localization procedure*.

5.2.2 Balance of Angular Momentum

For the balance of angular momentum, we compute the total couple with respect to the origin and the total angular momentum about the same point. The total angular momentum is given by

$$\int_{S-\Delta S}^S dS \int_S dx_1 dx_2 \rho (\mathbf{r} + x_1 \mathbf{d}_1 + x_2 \mathbf{d}_2) \times \frac{\partial}{\partial T} (\mathbf{r} + x_1 \mathbf{d}_1 + x_2 \mathbf{d}_2). \quad (5.35)$$

We choose the vectors $\mathbf{d}_1$ and $\mathbf{d}_2$ so that they lie along the principal directions of inertia of the cross section. Therefore, the product of inertia $\int_S dx_1 dx_2 x_1 x_2$ vanishes identically and the only nonvanishing terms in (5.35) are

$$\int_{S-\Delta S}^S dS \left[(\rho A) \mathbf{r} \times \frac{\partial \mathbf{r}}{\partial T} + \rho \left(I_2 \mathbf{d}_1 \times \frac{\partial \mathbf{d}_1}{\partial T} + I_1 \mathbf{d}_2 \times \frac{\partial \mathbf{d}_2}{\partial T} \right) \right], \quad (5.36)$$

where the second moments of area I_1 and I_2 are defined as

$$I_1 = \int_S x_2^2 dx_1 dx_2, \quad I_2 = \int_S x_1^2 dx_1 dx_2. \quad (5.37)$$

We define $\mathbf{m}(S, T)$, the *resultant couple*, as the couple acting on a section at S due to the adjacent segment $S(S')$ with $S' > S$. However, the total couple exerted on the reference segment is not simply $\mathbf{m}(S, T) - \mathbf{m}(S - \Delta, T)$, because the moments $\mathbf{m}(S, T)$ and $\mathbf{m}(S - \Delta S, T)$ are not taken with respect to the same point. Integrating over the section, the resultant couple produced by the contact force $\mathbf{p}$ is

$$\begin{aligned}
& \mathbf{m}(S, T) - \mathbf{m}(S - \Delta S, T) \\
& + \mathbf{r}(S, T) \times \mathbf{n}(S, T) - \mathbf{r}(S - \Delta S, T) \times \mathbf{n}(S - \Delta S, T) \\
& + \int_{S-\Delta S}^S dS [\mathbf{r}(S, T) \times \mathbf{f}(S, T) + \mathbf{l}(S, T)] \\
& = \int_{S-\Delta S}^S dS \left[\frac{\partial \mathbf{m}}{\partial S} + \frac{\partial}{\partial S} (\mathbf{r} \times \mathbf{n}) + \mathbf{r} \times \mathbf{f} + \mathbf{l} \right], \quad (5.38)
\end{aligned}$$

where we have taken into account both the couple created by the body force and an external *body couple* $\mathbf{l}(S)$. The conservation of angular momentum now reads

$$\begin{aligned}
& \int_{S-\Delta S}^S dS \left[\frac{\partial \mathbf{m}}{\partial S} + \frac{\partial}{\partial S} (\mathbf{r} \times \mathbf{n}) + \mathbf{r} \times \mathbf{f} + \mathbf{l} \right] \\
& = \frac{\partial}{\partial T} \int_{S-\Delta S}^S dS \left[(\rho A) \mathbf{r} \times \frac{\partial \mathbf{r}}{\partial T} + \rho \left(I_2 \mathbf{d}_1 \times \frac{\partial \mathbf{d}_1}{\partial T} + I_1 \mathbf{d}_2 \times \frac{\partial \mathbf{d}_2}{\partial T} \right) \right]. \quad (5.39)
\end{aligned}$$

Assuming again continuity of the integrands and using Equation (5.34) to simplify derivatives of $\mathbf{n}$, we can localize this relation to obtain

$$\frac{\partial \mathbf{m}}{\partial S} + \frac{\partial \mathbf{r}}{\partial S} \times \mathbf{n} + \mathbf{l} = \rho \left(I_2 \mathbf{d}_1 \times \frac{\partial^2 \mathbf{d}_1}{\partial T^2} + I_1 \mathbf{d}_2 \times \frac{\partial^2 \mathbf{d}_2}{\partial T^2} \right). \quad (5.40)$$

In problems with adhesion or contact, the integrands appearing in (5.33) and (5.39) may not be continuous. In this case, the possibility of jumps has to be taken into account [990]. However, this case will not be considered here.

5.2.3 Local Mechanics of Rods

To summarize, the stress acting on the cross section at $\mathbf{r}(S)$ from the part of the rod with $S' > S$ gives rise to a resultant force $\mathbf{n}(S, T)$ and resultant moment $\mathbf{m}(S, T)$ attached to the central curve. The balance of linear and angular momenta yields the two fundamental equation of mechanical balance in elastic rods [33]:

$$\frac{\partial \mathbf{n}}{\partial S} + \mathbf{f} = \rho A \frac{\partial^2 \mathbf{r}}{\partial T^2}, \quad (5.41)$$

$$\frac{\partial \mathbf{m}}{\partial S} + \frac{\partial \mathbf{r}}{\partial S} \times \mathbf{n} + \mathbf{l} = \rho \left(I_2 \mathbf{d}_1 \times \frac{\partial^2 \mathbf{d}_1}{\partial T^2} + I_1 \mathbf{d}_2 \times \frac{\partial^2 \mathbf{d}_2}{\partial T^2} \right), \quad (5.42)$$

where $\mathbf{f}(S, T)$ and $\mathbf{l}(S, T)$ are the body force and body couple per unit reference length applied on the cross section at S . These body forces and couples can be used to model different effects such as short- and long-range interactions between

different parts of the rod, or can be the result of active stress, self-contact, or contact with another body.

The quantity $A(S)$ denotes the cross-sectional area, in the reference configuration and $\rho(S)$ is the mass density, defined as a mass per unit reference volume. Here $I_1(S)$ and $I_2(S)$ are the second moments of area of the cross section corresponding to the directions $\mathbf{d}_1$ and $\mathbf{d}_2$, respectively, at a material point S . They are given explicitly in (5.37) and several examples are given in Section 5.5.

To close the system, we must specify a constitutive relationship between the resultant stresses and strains, that is, in the case of rods, between the resultant force and couple and the curvature and stretch vectors.

5.3 Constitutive Laws for Elastic Rods

5.3.1 Extensible and Shearable Elastic Rods

First, we consider the case where the rod is both extensible and shearable. We further assume that the rod is *hyperelastic*: We assume that there exists a *strain-energy density function* (also referred to simply as a *strain-energy function*) $W = W(\mathbf{u} - \hat{\mathbf{u}}, \mathbf{v} - \hat{\mathbf{v}}, S)$ such that the constitutive relations for the resultant moment and force in the local basis are given by

$$\mathbf{m} = \mathbf{f}(\mathbf{u} - \hat{\mathbf{u}}, \mathbf{v} - \hat{\mathbf{v}}, S) = \partial_{\mathbf{y}} W(\mathbf{u} - \hat{\mathbf{u}}, \mathbf{v} - \hat{\mathbf{v}}, S), \quad (5.43)$$

$$\mathbf{n} = \mathbf{g}(\mathbf{u} - \hat{\mathbf{u}}, \mathbf{v} - \hat{\mathbf{v}}, S) = \partial_{\mathbf{z}} W(\mathbf{u} - \hat{\mathbf{u}}, \mathbf{v} - \hat{\mathbf{v}}, S), \quad (5.44)$$

where $\mathbf{y} = \mathbf{u} - \hat{\mathbf{u}}$ and $\mathbf{z} = \mathbf{v} - \hat{\mathbf{v}}$.

Here, $\hat{\mathbf{v}}, \hat{\mathbf{u}}$ are the strains in the unstressed reference configuration, that is, $\mathbf{m} = \mathbf{n} = \mathbf{0}$ when $\mathbf{u} = \hat{\mathbf{u}}$, and $\mathbf{v} = \hat{\mathbf{v}}$. Without loss of generality, one can choose the general frame so that $\hat{\mathbf{v}}_1 = \hat{\mathbf{v}}_2 = 0$. Furthermore, if S is the arc length of the unstressed configuration then $\hat{\mathbf{v}}_3 = 1$.

Typically, W is assumed to be continuously differentiable, convex, and to satisfy the growth condition at infinity:

$$\frac{W(\mathbf{y}, \mathbf{z})}{|\mathbf{y}|^2 + |\mathbf{z}|^2} \rightarrow \infty, \quad \text{as } |\mathbf{y}|^2 + |\mathbf{z}|^2 \rightarrow \infty. \quad (5.45)$$

The rod is *uniform* if its material properties do not change along its length (i.e., W has no explicit dependence on S) and the stress-free strains $\hat{\mathbf{v}}, \hat{\mathbf{u}}$ are independent of S as well.

5.3.2 Inextensible and Unshearable Rods

In the second case, we assume that the rod is inextensible and unshearable. Therefore, we take $\mathbf{v} = \mathbf{d}_3$ and the material parameter becomes the arc length in all

configurations, that is, $S = s$. In this case, there is no constitutive relationship for the resultant force and the strain-energy function is a function of only $(\mathbf{u} - \hat{\mathbf{u}})$:

$$\mathbf{m} = \partial_{\mathbf{y}} W(\mathbf{u} - \hat{\mathbf{u}}) = \mathbf{f}(\mathbf{u} - \hat{\mathbf{u}}). \quad (5.46)$$

For a quadratic strain-energy $W = \mathbf{y}^T \mathbf{K} \mathbf{y}$, the constitutive relations for the local basis components $\mathbf{m}$ are

$$\mathbf{m} = \mathbf{K}(\mathbf{u} - \hat{\mathbf{u}}), \quad \mathbf{K} = \begin{bmatrix} K_1 & K_{12} & K_{13} \\ K_{12} & K_2 & K_{23} \\ K_{13} & K_{23} & K_3 \end{bmatrix}, \quad K_1 \geq K_2. \quad (5.47)$$

The condition $K_1 \geq K_2$ corresponds to the choice of labeling of the vectors $\mathbf{d}_1$ and $\mathbf{d}_2$. If, in a basis $K_1 < K_2$ then a proper relabeling of these vectors leads to $K_1 \geq K_2$. Also, note that, in general, we can choose the vector $\mathbf{d}_1$ so that either $K_{12} = K_{21} = 0$ or $\hat{u}_1 = 0$ or $\hat{u}_2 = 0$.

In the simplest, and most widely used case, the energy is further simplified by taking the matrix $\mathbf{K}$ to be diagonal, in which case

$$W_1 = K_1(u_1 - \hat{u}_1)^2 + K_2(u_2 - \hat{u}_2)^2 + K_3(u_3 - \hat{u}_3)^2, \quad (5.48)$$

where $\hat{\mathbf{u}}$ is the intrinsic Darboux vector that defines the shape of the rod when unloaded. The coefficients K_1 and K_2 are the *principal bending stiffnesses* of the rod, and K_3 is the *torsional stiffness*.

In order to obtain explicit relationships between the geometric properties of the cross sections and the material properties of the elastic material that make up the rod, the classic approach is to compute the response of an elastic cylinder under bending and torsion within the framework of linear elasticity. We outline these results in Section 5.5. Explicitly, the resultant moment and coefficients $\{K_1, K_2, K_3\}$ are

$$\mathbf{m} = EI_1(u_1 - \hat{u}_1)\mathbf{d}_1 + EI_2(u_2 - \hat{u}_2)\mathbf{d}_2 + \mu J(u_3 - \hat{u}_3)\mathbf{d}_3, \quad (5.49)$$

where E is the Young's modulus, μ is the shear modulus, J is a parameter that depends on the cross-sectional shape and I_1 and I_2 are the second moments of area given by (5.37). By identification with (5.48), we have $EI_1 \equiv K_1$ and $EI_2 \equiv K_2$, as well as $\mu J \equiv K_3$. Explicit forms for J and I_1, I_2 are given in Section 5.5.

From (5.49), we can obtain two important dimensionless parameters

$$a = \frac{I_2}{I_1}, \quad b = \frac{\mu J}{EI_1} = \frac{J}{2I_1(1 + \sigma)}, \quad (5.50)$$

where we have used the relations $\mu = 2E(1 + \sigma)$. Here, σ denotes the *Poisson's ratio*, a measure of a material compressibility defined for an isotropic linear elastic material as the ratio of transverse contraction strain to longitudinal extension strain

in the direction of a stretching force. For most materials, it varies between 0 and $1/2$, the latter value corresponding to incompressible materials.

The constant a measures the asymmetry of the cross section. Our convention is to orient the vector fields $\mathbf{d}_1$ and $\mathbf{d}_2$ such that I_1 and I_2 are the larger and smaller second moments of area, respectively. In this case, we have

$$0 < a \leq 1, \quad (5.51)$$

the value 1 being reached in the dynamically symmetric case in which the second moments of area are identical.

The constant b is the *scaled torsional stiffness*. It involves the constant $1/(1 + \sigma)$, which ranges from $2/3$ attained for incompressible materials to 1, corresponding to materials for which there is no restriction under stretching.

5.3.3 Isotropic, Extensible, but Unshearable Rods

For many applications, rods can be modeled as inextensible and unshearable. However, for the modeling of a growing rod, it will be interesting to consider the case where the rod is unshearable and extensible with a quadratic energy. In this case, in addition to (5.49), we have an equation relating the elastic stretch $\alpha \equiv v_3 \equiv \partial s / \partial S$ to the tension:

$$\mathbf{m} = E I_1 (u_1 - \hat{u}_1) \mathbf{d}_1 + E I_2 (u_2 - \hat{u}_2) \mathbf{d}_2 + \mu J (u_3 - \hat{u}_3) \mathbf{d}_3, \quad (5.52)$$

$$n_3 = E A (\alpha - 1). \quad (5.53)$$

For a straight rod under uniaxial tension, this last constitutive equation is simply Hooke's law. Note that since S is not the arc length, the Darboux vector $\mathbf{u}$ is not given by (5.23), but it is scaled by an elastic stretch factor α so that

$$\mathbf{u} = \alpha (\kappa \sin \varphi, \kappa \cos \varphi, \tau + \frac{\partial \varphi}{\partial s}). \quad (5.54)$$

However, the intrinsic Darboux vector $\hat{\mathbf{u}}$ is given by the intrinsic geometric curvatures in the reference configuration; it is not scaled by α since it is a material property of the rod in the reference configuration.

5.4 Scaling

To further simplify the system in the quadratic inextensible case with equal second moments of area $I = I_1 = I_2$, we scale the variables by choosing a combination of the length $[L]$, time $[T]$, and mass $[M]$ units in the following way:

$$[M] = \rho\sqrt{AI}, \quad \frac{[M][L]^3}{[T]^2} = EI. \quad (5.55)$$

Explicitly, this scaling reads

$$\begin{aligned} t &\rightarrow t\sqrt{I\rho/AE} & s &\rightarrow s\sqrt{I/A}, \\ \mathbf{n} &\rightarrow A\mathbf{E}\mathbf{n} & \mathbf{m} &\rightarrow \mathbf{m}E\sqrt{AI}, \\ \mathbf{u} &\rightarrow \mathbf{u}\sqrt{A/I} & \mathbf{w} &\rightarrow \mathbf{w}\sqrt{AE/I\rho}. \end{aligned} \quad (5.56)$$

Under this rescaling, the properties of a rod with a circular cross section can be conveniently described by a single parameter: the ratio of bending to torsional stiffnesses, given by

$$\Gamma \equiv \frac{\mu J}{EI_1} = \frac{1}{1+\sigma} \in \left[\frac{2}{3}, 1\right], \quad (5.57)$$

where σ denotes the Poisson's ratio.

5.5 Bending and Torsional Stiffnesses

Within the framework of linear elasticity theory [761, 806, 1179] it is known that the parameter J , introduced in (5.49), is determined by

$$J = I_1 + I_2 + \int_S dx_1 dx_2 \left(x_1 \frac{\partial \varphi}{\partial x_2} - x_2 \frac{\partial \varphi}{\partial x_1} \right). \quad (5.58)$$

The *warping function* $\varphi(x_1, x_2)$ provides a measure of the displacement, δs , that each material point in a given cross section experiences when the rod is twisted uniformly. In the linear theory, this displacement is determined by

$$\delta s(x_1, x_2) = \mathbf{u}_3 \varphi(x_1, x_2). \quad (5.59)$$

The warping function is the solution of a Neumann problem for the Laplace equation, namely

$$\frac{\partial^2 \varphi}{\partial x_1^2} + \frac{\partial^2 \varphi}{\partial x_2^2} = 0 \quad \text{inside } S, \quad (5.60)$$

$$\frac{\partial \varphi}{\partial x_1} N_1 + \frac{\partial \varphi}{\partial x_2} N_2 = x_2 N_1 - x_1 N_2 \quad \text{on } \partial S, \quad (5.61)$$

where N_1 and N_2 are the components of the exterior unit vector normal to the boundary ∂S of the cross section in the $\mathbf{d}_1$ and $\mathbf{d}_2$ directions.

In the case of simply connected cross sections, the expression (5.58) for J can be formulated in terms of the *stress function* ψ , defined as the harmonic function conjugate to φ :

$$\frac{\partial \varphi}{\partial x_1} = \frac{\partial \psi}{\partial x_2}, \quad \frac{\partial \varphi}{\partial x_2} = -\frac{\partial \psi}{\partial x_1}. \quad (5.62)$$

The stress function ψ is the solution of the following Dirichlet problem for the Laplace equation:

$$\frac{\partial^2 \psi}{\partial x_1^2} + \frac{\partial^2 \psi}{\partial x_2^2} = 0 \quad \text{inside } S, \quad (5.63)$$

$$\psi = \frac{x_1^2 + x_2^2}{2} \quad \text{on } \partial S. \quad (5.64)$$

Substituting (5.62) into (5.58), we obtain

$$J = I_1 + I_2 - \int_S \left(x_1 \frac{\partial \psi}{\partial x_1} + x_2 \frac{\partial \psi}{\partial x_2} \right) dx_1 dx_2, \quad (5.65)$$

which, using the divergence theorem and (5.64), can be simplified to

$$J = 2 \int_S \psi \, dx_1 dx_2 - I_1 - I_2. \quad (5.66)$$

The explicit computations of I_1 , I_2 , and J for various shapes can be found in classic textbooks [1179]. Here, we give the results for elliptic, circular, and rectangular sections:

- **Elliptic cross sections:** If we take A and B ($A < B$) to be the semi-axes of an ellipse in the $\mathbf{d}_1$ and $\mathbf{d}_2$ directions, respectively, we have

$$I_1 = \frac{\pi A B^3}{4}, \quad I_2 = \frac{\pi A^3 B}{4}, \quad (5.67)$$

$$J = \frac{\pi A^3 B^3}{A^2 + B^2} = \frac{4 I_1 I_2}{I_1 + I_2}, \quad a = \frac{A^2}{B^2}, \quad b = \frac{1}{1 + \sigma} \frac{2a}{1 + a}. \quad (5.68)$$

Applying the scaling (5.56), the scaled semi-axes become, respectively, $2\sqrt{a}$ and 2.

- **Circular cross sections:** In the particular case of rods with uniform circular cross section of radius R , the specialization of the previous case with $A = B = R$ gives

$$I_1 = I_2 = \frac{J}{2} = \frac{\pi R^4}{4}, \quad (5.69)$$

which implies $a = 1$ and $b = \Gamma$.

- **Rectangular cross sections:** If A and B denote the lengths of the rectangle in the $\mathbf{d}_1$ and $\mathbf{d}_2$ directions, respectively, where $A < B$, we have

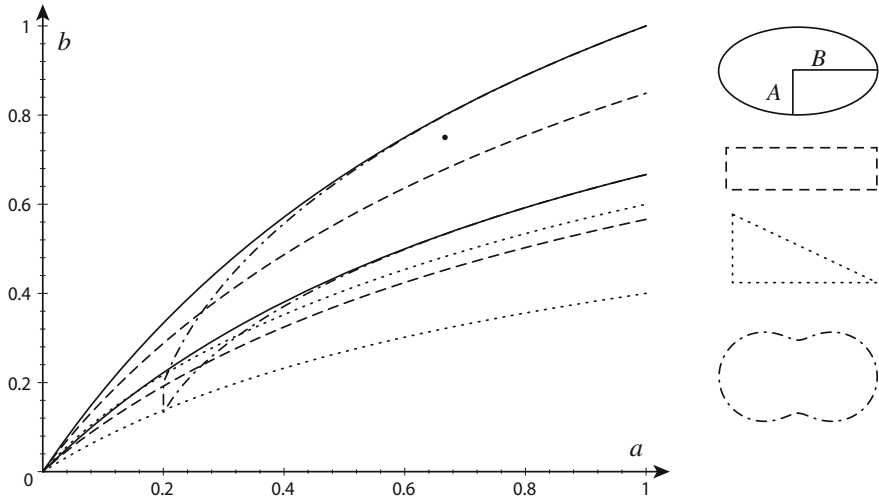


Figure 5.5 The domains covered in the (a, b) plane by various cross section shapes are enclosed in black lines (solid = ellipses, dash = rectangles, dot = right triangles, dash-dot = limaçons).

$$I_1 = \frac{AB^3}{12}, \quad I_2 = \frac{A^3B}{12}, \quad (5.70)$$

$$J = \frac{A^3B}{3} - \frac{64A^4}{\pi^5} \tanh \frac{\pi B}{2A} \pm 0.502\%, \quad (5.71)$$

$$a = \frac{A^2}{B^2}, \quad b = \frac{1}{1 + \sigma} \left(2a - \frac{384a^{\frac{3}{2}}}{\pi^5} \tanh \frac{\pi B}{2A} \right) \pm 0.502\%. \quad (5.72)$$

Under the scaling (5.56), the scaled lengths of the rectangle are $2\sqrt{3}$ and $2\sqrt{3}a$. In the case of a square cross section ($a = 1$), the expression for b reduces to

$$b = 0.859 \frac{1}{1 + \sigma} \pm 0.502\%. \quad (5.73)$$

Figure 5.5 shows the domain covered in the (a, b) plane for different particular shapes. More data can be found, for example, in [1119]. Rods with cross sections made up of assembled flat pieces, like X or H shapes, have low torsional stiffnesses (small b).

5.6 The Kirchhoff Elastic Rod Model: A Summary

The most commonly used model of elastic rods is obtained by assuming that the rod is unshearable and inextensible as detailed in Section 5.3.2 with a diagonal constitutive relationship. In this case, we have the following set of equations for the position

vector $\mathbf{r}$, basis $\mathbf{D} = [\mathbf{d}_1, \mathbf{d}_2, \mathbf{d}_3]$, Darboux and spin matrices $\mathbf{U}$, $\mathbf{W}$, and resultant force and couple $\mathbf{n}$ and $\mathbf{m}$

1. Kinematics

$$\frac{\partial \mathbf{r}}{\partial s} = \mathbf{d}_3, \quad (5.74)$$

$$\frac{\partial \mathbf{D}}{\partial s} = \mathbf{D}\mathbf{U}, \quad (5.75)$$

$$\frac{\partial \mathbf{D}}{\partial t} = \mathbf{D}\mathbf{W}, \quad (5.76)$$

$$\mathbf{U} = \begin{bmatrix} 0 & -u_3 & u_2 \\ u_3 & 0 & -u_1 \\ -u_2 & u_1 & 0 \end{bmatrix}, \quad (5.77)$$

$$\mathbf{W} = \begin{bmatrix} 0 & -w_3 & w_2 \\ w_3 & 0 & -w_1 \\ -w_2 & w_1 & 0 \end{bmatrix}. \quad (5.78)$$

2. Mechanics

$$\frac{\partial \mathbf{n}}{\partial s} + \mathbf{f} = \rho A \frac{\partial^2 \mathbf{r}}{\partial t^2}, \quad (5.79)$$

$$\frac{\partial \mathbf{m}}{\partial s} + \frac{\partial \mathbf{r}}{\partial s} \times \mathbf{n} + \mathbf{l} = \rho \left(I_2 \mathbf{d}_1 \times \frac{\partial^2 \mathbf{d}_1}{\partial t^2} + I_1 \mathbf{d}_2 \times \frac{\partial^2 \mathbf{d}_2}{\partial t^2} \right). \quad (5.80)$$

3. Constitutive law

$$\mathbf{m} = EI_1(u_1 - \hat{u}_1)\mathbf{d}_1 + EI_2(u_2 - \hat{u}_2)\mathbf{d}_2 + \mu J(u_3 - \hat{u}_3)\mathbf{d}_3. \quad (5.81)$$

A few comments are in order:

1. The material is described by three stiffnesses, EI_2 , EI_2 , and μJ , its density ρ and by its geometry defined by the cross-sectional area A , the length L , and the intrinsic Darboux curvatures $\hat{\mathbf{u}}$.
2. The system is characterized by 15 variables: three coordinates $\mathbf{r}$, three curvatures $\mathbf{u}$, three spins $\mathbf{w}$, three resultant forces $\mathbf{n}$, and three resultant moments $\mathbf{m}$. The last three sets of equations (5.79–5.81) provide nine equations. The first equation (5.74) provides another three equations. The second and third equations (5.75–5.76) are a set of nine equations, but only three of these nine equations are independent since the matrix $\mathbf{D}$ is orthonormal, and these two sets are connected to each other by the compatibility condition (5.20).
3. The body force $\mathbf{f}$ and body couple $\mathbf{l}$ are given based on the physics of the problem. They can represent gravity, magnetic forces, electrical forces, self-contact, etc. In most problems of interest, body couples are not generated and can therefore be neglected.

4. The rotary inertia terms, given by the right-hand side of (5.80), are often ignored based on an analysis of typical time scales [46]. They can, nevertheless, be of importance in some dynamic phenomena. For instance, they are required to capture the vibration frequencies of a loaded rod close to its buckling point [942].
5. A rod is said to be *initially straight* if the intrinsic curvatures vanish identically $\hat{\mathbf{u}} = \mathbf{0}$.
6. A remarkable feature of the model, known as the *Kirchhoff kinetic analogy*, is that the equations governing the equilibrium solutions are formally equivalent to the Euler equations describing the motion of a top, that is, a rigid body with a fixed point under an external force field. This equivalence is achieved by identifying the axis of the top with the tangent vector of the rod, and the time with the rod's arc length. For each equilibrium configuration of a rod, the tangent vector as a function of the arc length defines a curve on a unit sphere as time evolves. Similarly, in the motion of a top, the axis draws a curve on the unit sphere. The Kirchhoff analogy establishes that to each solution of the Euler equations for tops in time, there exists an equilibrium solution of the Kirchhoff equations for rods in space. In the case of planar motion (where the rigid body reduces to a simple pendulum) this analogy was already known by Bernoulli and Euler [685, art. 620]. The statics of rods is thus intimately connected to the dynamics of spinning tops. For instance, if $\hat{\mathbf{u}}_2$ vanishes identically, the equations for the rods are equivalent to the Lagrange case of the Euler equation (a symmetric top) which are known to be completely integrable [471, 959]. An example of a solution of the top, together with the corresponding elastic rod, is shown in Figure 5.6.

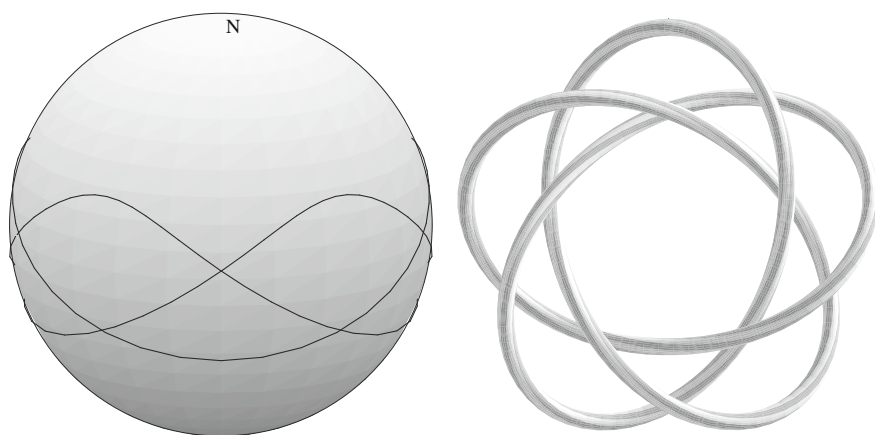


Figure 5.6 The Kirchhoff analogy. The evolution in time of the axis of the Lagrange top is equivalent to the evolution in space of the tangent vector of an inextensible transversely isotropic rod with quadratic elastic energy. Left. The tip of the top axis draws a periodic curve on the unit sphere. Right. The equivalent rod forms a torus knot in space.

5.7 Example: Helical Rods

An important class of solutions consists of elastic rods with constant Frenet curvature and torsion. They can be either straight rods if both curvature and torsion vanish, circular rods if only torsion vanishes, or helical if neither vanishes. Helices arise in nanosprings [846], carbon nanotubes, α -helices [831], proteins [943, 944], DNA [92, 826] and macromolecules [675, 1261], lipid bilayers [565, 1129], bacterial flagella in *Salmonella* and *Escherichia coli* [679, 817], aerial hyphae in actinomycetes [814], bacterial shapes in spirochetes [454], horns, tendrils, vines [470], screws [133], springs, and helical staircases [226, 417]. In many situations it is beneficial to model such structures as elastic rods.

We first show that there is a large family of helical structures that are solutions of the static inextensible Kirchhoff equations in the absence of distributed body forces and couples, i.e., $\mathbf{f} = \mathbf{l} = \mathbf{0}$ in (5.79–5.80). For simplicity, we consider here the transversely isotropic quadratic case where W has the form (5.48) with $K_2 = K_1$. The existence of helical equilibria for arbitrary strain-energy functions W was considered in [205].

5.7.1 Geometry of Helices

We consider a helical space curve, parameterized by arc length, s , turning around a cylinder of radius R whose central axis points along the fixed $\mathbf{e}_1$ -axis:

$$\mathbf{r} = P\delta s\mathbf{e}_1 + R\cos(\delta s)\mathbf{e}_2 + R\sin(\delta s)\mathbf{e}_3, \quad (5.82)$$

where $\delta = \pm 1/\sqrt{P^2 + R^2}$. The choice $+$ ($P > 0$) defines a right-handed helix. We use Maxwell's convention [844] and define right-handedness as the handedness of a common screw. The height (along the $\mathbf{e}_1$ -axis) per turn of the helix, known as the *pitch*, is $h = 2\pi|P|$ and the length of the curve per turn is $l = 2\pi/\delta$. For a helix of N turns, the total height is $H = 2\pi|P|N$ and the total filament length is $L = 2\pi N/|\delta|$. A sketch of a helical rod with an applied twist $L\gamma$ is shown in Figure 5.7. The Frenet frame for this helix is

$$\boldsymbol{\tau}(s) = P\delta\mathbf{e}_1 - R\delta\sin(\delta s)\mathbf{e}_2 + R\delta\cos(\delta s)\mathbf{e}_3, \quad (5.83)$$

$$\boldsymbol{\nu}(s) = -\cos(\delta s)\mathbf{e}_2 - \sin(\delta s)\mathbf{e}_3, \quad (5.84)$$

$$\boldsymbol{\beta}(s) = -R\delta\mathbf{e}_1 + P\delta\sin(\delta s)\mathbf{e}_2 - P\delta\cos(\delta s)\mathbf{e}_3, \quad (5.85)$$

with Frenet curvature, κ , and torsion, τ given by

$$\kappa = R\delta^2 = \frac{R}{P^2 + R^2}, \quad \tau = P\delta^2 = \frac{P}{P^2 + R^2}. \quad (5.86)$$

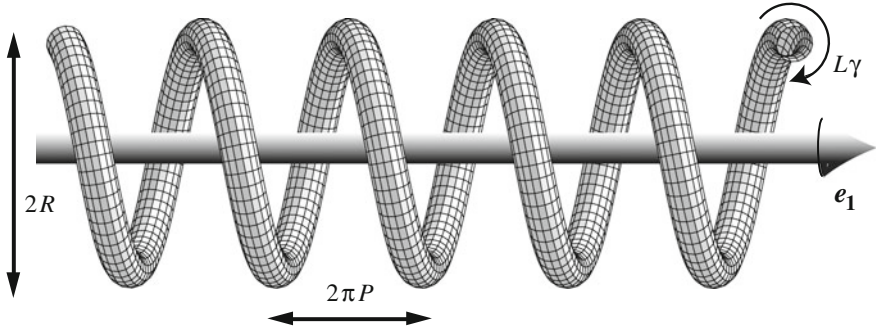


Figure 5.7 A right-handed helical rod characterized by an applied twist $L\gamma$, a radius R , and a pitch $2\pi P$.

A twisted helical rod is obtained by a rotation of the Frenet frame in the plane normal to τ by an angle γ :

$$\mathbf{d}_1 = \nu \cos(\gamma s) + \beta \sin(\gamma s), \quad (5.87)$$

$$\mathbf{d}_2 = -\nu \sin(\gamma s) + \beta \cos(\gamma s), \quad (5.88)$$

$$\mathbf{d}_3 = \tau. \quad (5.89)$$

We only consider solutions with constant excess twist ($\frac{\partial \varphi}{\partial s}$ in (5.23) constant) since it was shown that helical rod solutions with nonconstant excess twist do not exist for our choice of strain-energy function. Such solutions only exist for very particular choices of W [205]. The Darboux vector for this rod is

$$\mathbf{u} = (\kappa \sin(\gamma s), \kappa \cos(\gamma s), \tau + \gamma). \quad (5.90)$$

5.7.2 Helical Equilibria

We restrict our attention to inextensible rods with constitutive law (5.48) and $K_2 = K_1$. We further assume that the unstressed state of the rod is also a helix defined by

$$\hat{\mathbf{u}} = (0, \hat{\kappa}, \hat{\tau}). \quad (5.91)$$

For an inextensible rod in the absence of body loads, the equilibrium equations are

$$\mathbf{n}' = \mathbf{0}, \quad (5.92)$$

$$\mathbf{m}' + \mathbf{d}_3 \times \mathbf{n} = \mathbf{0}, \quad (5.93)$$

where $(\cdot)' = \partial_s(\cdot)$. We write the force and moment vectors in the director basis

$$\mathbf{n} = n_1 \mathbf{d}_1 + n_2 \mathbf{d}_2 + n_3 \mathbf{d}_3, \quad (5.94)$$

$$\mathbf{m} = m_1 \mathbf{d}_1 + m_2 \mathbf{d}_2 + m_3 \mathbf{d}_3, \quad (5.95)$$

and introduce $\mathbf{n} = (n_1, n_2, n_3)$ and $\mathbf{m} = (m_1, m_2, m_3)$. The equilibrium equations can then be written as

$$\mathbf{n}' + \mathbf{u} \times \mathbf{n} = \mathbf{0}, \quad (5.96)$$

$$\mathbf{m}' + \mathbf{u} \times \mathbf{m} + \mathbf{v} \times \mathbf{n} = \mathbf{0}, \quad \mathbf{v} = (0, 0, 1). \quad (5.97)$$

There are three limiting and exceptional families of helices with either $\hat{\mathbf{u}} = \mathbf{0}$, $\mathbf{u} = \mathbf{0}$, or $\mathbf{n} = \mathbf{0}$.

- **Naturally straight rods:** If $\hat{\mathbf{u}} = \mathbf{0}$, i.e., $\hat{\kappa} = \hat{\tau} = 0$, a helical solution exists with

$$\mathbf{n} = [K_3\omega + (K_3 - K_1)\tau] (\kappa \sin(\omega s), \kappa \cos(\omega s), \tau), \quad (5.98)$$

$$\mathbf{m} = (K_1\kappa \sin(\omega s), K_1\kappa \cos(\omega s), K_3(\tau + \omega)), \quad (5.99)$$

where ω is arbitrary. If we further assume that $\tau = 0$ and $L = 2\pi/\kappa$, the rods are twisted circular rings. These twisted helical and ring solutions are illustrated in Figure 5.8ABC.

- **Straight rods:** When $\mathbf{u} = \mathbf{0}$, the general frame steadily translates, that is, the centerline is a straight line, as illustrated in Figure 5.8D. The moment $\mathbf{m}$ is given by the constitutive relations, and the force $\mathbf{n}$ is parallel (or anti-parallel) to the helix centerline with arbitrary magnitude.
- **Zero-force helices:** The third family of singular equilibria are solutions with $\mathbf{n} = \mathbf{0}$, which implies $\omega = 0$. In this case, $\mathbf{m}$ is parallel to $\mathbf{u}$. Therefore, the vector $\mathbf{m}$ is constant and parallel to the axis of the helical centerline.

All other helical equilibria have $\kappa \neq 0$ and are *twistless*, i.e., $\omega = 0$. These solutions are maintained by a resultant force and moment given by

$$\mathbf{n} = [K_3\kappa(\tau - \hat{\tau}) - K_1\tau(\kappa - \hat{\kappa})] (0, 1, \tau/\kappa), \quad (5.100)$$

$$\mathbf{m} = (0, K_1(\kappa - \hat{\kappa}), K_3(\tau - \hat{\tau})). \quad (5.101)$$

In terms of a fixed basis, the moment and force necessary to maintain a helical shape can be expressed as a *wrench*, that is, a combination of a force N and moment M along the helical axis $\mathbf{e}_1$. Explicitly, we have

$$M \equiv \mathbf{n} \cdot \mathbf{e}_1 = \delta^{-1} [K_1\kappa(\kappa - \hat{\kappa}) + K_3\tau(\tau - \hat{\tau})], \quad (5.102)$$

$$N \equiv \mathbf{m} \cdot \mathbf{e}_1 = \delta\kappa^{-1} [K_3\kappa(\tau - \hat{\tau}) - K_1\tau(\kappa - \hat{\kappa})]. \quad (5.103)$$

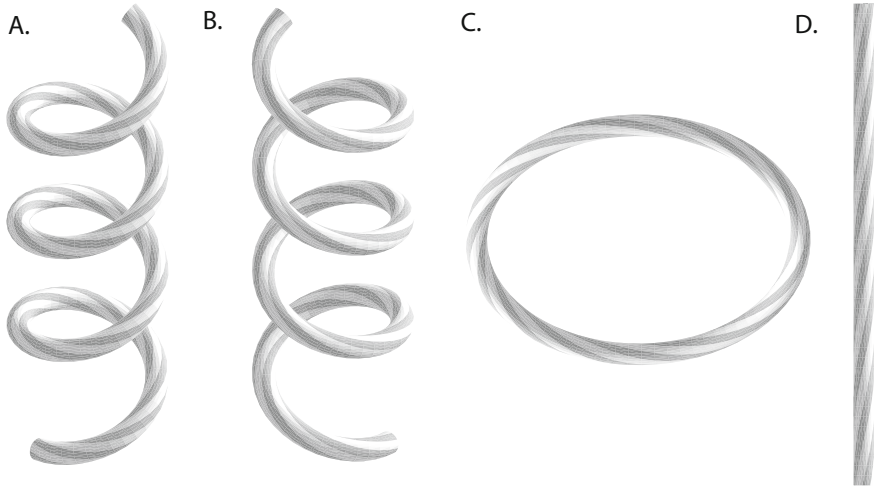


Figure 5.8 Particular twisted solutions. ABC. Twisted helical rods and twisted rings require $\hat{\kappa} = 0$. D. If $\hat{\kappa} \neq 0$, then $\kappa = 0$ and only straight-twisted solutions exist. (A. $\kappa = 3$, $\tau = 1$, $\omega = 5$, B. $\kappa = 3$, $\tau = -1$, $\omega = 5$, C. $\kappa = 1$, $\tau = 1$, $\omega = 3$, D. $\kappa = 0$, $\tau = 0$, $\omega = 3$).

These relationships for the wrench in terms of the material parameters and geometry of a helix are the classic *helical spring formulas* first studied by Thomson and Tait in 1867 [1229, Sect. 605] (see also Love [806, Sect. 271]).

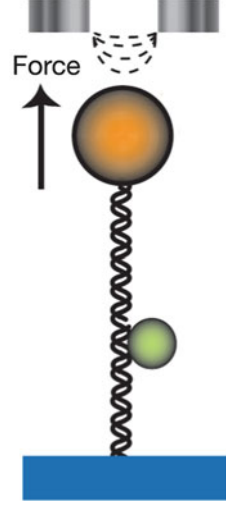
5.7.3 Overwinding or Underwinding Helices

An interesting application of the helical spring formula is found when we restrict our attention to helices maintained solely by axial tension, that is, $M = 0$. This condition can be easily realized by pulling a spring.

Physically, the spring is extended but free to twist around its axis. The same experimental conditions have been reproduced in single-molecule experiments [459, 792]. As sketched in Figure 5.9, in these experiments, molecules of DNA are pulled by optical and magnetic tweezers while the angular rotation of a bead attached along the DNA is tracked. The key question is to understand the rotation of the helical structure as the axial load increases. Experiments show an unexpected behavior where the DNA systematically overwinds before unwinding. In Figure 5.10, overwinding means that as N increases, θ also increases. The authors write “*simple intuition suggests that DNA should unwind under tension*” [459]. A simple question is to understand the rotation of a helical spring as it extends: Will it unwind or overwind?

The helical spring formulas (5.102–5.103) imply that for constitutive relations appropriate for metal springs with circular cross section; as tension $N > 0$ is

Figure 5.9 In a single-molecule experiment, a molecule of DNA is attached to a substrate and pulled or twisted at the other end where a paramagnetic bead is attached. The rotation can be observed by tracking the motion of an attached fluorescent bead (adapted from [459]).



increased monotonically from zero with $M = 0$, the rotation first increases (overwinding the helical axis in the same direction as the reference handedness) and then decreases, returning to its initial value and then unwinding as illustrated in Figure 5.10C.

We define the *coiling angle per unit arc length* to be $\rho = |\mathbf{u}|$, so that in the unstressed state $\hat{\rho} = |\hat{\mathbf{u}}|$. Close to the unstressed state, we can then express the axial stretch $z = \tau/\rho - \hat{\tau}/\hat{\rho}$ and rotation angle $\theta = \rho - \hat{\rho}$ as a function of N :

$$z = \frac{N(K_1\hat{\kappa}^4 + K_3\hat{\kappa}^2\hat{\tau}^2)}{K_1K_3(\hat{\kappa}^2 + \hat{\tau}^2)^3} + \mathcal{O}(N^2), \quad (5.104)$$

$$\theta = \frac{N(K_1 - K_3)\hat{\kappa}^2\hat{\tau}}{K_1K_3\sqrt{\hat{\kappa}^2 + \hat{\tau}^2}} + \mathcal{O}(N^2). \quad (5.105)$$

The second equation gives the linear approximation at the origin to the graph in Figure 5.10C, which demonstrates that a helix will initially overwind when pulled from its minimum energy state if and only if $\Gamma = K_3/K_1 < 1$. We remark that if the filament is formed from a three-dimensional homogeneous linearly elastic material with Poisson's ratio in $[0, 1/2]$, e.g., standard metals, then $\Gamma \in [2/3, 1]$, so that initial overwinding in response to positive tension always arises for simple helical springs; a slightly surprising yet completely classic effect. Equation (5.104) defines an effective Hooke constant for small extension.

Geometrically, the condition $M = 0$ implies, from (5.102), that all helical equilibria lie on an ellipse in the curvature–torsion plane, given by

$$\kappa(\kappa - \hat{\kappa}) + \Gamma\tau(\tau - \hat{\tau}) = 0. \quad (5.106)$$

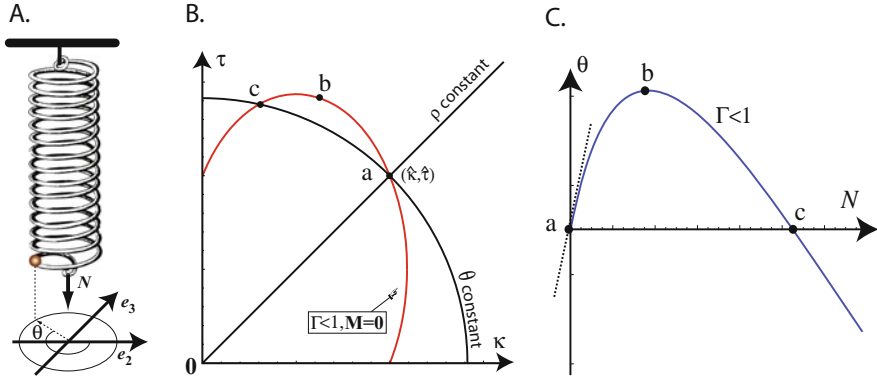


Figure 5.10 A. A pure axial tension applied to a helical spring gives rise to another helical equilibrium (adapted from Hooke’s 1678 “De Potentia Restitutiva” [611]). B. The solutions with $M = 0$ zero axial torque helical equilibria lie on an ellipse in the curvature–torsion plane determined by the value of Γ . Close to the unstressed helix with $N = 0$ (point **a**), $N > 0$ equilibria correspond to $|\tau| > |\hat{\tau}|$ (case $\tau > 0$ shown). Initial overwinding in extension occurs for $\Gamma < 1$. C. The relative coiling angle as a function of the axial force. For $\Gamma < 1$ and $N > 0$ the helix first overwinds ($\theta > 0$), and then unwinds ($\theta < 0$).

For given material parameters Γ , $\hat{\kappa}$, $\hat{\tau}$, all $M = 0$ helical solutions lie on this ellipse and the helix always extends when pulled ($|\tau| > |\hat{\tau}|$ for $N > 0$). A point on the ellipse corresponds to overwound configurations with respect to $(\hat{\kappa}, \hat{\tau})$ when it lies outside the circle centered at the origin and of radius $\hat{\rho}$. It follows that for $N > 0$ a helix will initially overwind when pulled from rest if and only if $\Gamma < 1$. Furthermore, the maximum overwinding, corresponding to point **b** in Figure 5.10B, is obtained when the ellipse (5.106) intersects the hyperbola

$$2(1 - \Gamma)\kappa\tau + \Gamma\hat{\tau}\kappa - \hat{\kappa}\tau = 0, \quad (5.107)$$

which comes from (5.103), and the coiling angle returns to its original value when the ellipse re-intersects the circle $\rho^2 = \hat{\rho}^2$ (corresponding to the point **c**).

We conclude that the seemingly counterintuitive behavior found in DNA experiments is in fact generic for most macroscopic helical elastic filaments. This behavior is found in the classic Kirchhoff equations and has been confirmed experimentally as early as 1902 [891, 1093].

Confusion over the sign of rotation in helical structures also arises in the problem of growth of stems and roots where cell wall anisotropy is responsible for the overall handedness that is observed. A typical argument is that the cell wall is a cylindrical structure with reinforced, say, right-handed helical microfibrils that rotate clockwise during growth (viewed from the top) [155, 483]. Therefore, unwinding is expected because “*helices unwind when they are stretched*” [797]. This explanation of handedness is again falsidical and will be further discussed in Section 16.9.

5.8 The Planar Elastica: Bernoulli–Euler Equations

We now consider a reduction of the three-dimensional basic rod above. We assume that the rod is planar unshearable, inextensible, has a circular cross section, is naturally straight, and that there are no body forces or couples acting on it. Therefore, it has no torsion and we further assume that it has no twist. The Darboux vector is then simply given by

$$\mathbf{u} = (0, \kappa, 0). \quad (5.108)$$

A convenient representation of the rod is obtained by assuming that it lies in the $\mathbf{e}_1 - \mathbf{e}_2$ plane and by introducing the angle θ between the tangent vector and the $\mathbf{e}_1$ -axis. That is, we have

$$\boldsymbol{\tau} = \mathbf{d}_3 = \cos \theta \mathbf{e}_1 + \sin \theta \mathbf{e}_2, \quad (5.109)$$

which implies

$$\kappa = \theta', \quad (5.110)$$

and $\mathbf{d}_2 = \mathbf{e}_3$. By writing $\mathbf{n} = F\mathbf{e}_1 + G\mathbf{e}_2$, $\mathbf{f} = f\mathbf{e}_1 + g\mathbf{e}_2$, $\mathbf{r} = x\mathbf{e}_1 + y\mathbf{e}_2$, we can simplify the equations of motion (5.79–5.80) to

$$F' + f = \rho A \ddot{x}, \quad (5.111)$$

$$G' + g = \rho A \ddot{y}, \quad (5.112)$$

$$EI\theta'' + G \cos \theta - F \sin \theta = \rho I \ddot{\theta}. \quad (5.113)$$

These equations form a system of three equations for the three unknowns (F, G, θ) .

5.8.1 Static Solutions

We consider the static case of (5.111–5.113) in the absence of body forces. Therefore, $\ddot{x} = \ddot{y} = 0$ and we conclude that F and G are constant meaning that $\mathbf{n}$ is a constant vector. Without loss of generality, we choose $\mathbf{e}_1$ to be along this constant force, so that $G = 0$ and

$$EI\theta'' - F \sin \theta = 0, \quad (5.114)$$

or

$$\theta'' + \alpha \sin \theta = 0, \quad (5.115)$$

where $\alpha = -F/EI$ is positive for compressive forces, i.e., $F < 0$. We recognize in (5.115) the equation for a hanging pendulum under gravitation. For the pendulum θ is the angle with respect to the vertical, and α is the ratio of the gravity acceleration by the length of the pendulum. Therefore, any solution of the pendulum is a solution

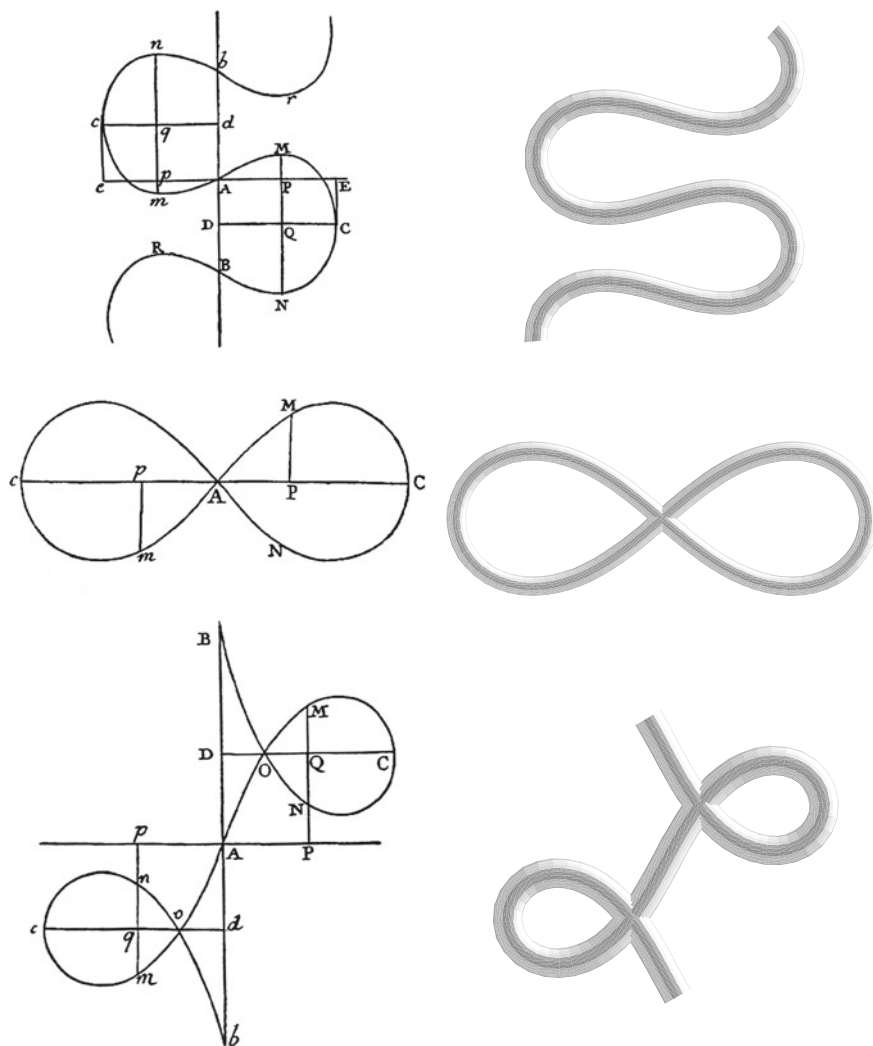


Figure 5.11 Euler's drawings of spatial equilibria of the elastica [350] together with the solutions of (5.115) (adapted from [959]).

of the elastica. This equivalence is the two-dimensional version of the Kirchhoff analogy between Lagrange tops and rods at equilibrium and was already known by Euler [350]. Since all the solutions of the pendulum are known in terms of elliptic functions, all the solutions of the planar elastica can be obtained systematically [959] as illustrated in Figure 5.11.

Chapter 6

Morphoelastic Rods



We can now adapt the theory of elastic rods presented in the previous chapter to include the contribution of growth and remodeling in filamentary structures. Growth takes place on time scales much longer than any time scales associated with elastic propagation or viscous relaxation. Indeed, elastic wave propagation takes place at the speed of sound, whereas growth time scales are of the order of minutes, hours, and days. Growth is therefore slow enough so that it is uncoupled with inertial terms and it can therefore be considered as a quasi-static process. Different attempts have been made to model growing rods. Essentially, one can distinguish three different approaches.

In the first approach, which we refer to as *parameter variation*, we consider families of rod solutions parameterized by one of the material parameters. For instance, in the growth of a tree, one may consider the length and width as two parameters that evolve in time. At each growth time, the value of such parameters is increased and a new static solution is recomputed [470].

The second approach is *remodeling*. The idea is to consider a separate evolution law for the material parameters that may depend on both time and on the history of the material. For instance, through differential growth, an initially straight rod can develop intrinsic curvature and the resulting equilibrium configurations for given boundary conditions can be studied [451, 853]. This is fundamentally different from

the previous approach since the material parameters are now coupled with the evolution of the rod in space and time.

The third approach, *morphoelasticity*, combines all aspects of growth and remodeling by considering the evolution of the reference configuration separately from the mechanical response of the rod. In the general theory of morphoelasticity, a distinction between growth and remodeling is usually made. Growth is associated with a change of volume of the unstressed elastic material, whereas remodeling refers to a change of material properties. This distinction is clear in the general three-dimensional theory of growing elastic bodies, presented in Part IV. However, in the theory of rods, growth and remodeling are irretrievably intertwined. Indeed, rod theory is a reduction from three-dimensional elastic bodies to one-dimensional structures that mixes geometry and material parameters. For instance, the bending stiffness, $K_1 = EI_1$ in Equation (5.48), is a product of a material coefficient, the Young's modulus, E and a geometric property, I_1 , the second moment of area. As the rod grows and remodels, the material can become stiffer or increase its radius, both changing the stiffness K_1 .

Rods can also grow in length. Again, the effect of this type of growth is not obvious as a uniform change of length in a rod can easily be rescaled without affecting the basic equations. Therefore, the effect of a change of length in a rod can only be appreciated through nonhomogeneous or boundary effects arising from the interactions of the rod with its environment, either through boundary conditions at each end of the rod or through body forces and couples coupling the rod with its surrounding. The special case where a rod interacts with itself, nonlocally, through periodic boundary conditions can also lead to stressed configurations even in the absence of external forces or couples.

In order to describe interesting aspects of growing rods in space, we first define the mechanics of a single growing rod through the evolution of its reference configuration. Second, we consider the case of a growing rod attached to a given rigid curve in space via an elastic force. For instance, one may consider the case of a growing rod either attached to a substrate, growing inside a sphere, or lying on a cylinder. Finally, we can consider the case of two rods growing at different rates while attached together [786].

For the rest of this chapter, our basic assumptions are:

1. The growth dynamics is slow enough so that the unstressed rod is in elastic equilibrium at all times. We use the variable t to denote this slow time evolution. This assumption implies that the growth dynamics is decoupled from the elastic dynamic of the rod. We assume the existence of a dissipative process that takes the rod back to a stable equilibrium and we consider the effects of inertial terms to assess the stability of such equilibria.
2. The rod is assumed to be hyperelastic and characterized by a quadratic strain-energy function W . Due to remodeling and growth, the parameters defining the intrinsic shape $\hat{\mathbf{u}}$ and the coefficients of W are also functions of the growth time t .

6.1 Kinematics of a Growing Rod

Based on the general approach of growth in nonlinear elasticity through a multiplicative decomposition [80, 1091], we consider three different configurations for the rod. The *initial configuration* $\mathcal{B}_0$ is the unstressed configuration of the rod at time $t = 0$; all quantities in this state are denoted by a subscript 0. The *virtual configuration* $\mathcal{V}$ is the unstressed configuration at a given time t and the *current configuration* $\mathcal{B}$ is the actual configuration of the rod at time t for given external loads, body loads, and boundary conditions. Note that the unstressed configuration may not be realizable in Euclidean space. For instance, given a ring of radius one and intrinsic curvature one, an increase in its length would create a stress-free configuration that would be self-penetrating, as shown in Figure 6.1. However, unlike the three-dimensional case studied in Chapter 12, there is no problem with local compatibility or generation of residual stress associated with the local definition of a growth and elastic tensor [468]. Therefore, all local quantities are well defined and the virtual configuration is appropriate for the computation of the current configuration.

At time $t = 0$, the rod is described by its intrinsic curvature $\hat{\mathbf{u}}_0$ defined with respect to its arc length S_0 , its total length L_0 , density $\rho_0(S_0)$, cross-section area $A_0(S_0)$, and a stiffness matrix $\mathbf{K}_0$. This intrinsic curvature evolves so that at any given time t the rod has unstressed curvature $\hat{\mathbf{u}} = \hat{\mathbf{u}}(S_0, t)$, with arc length S , total length $L(t)$, density $\rho(S_0, t)$, cross-section area $A(S_0, t)$ and a stiffness matrix $\mathbf{K}(t)$. In this description, S_0 is a material parameter for all other configurations. Following the discussion of Section 4.4, it is related to the arc length S of the virtual configuration $\mathcal{V}$ by the *growth stretch* γ , i.e.

$$\gamma(S_0, t) = \frac{\partial S}{\partial S_0}, \quad (6.1)$$

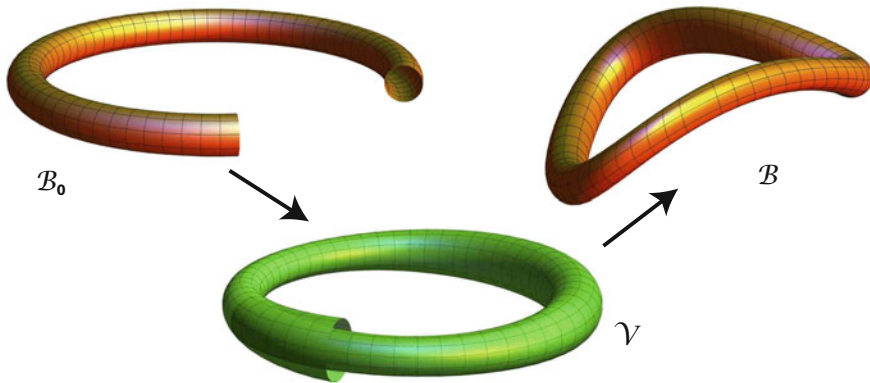


Figure 6.1 The three configurations of a morphoelastic rod: initial $\mathcal{B}_0$, reference $\mathcal{V}$, and current $\mathcal{B}$. The virtual configuration is stress free. It evolves in time and reflects the change due to growth. Initially, the rod has intrinsic curvature. As growth proceeds the cross section and length change inhomogeneously. The virtual reference configuration can also intersect itself as it does not represent a possible physical realization of the rod. The current configuration is the actual configuration with imposed boundary conditions and body loads.

so that γ characterizes the local increase of length of a material segment located at a material point S_0 at time t . This virtual configuration is required in order to compute the current shape of the rod at a later time $t > 0$ for given loads and boundary conditions. This decomposition is illustrated in Figure 6.1.

6.2 Mechanics of a Growing Rod

At time t , the balance of linear and angular momenta in the virtual configuration yields

$$\frac{\partial \mathbf{n}}{\partial S} + \mathbf{f} = \mathbf{0}, \quad (6.2)$$

$$\frac{\partial \mathbf{m}}{\partial S} + \frac{\partial \mathbf{r}}{\partial S} \times \mathbf{n} + \mathbf{l} = \mathbf{0}, \quad (6.3)$$

where $\mathbf{f}$ and $\mathbf{l}$ are the body force and couple per unit *reference* length. The reference variable S is the natural choice to express all quantities as the constitutive equations are given in this configuration. This equation together with the appropriate boundary conditions and with one of the two constitutive models proposed (either (5.47) for inextensible rods or (5.52) for extensible rods), can be solved to obtain the current configuration.

We define α to be the *elastic stretch* and λ the *total stretch* between the initial and current configuration. We have

$$\lambda = \alpha \gamma \iff \frac{\partial s}{\partial S_0} = \frac{\partial s}{\partial S} \frac{\partial S}{\partial S_0}. \quad (6.4)$$

A change of independent variable leads to an alternative formulation in the current and initial configuration. Namely, in the current configuration we have

$$\frac{\partial \mathbf{n}}{\partial s} + \alpha^{-1} \mathbf{f} = \mathbf{0}, \quad (6.5)$$

$$\frac{\partial \mathbf{m}}{\partial s} + \frac{\partial \mathbf{r}}{\partial s} \times \mathbf{n} + \alpha^{-1} \mathbf{l} = \mathbf{0}, \quad (6.6)$$

where $\alpha^{-1} \mathbf{f}$ and $\alpha^{-1} \mathbf{l}$ are the body force and couple per unit *current* length. Finally, in the initial configuration, we have

$$\frac{\partial \mathbf{n}}{\partial S_0} + \gamma \mathbf{f} = \mathbf{0}, \quad (6.7)$$

$$\frac{\partial \mathbf{m}}{\partial S_0} + \frac{\partial \mathbf{r}}{\partial S_0} \times \mathbf{n} + \gamma \mathbf{l} = \mathbf{0}, \quad (6.8)$$

where $\gamma \mathbf{f}$ and $\gamma \mathbf{l}$ are the body force and couple per unit *initial* length.

6.3 Evolution Laws for Growing Rods

Following the slow-growth assumption, the rod is characterized by one of the three constitutive models described in Section 5.3. Since both reference arc length and stretch can change at time t , great care must be exercised to ensure that these changes in length are taken into account correctly. To avoid confusion, we use the simple principle of first defining all material properties in the virtual reference configuration $\mathcal{B}$ with respect to the arc length S . All other formulations of the rod equations follow directly from a change of dependent variables as shown above. Note that the parameters entering the constitutive equations, such as stiffnesses and intrinsic curvatures, may also evolve with the slow time t .

We now consider a possible law for the evolution of intrinsic curvature. We first consider the case of an inextensible rod. In this case, the only material and structural parameters evolving in time are the radius, density, stiffness matrix $\mathbf{K}$, and intrinsic Darboux vector. Whereas, radii, density, and stiffnesses are quantities whose evolution must be prescribed from biological laws, the intrinsic curvatures $\hat{\mathbf{u}}$ depend both on intrinsic quantities and on the geometry of the deformation. To understand this dependence, we adapt the reasoning of [991] to the present situation.

First, we consider an inner rod with uniform intrinsic curvatures $\hat{\mathbf{u}}_{\text{in}}$ and stiffness matrix $\mathbf{K}_{\text{in}}$. Next, we apply a moment so that the new shape has uniform curvatures $\hat{\mathbf{u}}_{\text{out}}$. In this new configuration, we add an external outer cylindrical layer with the current curvature and with bending stiffness $\mathbf{K}_{\text{out}}$. Ignoring the possibility of internal residual stresses in the material and treating this new structure as an elastic rod, the problem is to determine its new properties: its curvature $\hat{\mathbf{u}}$ and stiffness matrix $\mathbf{K}$. For any given uniform shape given by $\mathbf{u}$, the total moment of the composite rod is $\mathbf{K}(\mathbf{u} - \hat{\mathbf{u}})$, which is also equal to the sum of both moments due to the inner and outer rods. Hence, we have

$$\mathbf{K}_{\text{in}}(\mathbf{u} - \hat{\mathbf{u}}_{\text{in}}) + \mathbf{K}_{\text{out}}(\mathbf{u} - \hat{\mathbf{u}}_{\text{out}}) = \mathbf{K}(\mathbf{u} - \hat{\mathbf{u}}). \quad (6.9)$$

This relation must be valid for all $\mathbf{u}$ so that we have both

$$\mathbf{K} = \mathbf{K}_{\text{in}} + \mathbf{K}_{\text{out}}, \quad (6.10)$$

and

$$\hat{\mathbf{u}} = \mathbf{K}^{-1} (\mathbf{K}_{\text{in}} \hat{\mathbf{u}}_{\text{in}} + \mathbf{K}_{\text{out}} \hat{\mathbf{u}}_{\text{out}}). \quad (6.11)$$

It is now possible to generalize this procedure by continuously adding new layers. Consider a deformed rod and assume that at time t it has curvatures $\mathbf{u}(t)$, and material properties $\hat{\mathbf{u}}(t)$ and $\mathbf{K}(t)$. At time $t + \Delta t$, a thin new layer is applied to the rod. The balance of moment now reads

$$\begin{aligned} \mathbf{K}(t)[\mathbf{u}(t + \Delta t) - \hat{\mathbf{u}}(t) - \mathbf{k}_2(t)\Delta t] + \Delta \mathbf{K}[\mathbf{u}(t + \Delta t) - \mathbf{u}(t) - \mathbf{k}_1(t)] \\ = \mathbf{K}(t + \Delta t)[\mathbf{u}(t + \Delta t) - \hat{\mathbf{u}}(t + \Delta t)], \end{aligned} \quad (6.12)$$

where $\Delta \mathbf{K} = \dot{\mathbf{K}}\Delta t$ is the bending stiffness of the new layer, $\mathbf{k}_1(t)$ is the difference between the curvatures of the new layer and the curvatures of the inner rod, and $\mathbf{k}_2(t)$ is a source term for the intrinsic curvature of the inner structure. By expanding all quantities to order Δt , we obtain

$$\dot{\mathbf{K}}(\mathbf{u} - \hat{\mathbf{u}} + \mathbf{k}_1) = \mathbf{K}(\dot{\hat{\mathbf{u}}} - \mathbf{k}_2). \quad (6.13)$$

If there is no increase of mass or change of stiffness in the section, we have $\dot{\mathbf{K}} = \mathbf{0}$ and the evolution of the curvatures is simply governed by $\dot{\hat{\mathbf{u}}} = \mathbf{k}_2$ and a choice for $\mathbf{k}_2$ must be made. For instance, in the plane, the only nonzero component of the curvatures is the Frenet curvature $\kappa = u_2$. If we assume that the intrinsic curvature relaxes to the current curvature with a relaxation time η^{-1} , we have

$$\dot{\hat{\kappa}} = \eta(\kappa - \hat{\kappa}). \quad (6.14)$$

The implication of this law and its application to the remodeling of vines is explored next.

6.4 Example: The Remodeling of Stems

In many growth processes, the evolution of a structure directly influences the evolution of the material parameters. For instance, the branch of a tree can be trained to grow in a certain shape, which makes for beautiful alleys in French formal gardens such as in the Jardin des Plantes in Paris. At first, the elastic structure is loaded and stressed into a particular shape. As time passes, the structure remodels itself in such a way as to relieve the stresses, and the structure permanently sets in, even in the absence of loading.

An example of such a process is shown in Figure 6.2 where an initially straight tendril coils and eventually adopts the coiled shape. The cut shape differs little from the intact one, showing that the tendril actually passes slowly through a continuum of quasi-equilibrium states to reach its current steady state. For a morphoelastic filament, this property can be modeled by considering an evolution of the rod's material properties. In the simplest case, the intrinsic curvatures evolve slowly in time to match the current configuration, hence releasing all stresses.

As a simple example, consider the case of an unshearable, inextensible planar rod under end compression [451]. As the rod buckles it takes a new shape. At this point it is assumed that the natural state of the rod will evolve toward this equilibrium shape, that is, its intrinsic curvature $\hat{\kappa} = \hat{u}_2$ evolves in time toward its actual curvature. Following the previous discussion, we use a simple morphoelastic model for the

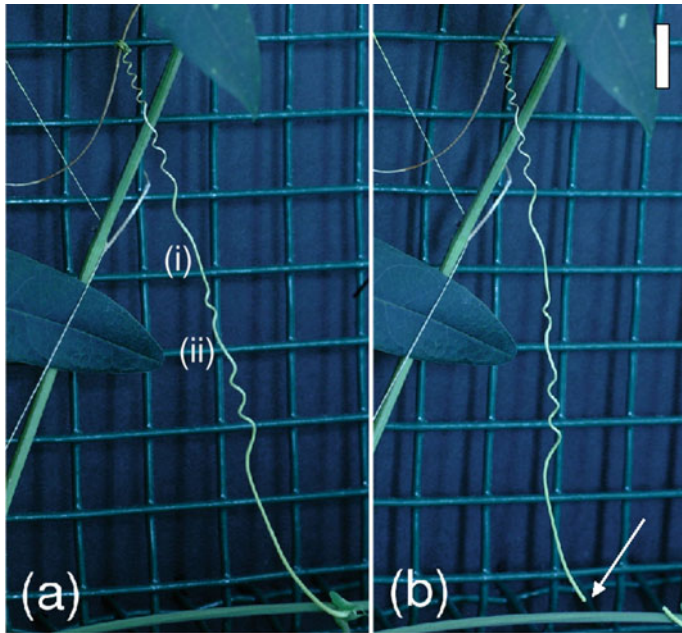


Figure 6.2 A tendril of the genus *Passiflora* (passion flowers). An intact tendril (a) with perversions (i, ii) maintains its shape when its connection to the plant is cut (b, arrow). Scale bar is 1 cm (reproduced from [451], picture courtesy of Ray Goldstein).

relaxation of curvature:

$$\frac{\partial \hat{\kappa}}{\partial t} = \eta(\kappa - \hat{\kappa}), \quad (6.15)$$

where $1/\eta$ is a characteristic time for relaxation. It is important to notice here that, after buckling, the curvature changes at all points and when the intrinsic curvature relaxes it takes different values at all points. The process depends on the loading and the parameters, but also on the history of the loading process which makes it fundamentally different from previous modeling through parameter variation.

To emphasize this point, consider Figure 6.3 where an initially straight rod was loaded with a given ramp and allowed to relax following (6.15). If the thrusting force is gradually removed at some time following a ramp, then the filament shape will soon adapt to the preferred curvature and it will then reach the minimum of the elastic energy, with $\kappa(s) = \hat{\kappa}(s)$ everywhere.

Figure 6.3 shows five sequences of trained shapes which result from a protocol of the force consisting of a ramp followed by exponential relaxation (with varying decay rates), where the total thrust vanishes. As the force is removed ever more slowly, the filament shape remains highly bent. Each final trained shape is typically very close to that of an elastic filament subjected to some particular external force, but of course the latter would not remain in place after the removal of that force.

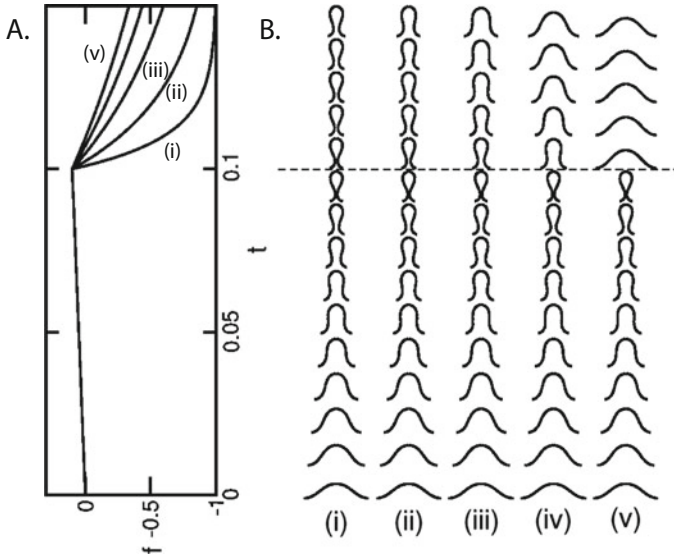


Figure 6.3 Filaments trained with time-dependent forces. A. For each of the force-time profiles shown, the corresponding sequence of filament shapes is shown at intervals of $\Delta t = 0.01$ in (B). The dashed line indicates the end of the linear ramp. As can be clearly seen in picture (i), the filament has remodeled into its shape and retains it after the load is removed. With longer unloading times ((ii) to (v)), the filament when unloaded, partially relaxes to its original shape (reproduced from [451]).

6.5 A Buckling Criterion

An interesting aspect of growing rods is the possibility of growth-induced buckling instabilities. We first derive a general formulation to obtain a bifurcation criterion for a rod with arbitrary body force and couple. We assume here that the rod has constant intrinsic curvature $\hat{\mathbf{u}}$. Our starting point is the full kinematic and mechanics description for an unshearable rod in the steady state, expressed in the virtual configuration as

$$\mathbf{r}' = \alpha \mathbf{d}_3, \quad (6.16)$$

$$\mathbf{d}' = \mathbf{u} \times \mathbf{d}_i, \quad i = 1, 2, 3, \quad (6.17)$$

$$\mathbf{n}' + \mathbf{f} = \mathbf{0}, \quad (6.18)$$

$$\mathbf{m}' + \frac{\partial \mathbf{r}}{\partial S} \times \mathbf{n} + \mathbf{l} = \mathbf{0}, \quad (6.19)$$

$$\mathbf{m} = K_1(u_1 - \hat{u}_1)\mathbf{d}_1 + K_2(u_2 - \hat{u}_2)\mathbf{d}_2 + K_3(u_3 - \hat{u}_3)\mathbf{d}_3, \quad (6.20)$$

$$n_3 = EA(\alpha - 1), \quad (6.21)$$

where $(\cdot)' = \partial(\cdot)/\partial S$.

We assume the existence of a one-parameter family of solutions. This base solution is defined by $\{\alpha^{(0)}, \mathbf{r}^{(0)}, \mathbf{n}^{(0)}, \mathbf{u}^{(0)}, \mathbf{d}_1^{(0)}, \mathbf{d}_2^{(0)}, \mathbf{d}_3^{(0)}\}$. Viewed as a bifurcation problem, the general idea is to consider a small perturbation to this solution and determine the critical value of the control parameter at which a different solution to the perturbed system exists. In the case of growing rods, a natural choice for the growth parameter is γ . The question is then to find the critical value of the parameter $\gamma = \gamma^*$ such that the Kirchhoff equations admit a solution that is different from the base solution.

6.5.1 Example: Michell's Instability

Before giving the general formulation for the bifurcation of a rod, we consider the simple case of a twisted elastic ring as depicted in Figure 6.4. This problem was first stated by Thomson and Tait in their classic, “Treatise on Natural Philosophy” [1229]. In paragraph 123, they discuss the problem of the respective stability of the circle versus the eight-form shown in Figures 6.4 and 6.5 and state that, “*the circular form, which is always a figure of free equilibrium, may be stable or unstable, according as the ratio of torsional to flexural rigidity is more or less than a certain value depending on the actual degree of twist.*” Motivated by this statement, John Henry Michell solved the problem in 1889 by determining the exact value of the twist necessary to trigger an instability in a ring [462, 885]. Michell writes: “*If a wire of isotropic section and naturally straight be twisted, and the ends joined so as to form a continuous curve, the circle will be a stable form of equilibrium for less than a certain amount of twist.*”

Reformulated in our terminology, the problem is to assess the stability of an inextensible, transversely isotropic, elastic ring with no intrinsic curvature. The system can be easily realized in an experiment: Take a straight uniform elastic rod with circular cross section, paint a straight line on it and shape the rod so that the rod's centerline is a circle. At the junction, the tangent from the two ends agrees, but the cross sections can be rotated so that the line painted on the straight intrinsic shape

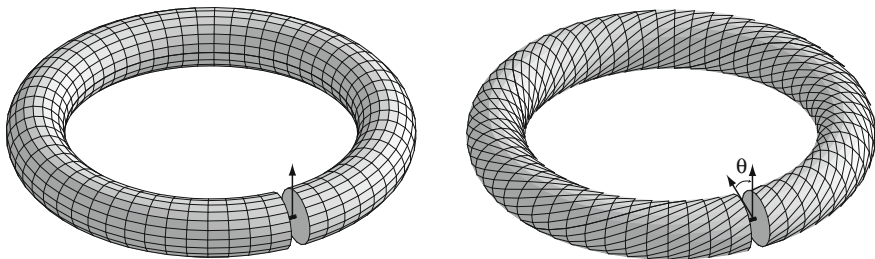


Figure 6.4 Untwisted (left) and twisted rings (right). The total twist is given by the total angular rotation of an arrow pointing at any circle on the surface of the untwisted ring. Here the total twist is $13\pi/2$.

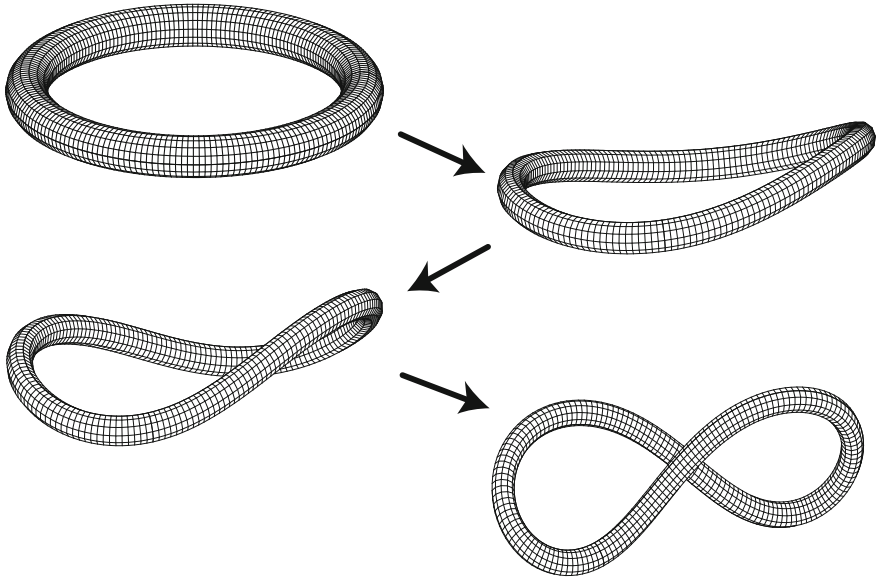


Figure 6.5 Buckling of an unstable ring when the critical twist is first reached. The twist is not shown on the ring. The solution shown is obtained as an asymptotic solution close to the bifurcation point [478].

twists around the central curve. The twist is the total angular rotation of the line with respect to the central curve. The line will close on itself at the junction if the twist is an integral multiple of 2π . After closure, the rod is glued and released.

For small values of the twist, the twisted ring is observed to be stable. For sufficiently high twist, the elastic ring will become unstable and will start writhing out of the plane. The phenomenon is quite striking as the instability is subcritical; the ring suddenly buckles and loops back on itself by forming an eight-shape with self-contact, as shown in Figure 6.5. We refer to the twisted elastic ring instability as *Michell's instability* and the problem is to identify the value of the critical twist at which the instability sets in.

For an inextensible rod $\alpha = 1$, (6.21) is neglected, and S is the arc length for all deformations. In the absence of body force or couple $\mathbf{f} = \mathbf{l} = 0$ and for naturally straight rods with transversely isotropic cross sections, (6.16)–(6.20) take the simple form

$$\mathbf{n}' = \mathbf{0}, \quad (6.22)$$

$$\mathbf{m}' + \mathbf{r}' \times \mathbf{n} = \mathbf{0}, \quad (6.23)$$

$$\mathbf{m} = K_1 \kappa \beta + K_3 \omega \tau, \quad (6.24)$$

where, as defined in Section 5.1, $\{\tau, \nu, \beta\}$ are, respectively, the tangent, normal, and binormal vectors to $\mathbf{r}$, and τ, κ are the Frenet torsion and curvature.

The twist ω describes the rotation of the material frame. By writing Equations (6.22–6.24) in the Frenet frame, the resultant force can be eliminated in terms of κ , τ , ω to obtain

$$\omega' = 0, \quad (6.25)$$

$$\kappa\tau' - \Gamma\omega\kappa' = 0, \quad (6.26)$$

$$\kappa^2 (\Gamma\omega - 2\tau) \tau' + \kappa'(\kappa^3 - \kappa'') + \kappa\kappa''' = 0, \quad (6.27)$$

where $\Gamma = K_3/K_1$. The first equation implies that the twist density ω must be constant. To identify bifurcation points, where the ring may lose stability with respect to out-of-plane and torsional deformations, we consider small variations of the curvature and torsion

$$\kappa = \kappa^{(0)} + \epsilon\kappa^{(1)}, \quad \tau = \tau^{(0)} + \epsilon\tau^{(1)}, \quad (6.28)$$

and expand Equations (6.26)–(6.27) to first order in ϵ .

The base solution is simply $\kappa^{(0)} = 1/R$, $\tau^{(0)} = 0$ and ω arbitrary, where R is the radius of the ring. This twisted ring solution is a one-parameter family of solutions parameterized by ω and is a particular case of the twisted helical equilibria discussed in Section 5.7. After simplification, to first order in ϵ , a single equation for $\kappa^{(1)} = k(S)$ is obtained

$$k''' + (R^{-2} + \Gamma^2\omega^2) k' = 0. \quad (6.29)$$

This equation supports periodic solutions of the form $k = \exp(inS/R)$ with n integer, such that (6.29) becomes

$$\Gamma^2\omega^2 R^2 = n^2 - 1. \quad (6.30)$$

The first nontrivial solution occurs for $n = 2$ and corresponds to

$$\omega_c = \frac{\sqrt{3}}{R\Gamma}. \quad (6.31)$$

The total twist Tw is the integral of the twist density ω over the circumference. It corresponds to the total angular rotation of the cross section along the rod; that is, $Tw = 2\pi R\omega$. The twisted ring becomes unstable for values of the total twist larger than

$$Tw_c = \frac{2\pi\sqrt{3}}{\Gamma}. \quad (6.32)$$

For most materials, typical values for Γ lie between 2/3, in the incompressible limit, to 1 with most metals around 4/5. Other filaments such as DNA may present higher values of twist to bending rigidity [1125]. Therefore, a ring becomes unstable when it has been twisted by about two full turns (with limits 1.73 to 2.6 corresponding to α between 2/3 and 1).

The problem of twisted elastic rings is important in the study of macromolecules such as DNA molecules [83, 84, 826, 1284] but also plants [477, 1156] and microbial filaments [452]. In particular, the analysis of mini-DNA rings made out of a few hundred bases offers a unique perspective to characterize physical properties of DNA [537, 1013, 1051]. Twisted elastic rings are the natural theory to understand and extract these properties [818, 985].

6.5.2 A General Perturbation Expansion

We can now generalize the linearization process for the general Kirchhoff equations assuming the existence of a one-parameter family of base solutions $\{\mathbf{r}^{(0)}, \mathbf{n}^{(0)}, \mathbf{u}^{(0)}, \mathbf{d}_1^{(0)}, \mathbf{d}_2^{(0)}, \mathbf{d}_3^{(0)}\}$ with elastic stretch $\alpha^{(0)}$. Let ϵ be a small parameter. Based on the general ideas outlined in [472, 474, 475, 478], we begin by expanding the basis itself,

$$\mathbf{d}_i = \mathbf{d}_i^{(0)} + \epsilon \mathbf{d}_i^{(1)} + \mathcal{O}(\epsilon^2). \quad (6.33)$$

If we express the correction terms $\mathbf{d}_i^{(1)}$ in terms of the unperturbed basis, and require orthonormality to $\mathcal{O}(\epsilon)$, we find that the $\mathcal{O}(\epsilon)$ corrections can be expressed in terms of a single vector

$$\mathbf{c} = c_1 \mathbf{d}_1^{(0)} + c_2 \mathbf{d}_2^{(0)} + c_3 \mathbf{d}_3^{(0)}, \quad (6.34)$$

such that

$$\mathbf{d}_i = \mathbf{d}_i^{(0)} + \epsilon \mathbf{c} \times \mathbf{d}_i^{(0)} + \mathcal{O}(\epsilon^2). \quad (6.35)$$

We now expand all quantities, such that the first-order perturbation of all vector quantities is expressed in the frame $\{\mathbf{d}_i^{(0)}, i = 1, 2, 3\}$. For any scalar a and vector

$$\mathbf{v} = v_1 \mathbf{d}_1 + v_2 \mathbf{d}_2 + v_3 \mathbf{d}_3, \quad (6.36)$$

we consider the following expansion in ϵ :

$$a = a^{(0)} + \epsilon a^{(1)} + \mathcal{O}(\epsilon^2), \quad (6.37)$$

$$\mathbf{v} = \sum_{i=1}^3 (v_i^{(0)} + \epsilon v_i^{(1)}) \mathbf{d}_i^{(0)} + \mathcal{O}(\epsilon^2). \quad (6.38)$$

Note the following relationship: If $\mathbf{v}_i = v_i^{(0)} + \epsilon v_i^{(1)}$, we have $v_i^{(0)} = \mathbf{v}_i^{(0)}$ and $v_i^{(1)} = \mathbf{v}_i^{(1)} - (\mathbf{c} \times \mathbf{v}^{(0)})_i$, where $\mathbf{v}^{(0)} = \sum_i v_i^{(0)} \mathbf{d}_i^{(0)}$.

We expand $\mathbf{r}$, $\mathbf{n}$, and $\mathbf{u}$ per (6.38), and $\alpha = \alpha^{(0)} + \epsilon \alpha^{(1)} + \mathcal{O}(\epsilon^2)$. We assume that the body force $\mathbf{f}$ and body couple $\mathbf{l}$ can be expanded similarly. By assumption, the base solution solves the Kirchhoff equations. We compute the linearized equations by expanding all equations and variables to order ϵ . Doing so, we obtain a linear system for the independent variables $\{r_1^{(1)}, r_2^{(1)}, r_3^{(1)}, n_1^{(1)}, n_2^{(1)}, n_3^{(1)}, u_1^{(1)}, u_2^{(1)}, u_3^{(1)}, c_1, c_2, c_3, \alpha^{(1)}\}$.

The kinematic equation $\partial \mathbf{r} / \partial S = \alpha \mathbf{d}_3$ is

$$(r_1^{(1)})' + u_2^{(0)} r_3^{(1)} - u_3^{(0)} r_2^{(1)} = \alpha^{(0)} \mathbf{c}_2, \quad (6.39)$$

$$(r_2^{(1)})' + u_3^{(0)} r_1^{(1)} - u_1^{(0)} r_3^{(1)} = -\alpha^{(0)} \mathbf{c}_1, \quad (6.40)$$

$$(r_3^{(1)})' + u_1^{(0)} r_2^{(1)} - u_2^{(0)} r_1^{(1)} = \alpha^{(1)}. \quad (6.41)$$

The frame equations $\partial \mathbf{d}_i / \partial S = \mathbf{u} \times \mathbf{d}_i$ is

$$\mathbf{c}'_1 = u_1^{(1)} + \mathbf{c}_3 u_2^{(0)} - \mathbf{c}_2 u_3^{(0)}, \quad (6.42)$$

$$\mathbf{c}'_2 = u_2^{(1)} + \mathbf{c}_1 u_3^{(0)} - \mathbf{c}_3 u_1^{(0)}, \quad (6.43)$$

$$\mathbf{c}'_3 = u_3^{(1)} + \mathbf{c}_2 u_1^{(0)} - \mathbf{c}_1 u_2^{(0)}. \quad (6.44)$$

The force balance $\mathbf{n}' + \mathbf{f} = \mathbf{0}$ to first order is given by

$$(n_1^{(1)})' = u_3^{(0)} n_2^{(1)} - u_2^{(0)} n_3^{(1)} - f_1^{(1)}, \quad (6.45)$$

$$(n_2^{(1)})' = u_1^{(0)} n_3^{(1)} - u_3^{(0)} n_1^{(1)} - f_2^{(1)}, \quad (6.46)$$

$$(n_3^{(1)})' = u_2^{(0)} n_1^{(1)} - u_1^{(0)} n_2^{(1)} - f_3^{(1)}, \quad (6.47)$$

and, similarly, the moment balance reads

$$(m_1^{(1)})' = u_3^{(0)} m_2^{(1)} - u_2^{(0)} m_3^{(1)} - l_1^{(1)} - \alpha^{(1)} n_1^{(0)} + \alpha^{(0)} (\mathbf{c}_2 n_3^{(0)} + n_2^{(1)}), \quad (6.48)$$

$$(m_2^{(1)})' = u_1^{(0)} m_3^{(1)} - u_3^{(0)} m_1^{(1)} - l_2^{(1)} + \alpha^{(1)} n_2^{(0)} + \alpha^{(0)} (\mathbf{c}_1 n_3^{(0)} - n_1^{(1)}), \quad (6.49)$$

$$(m_3^{(1)})' = u_2^{(0)} m_1^{(1)} - u_1^{(0)} m_2^{(1)} - l_3^{(1)} - \alpha^{(0)} (\mathbf{c}_1 n_1^{(0)} + \mathbf{c}_2 n_2^{(0)}), \quad (6.50)$$

where the first-order moment is given by the constitutive relationship also expanded to first order:

$$m_i^{(1)} = K_i u_i^{(1)} + \left(\mathbf{c} \times \sum_{j=1}^3 \left(K_j (u_j^{(0)} - \hat{u}_j) - u_j^{(0)} \right) \mathbf{d}_j^{(0)} \right)_i, \quad i = 1, 2, 3. \quad (6.51)$$

In the case of an inextensible rod, $\alpha^{(0)} = 1$, $\alpha^{(1)} = 0$ and there is no constitutive law for n_3 . For an extensible rod, the constitutive equation (6.21) gives

$$n_3^{(1)} = \mathbf{c}_2 n_1^{(0)} - \mathbf{c}_1 n_2^{(0)} + EA \alpha^{(1)}. \quad (6.52)$$

6.5.3 Bifurcation Criterion for Elastic Buckling

To obtain a bifurcation criterion, we define the nine-dimensional vector

$$\boldsymbol{\mu} = \{r_1^{(1)}, r_2^{(1)}, r_3^{(1)}, n_1^{(1)}, n_2^{(1)}, n_3^{(1)}, \mathbf{c}_1, \mathbf{c}_2, \mathbf{c}_3\}. \quad (6.53)$$

Note that we can eliminate $u_i^{(1)}$ immediately using (6.42–6.44), and $\alpha^{(1)}$ using (6.52). The system can be written in compact matrix form

$$\mathbf{M}_2 \boldsymbol{\mu}'' + \mathbf{M}_1 \boldsymbol{\mu}' + \mathbf{M}_0 \boldsymbol{\mu} = \mathbf{0}, \quad (6.54)$$

where each $\mathbf{M}_i$ is a 9×9 matrix whose coefficients are functions of the base solution.

If the family of equilibria can be written in a basis where it is constant in S , these matrices are also constant. In that case, we can look for a solution of the form $\boldsymbol{\mu} = \boldsymbol{\xi} e^{inS} + \bar{\boldsymbol{\xi}} e^{-inS}$. Inserting this form into (6.54), the system is satisfied if $\det(\mathbf{M}) = 0$, where

$$\mathbf{M} = -n^2 \mathbf{M}_2 + in \mathbf{M}_1 + \mathbf{M}_0. \quad (6.55)$$

For problems related to uniform growth, it is convenient to consider γ as a control parameter. Assuming that the base solution exists for a range of values of γ , the problem is to determine the critical growth γ^* at which a bifurcation takes place, that is, the values of γ at which the determinant vanishes. The corresponding value of n determines the mode or wavelength of the bifurcation mode, depending on the particular geometry.

6.5.4 Example: The Growing Ring

A classic problem in the theory of elastic rods is the buckling of a ring to a noncircular shape as discussed in Section 6.5.1 for the twisted ring. Similarly, the problem of the stability of a ring with intrinsic curvature under a variety of loadings and material parameters has been considered by many authors [462, 527, 825, 1150, 1237, 1238]. The case of multicovered rings, that is, rings that wrap around multiple times on themselves has also been studied in detail [474, 825, 827].

Here, we use this simple configuration to demonstrate the effect of growth on the buckling of rods. We further consider the role of remodeling and of an elastic foundation in the next sections. We assume that the ring is a constitutively isotropic, inextensible rod of initial and unstressed radius 1, with cross-section radius a . We assume that it grows linearly in time so that, without loss of generality, $\gamma = 1 + t$, while all other material properties are unchanged. In this case, we have $\hat{\mathbf{u}} = (0, 1, 0)$, $L = 2\pi\gamma$.

First, we study the buckling of the growing ring in the absence of external forces. In the absence of remodeling, the buckling is strictly determined by the critical

parameter γ . For this system there exist, for all $\gamma \geq 1$, circular solutions characterized by a curvature $u_2 = 1/\gamma$ and vanishing force $\mathbf{n} = \mathbf{0}$. These solutions are maintained by a bending moment $\mathbf{m} = EI(u_2 - 1)$ generated by the periodic boundary conditions. The ring is initially situated in the x - y plane with general frame

$$\mathbf{d}_1^{(0)} = -\cos(S/\gamma)\mathbf{e}_x - \sin(S/\gamma)\mathbf{e}_y, \quad (6.56)$$

$$\mathbf{d}_2^{(0)} = \mathbf{e}_z, \quad (6.57)$$

$$\mathbf{d}_3^{(0)} = -\sin(S/\gamma)\mathbf{e}_x + \cos(S/\gamma)\mathbf{e}_y. \quad (6.58)$$

Then, the only nonvanishing components of the base solution are

$$r_1^{(0)} = -\gamma, \quad u_2^{(0)} = 1/\gamma. \quad (6.59)$$

Inserting this into (6.39–6.50), the determinant condition can be solved explicitly for γ , and is found to be

$$\gamma(n) = \frac{1 - \Gamma + \sqrt{1 + (4n^2 - 2)\Gamma + \Gamma^2}}{2}, \quad (6.60)$$

where Γ is given by (5.57) and the buckling mode n must be an integer to satisfy the periodic boundary conditions of the closed ring. The critical growth is the smallest possible value of $\gamma > 1$, and it occurs for $n = 2$.

The first-order corrections for the centerline are shown in Figure 6.6. Equation (6.60) provides the critical point at which the ring buckles. After buckling, a full numerical solution for the post-buckled ring can be obtained by solving the full system via a shooting method [942] and parameter continuation. This solution is shown in Figure 6.7. Note that self-contact is not taken into account. Nevertheless, the ring follows an interesting deformation path. By $\gamma \approx 2.19$, the closed rod has collapsed back into a planar ring, tripling on itself. As γ continues to increase, this tripled ring grows, so that at $\gamma = 3$, it forms a tripled ring of radius 1. At this point, the curvature everywhere matches the intrinsic curvature; the ring is back to a stable stress-free state.

The tripled covered ring will become unstable if we further increase γ . The critical value of γ where it becomes unstable can be found by realizing that the buckling mode n in (6.60) is now an integer multiple of $1/3$, since the rod has tripled its length.

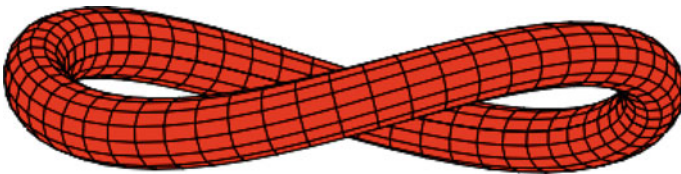


Figure 6.6 The shape of a growing ring after buckling, computed from a linear stability analysis.

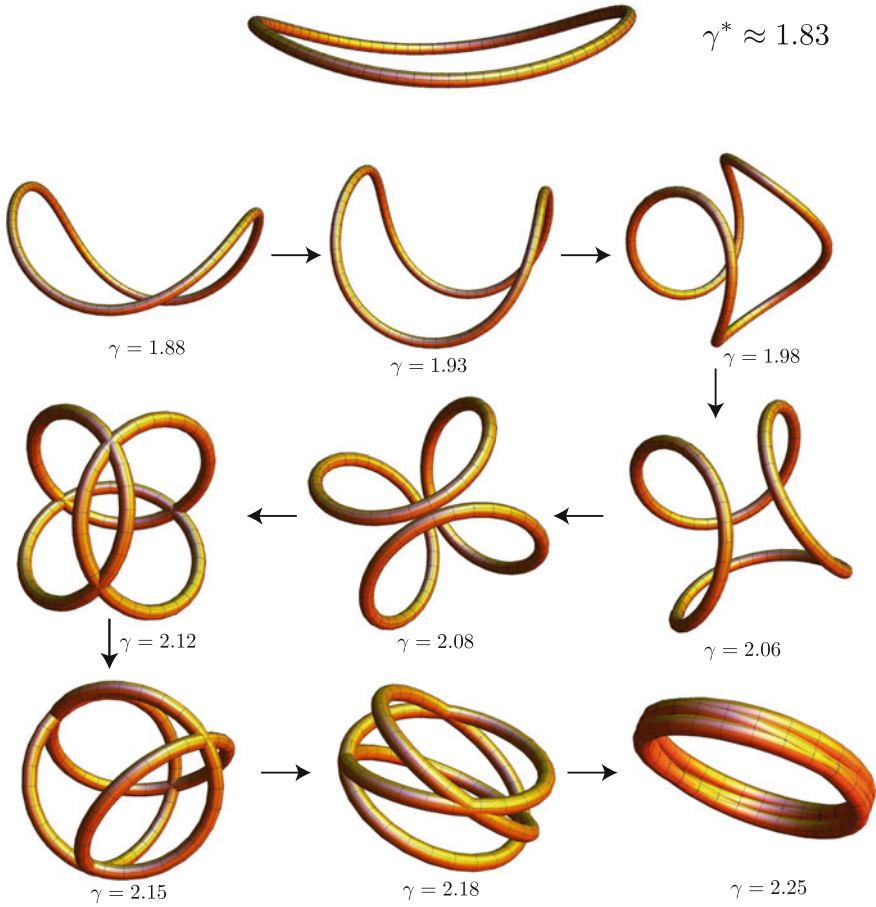


Figure 6.7 The shape of a growing ring after buckling, computed from a numerical analysis ($\Gamma = 0.7$) [917]. The parameter γ denotes the growth stretch.

For $\Gamma = 0.7$, the second bifurcation occurs at $\gamma \approx 3.83$, with mode $4/3$. This solution is shown in Figure 6.8 where the out-of-plane amplitude is plotted as a function of the growth parameter γ .

6.5.5 A Growing Ring with Remodeling

We look again at a growing ring of initial unstressed radius 1. We assume that it grows linearly in time so that $\gamma = 1 + t$, where t is the growth time. During growth, the intrinsic curvature also evolves to the current curvature following the law (6.14) in such a way that if growth is interrupted, the ring evolves to an intrinsic state with

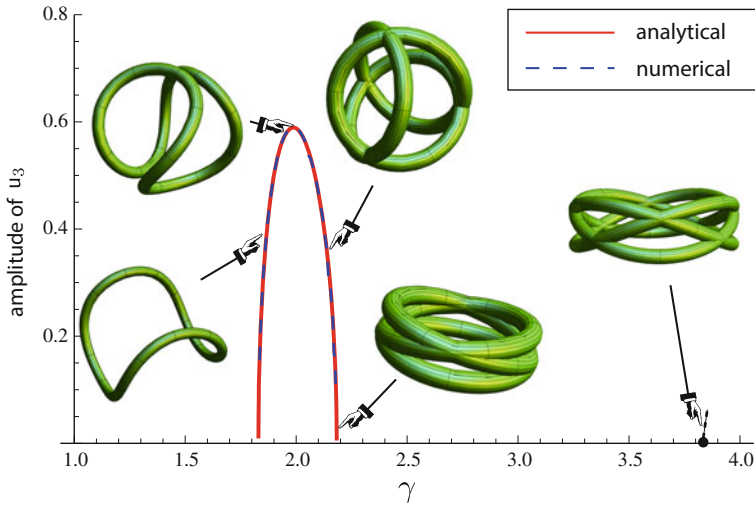


Figure 6.8 Comparison between the out-of-plane amplitude of the ring obtained from the numerical simulation (dashed) for $\Gamma = 0.7$ and the asymptotic value predicted by an asymptotic model (solid) given in [917].

a characteristic time $1/\eta$. As long as the central axis of the rod remains circular, the curvature is, as before, $u_2 = 1/(1+t)$, which can be used directly in (6.14), giving

$$\frac{\partial \hat{u}_2}{\partial t} = \eta \left(\frac{1}{1+t} - \hat{u}_2 \right). \quad (6.61)$$

The solution of this last equation is

$$\hat{u}_2(t) = e^{-\eta(1+t)} \left[e^\eta + \eta \text{Ei}(\eta(1+t)) - \eta \text{Ei}(\eta) \right], \quad (6.62)$$

where $\text{Ei}(\cdot)$ denotes the exponential integral function. We now have a competition between growth and the remodeling of the intrinsic curvature and the ring may become unstable as shown in Figure 6.9. A bifurcation happens when

$$\frac{u_2}{\hat{u}_2} \leq c_2 \equiv \frac{\Gamma - 1 + \sqrt{\Gamma^2 + 14\Gamma + 1}}{8\Gamma}, \quad (6.63)$$

at which time the solution does not remain planar and the expression for the intrinsic curvature (6.62) ceases to be valid. In this situation where we have two dynamical processes, the history of the deformation has to be taken into account. A similar situation for the Euler buckling of a straight rod and the twisted ring has been discussed in [451, 1337].

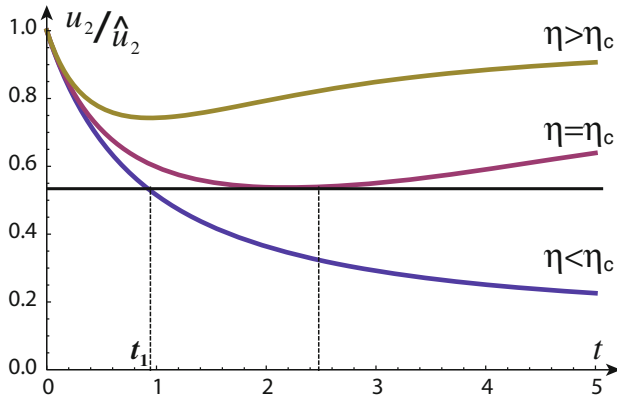
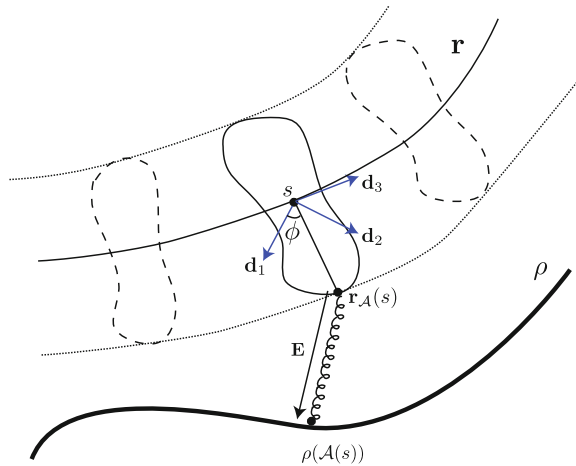


Figure 6.9 Stability of a growing ring with evolving intrinsic curvature ($\Gamma = 3/4$). The condition for buckling is $c_2 \approx 0.54$, for $\eta < \eta_c \approx 0.57$, whereby the instability occurs at time t_1 . For $\eta > \eta_c$, the intrinsic curvature evolves sufficiently fast so as to remove stresses in the ring and to prevent an instability developing (upper curve: $\eta = 2$, lower curve $\eta = 0.1$).

6.6 Growing Rods on a Rigid Foundation

Next, we consider a growing rod attached to a rigid foundation via an elastic force, and explore the effect of the body force $\mathbf{f}$ and body couple $\mathbf{l}$ generated by the attachment. We assume that the foundation is a rigid space curve to which the rod is attached via a restoring body force depending on the distance from the rod to the curve. This attachment induces a body force and body couple acting on the rod. The position of the rigid curve $\mathbf{r}_A(s)$ is specified with respect to the rod by a pair of functions $\phi : [0, l] \rightarrow [0, 2\pi[$ and $\mathcal{A} : [0, l] \rightarrow [0, \hat{l}]$ where l and $\hat{l}$ are the length of the rod and the rigid curve, respectively. The situation is depicted in Figure 6.10.

Figure 6.10 A rod is attached on a rigid foundation ρ by an elastic force.



The function $\phi(s)$ is the angle from the $\mathbf{d}_1$ axis at which the attachment occurs. Defining $a(s)$ to be the perpendicular distance from the centerline to the attachment point on the surface of the rod, the point $\mathbf{r}_{\mathcal{A}}(s)$ of attachment is

$$\mathbf{r}_{\mathcal{A}} = \mathbf{r} + a [\cos \phi \mathbf{d}_1 + \sin \phi \mathbf{d}_2]. \quad (6.64)$$

The function $\mathcal{A}(s)$ defines the location on the foundation to which a point with material coordinate s is attached, i.e., a map between the centerline of the rod and the foundation curve $\boldsymbol{\rho}(\hat{s})$. The *attachment map* $\mathcal{A}(s)$ is a one-to-one map from the rod to the foundations such that $\hat{s} = \mathcal{A}(s)$, $\mathcal{A}(0) = 0$. That is, the point $\mathbf{r}_{\mathcal{A}}(s)$ is attached to the point $\boldsymbol{\rho}(\mathcal{A}(s))$.

The two functions ϕ and $\mathcal{A}$, as well as the foundation curve $\boldsymbol{\rho}$, completely define the geometry of attachment. To describe the mechanical force connecting the curve to the rod, we introduce

$$\mathbf{E} = \boldsymbol{\rho}(\mathcal{A}(s)) - \mathbf{r}_{\mathcal{A}}(s), \quad (6.65)$$

and assume that the body force generated by the rigid foundation is along that direction, and only depends on the distance relative to a rest length $q(s)$,

$$\mathbf{f}(s) = f(|\mathbf{E}| - q(s)) \frac{\mathbf{E}}{|\mathbf{E}|}, \quad (6.66)$$

where $q(s)$ is the rest length of the spring, so that $f(0) = 0$ when $|\mathbf{E}| = q$. We further assume that f derives from a convex potential for which the origin is a minimum. The particular case where f is linear corresponds to the classic case of a Winkler foundation with a Hookean spring [100, 326, 983].

Since the attachment force acts on the rod, it also generates a body couple given by

$$\mathbf{l} = (\mathbf{r}_{\mathcal{A}} - \mathbf{r}) \times \mathbf{f}. \quad (6.67)$$

6.6.1 Example: A Growing Ring on a Foundation

We consider the case in which the inside edge of a growing rod of initial radius 1 is attached to a ring of radius $(1 - a)$, located in the x - y plane and centered at the origin. As the ring grows, the foundation exerts an increasing force directed toward the center of the ring, as illustrated in Figure 6.11. To compute the circular planar base solution, we consider a ring in the x - y plane with a frame given by (6.56–6.58). The foundation is attached at the point $\mathbf{r}_{\mathcal{A}} = \mathbf{r} + a\mathbf{d}_1$, where a is the cross-section radius of the rod, and the foundation force is assumed to be linear:

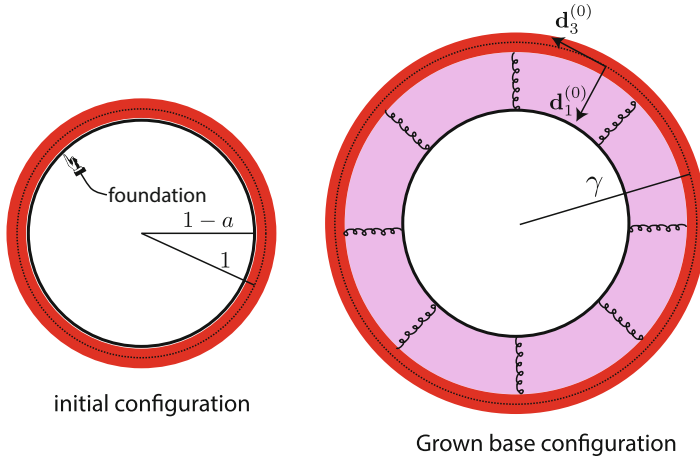


Figure 6.11 Circular solutions for the growing ring with foundation on inside edge, viewed from above. The intrinsic curvature is $\bar{u}_2 = 1$.

$$\mathbf{f} = k(\boldsymbol{\rho} - \mathbf{r}_A), \quad (6.68)$$

where k is the foundation stiffness.

Since $\boldsymbol{\rho} = -(1-a)\mathbf{d}_1^{(0)}$, the circular base solution is given by:

$$r_1^{(0)} = -\gamma, \quad r_2^{(0)} = r_3^{(0)} = 0, \quad (6.69)$$

$$f_1^{(0)} = k(\gamma - 1), \quad f_2^{(0)} = f_3^{(0)} = 0, \quad \mathbf{l}^{(0)} = \mathbf{0}, \quad (6.70)$$

$$u_2^{(0)} = 1/\gamma, \quad (6.71)$$

$$n_3^{(0)} = -k\gamma(\gamma - 1). \quad (6.72)$$

To compute the critical value of γ , the body force (6.68) and couple (6.67) are expanded to $\mathcal{O}(\epsilon)$, yielding

$$f_1^{(1)} = -kr_1^{(1)}, \quad f_2^{(1)} = -k(r_2^{(1)} + a\mathbf{c}_3), \quad f_3^{(1)} = -k(r_3^{(1)} - a\mathbf{c}_2), \quad (6.73)$$

$$l_1^{(1)} = 0, \quad l_2^{(1)} = -a(f_3^{(1)} + \mathbf{c}_2 f_1^{(0)}), \quad l_3^{(1)} = a(f_2^{(1)} - \mathbf{c}_3 f_1^{(0)}). \quad (6.74)$$

Following Section 6.5, a determinant condition is formed for the critical growth γ^* . The result, and the influence of the foundation on buckling, is illustrated in Figure 6.12, in which γ^* is plotted against the log of the foundation stiffness k for modes $n = 2, 3, 4$.

For small k , the solution is similar to the case of no foundation: The ring buckles at mode 2, and as $k \rightarrow 0$, the buckling criterion (6.60) is recovered. As the stiffness increases, the critical growth decreases for increasing buckling mode n and the ring buckles earlier. As the foundation force strengthens, it becomes energetically favor-

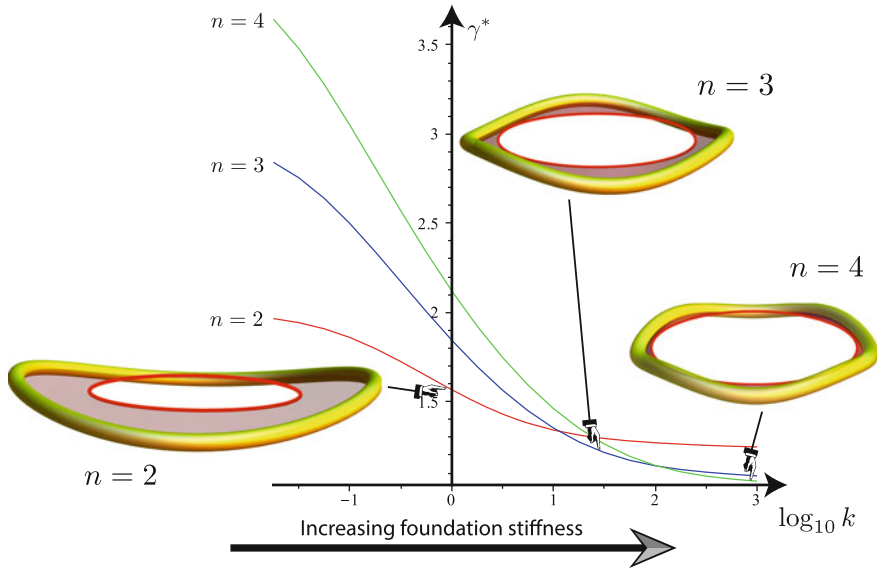


Figure 6.12 Critical buckling growth against the log of the foundation stiffness k , for modes 2, 3, and 4. As the stiffness increases, buckling occurs after less growth, and at higher modes ($\Gamma = 1$ and $a = 0.07$).

able to buckle at higher modes. These solutions have higher bending energy, but they reduce the foundation energy by remaining closer to the foundation.

6.6.2 Example: A Straight Rod Growing on a Foundation

Next, we consider the buckling of a growing planar rod on a foundation in the absence of body couples, as shown in Figure 6.13. This scenario is similar to the classic problem first studied by Winkler in 1867 [395, 983, 1287, 1328]. It is instructive to see how buckling emerges within our framework. The rod is naturally straight, initially planar, and constrained in the plane so that the Darboux vector is $\mathbf{u} = (0, \alpha\kappa, 0)$, where κ is the Frenet curvature and $\alpha = \partial_S s$ is the elastic stretch. It is convenient to use the planar representation of a rod given in Section 5.8. The rod lies in the x - y plane and is parameterized by the angle θ between the tangent vector and the x -axis:

$$\boldsymbol{\tau} = \mathbf{d}_3 = \cos \theta \mathbf{e}_x + \sin \theta \mathbf{e}_y, \quad (6.75)$$

which implies

$$\kappa = \frac{\partial \theta}{\partial s} = \alpha^{-1} \frac{\partial \theta}{\partial S}, \quad (6.76)$$

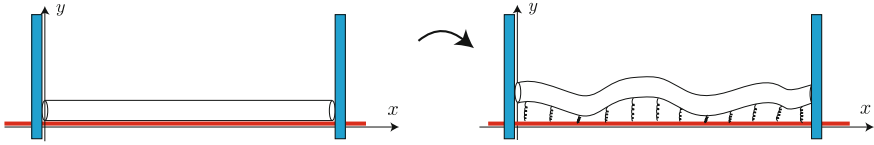


Figure 6.13 Setup of the buckling of a straight planar rod on a foundation. A rod is attached to a foundation and is allowed to deform only in the plane. An increase in length leads to a buckling instability.

and $\mathbf{d}_2 = \mathbf{e}_z$. By writing $\mathbf{n} = F\mathbf{e}_x + G\mathbf{e}_y$, $\mathbf{f} = f\mathbf{e}_x + g\mathbf{e}_y$, $\mathbf{r} = x\mathbf{e}_x + y\mathbf{e}_y$, we can simplify the equations of motion (6.2–6.3) to a system of five equations:

$$\frac{\partial x}{\partial S} = \alpha \cos \theta, \quad \frac{\partial y}{\partial S} = \alpha \sin \theta, \quad (6.77)$$

$$\frac{\partial F}{\partial S} + f = 0, \quad \frac{\partial G}{\partial S} + g = 0, \quad (6.78)$$

$$EI \frac{\partial^2 \theta}{\partial S^2} + \alpha G \cos \theta - \alpha F \sin \theta = 0. \quad (6.79)$$

These equations are supplemented by the constitutive law for the foundation, given below, and a constitutive law for tension

$$F \cos \theta + G \sin \theta = EA(\alpha - 1), \quad (6.80)$$

where A is the cross-sectional area as before. We use this last relationship to express α in terms of F , G , and θ in the equations above.

We consider the case of a clamped uniformly growing rod of initial length $L_0 = 1$ whose end positions are fixed for all time:

$$x(0) = 0, \quad x(L) = 1, \quad y(L) = y(0) = y_0, \quad \theta(0) = \theta(L) = 0, \quad (6.81)$$

where y_0 is the distance between the rod and the rigid foundation, taken to be the segment of the x -axis between 0 and 1.

Different assumptions about the nature of the attachment between the rod and the foundation can be made. We consider the case where the rod is initially glued to the axis: A point $(S_0, 0)$ on the x -axis is attached to a point (S_0, y_0) on the rod. In the current configuration, the two points are still connected elastically and are now located at $(S/\gamma, 0)$ and $(x(S), y(S))$. Therefore, the body force acting on the rod from the foundation is

$$\mathbf{f} = \frac{h(\Delta)}{\gamma \Delta} [(x - S/\gamma)\mathbf{e}_x + (y - y_0)\mathbf{e}_y], \quad (6.82)$$

where we have assumed that the rest length of the foundation is y_0 and $\Delta = \sqrt{(x - S/\gamma)^2 + (y - y_0)^2}$ is the distance between these two connected points. Note the factor $1/\gamma$ which indicates that the attachment was made in the initial configuration and no subsequent remodeling takes place. The function $h(\Delta)$ is chosen such that $h(0) = 0$ and $h'(0) = -Ek < 0$.

The base solution is a straight compressed rod given by

$$x^{(0)} = S/\gamma, \quad y^{(0)} = \theta^{(0)} = G^{(0)} = 0, \quad F^{(0)} = EA \frac{1-\gamma}{\gamma}. \quad (6.83)$$

To find the critical value of γ where a bifurcation first occurs, we expand our variables as

$$x = x^{(0)} + \epsilon x^{(1)} + \mathcal{O}(\epsilon^2), \quad y = y^{(0)} + \epsilon y^{(1)} + \mathcal{O}(\epsilon^2), \quad (6.84)$$

and, as before, linearize the system around the trivial compressed state. To first order, it is easy to show that $x^{(1)} = F^{(1)} = 0$, and the problem is reduced to a set of three linear equations

$$\frac{dy^{(1)}}{dS} = \frac{\theta^{(1)}}{\gamma}, \quad \frac{dG^{(1)}}{dS} = Ek \frac{y^{(1)}}{\gamma}, \quad (6.85)$$

$$EI \frac{d^2 \theta^{(1)}}{dS^2} + EA(\gamma - 1)\theta^{(1)} + \gamma G^{(1)} = 0, \quad (6.86)$$

which can be further reduced to a single fourth-order differential equation for $\theta^{(1)}$

$$\frac{d^4 \theta^{(1)}}{dS^4} + 2a \frac{d^2 \theta^{(1)}}{dS^2} + b^2 \theta^{(1)} = 0, \quad (6.87)$$

where

$$a = \frac{A(\gamma - 1)}{2I\gamma^2}, \quad b = \sqrt{\frac{k}{I\gamma^3}}, \quad (6.88)$$

and the boundary conditions, vanishing for all linearized variables, now read

$$\theta^{(1)}(0) = A(\gamma - 1) \frac{d\theta^{(1)}}{dS}(0) + I\gamma^2 \frac{d^3 \theta^{(1)}}{dS^3}(0) = 0, \quad (6.89)$$

$$\theta^{(1)}(\gamma) = A(\gamma - 1) \frac{d\theta^{(1)}}{dS}(\gamma) + I\gamma^2 \frac{d^3 \theta^{(1)}}{dS^3}(\gamma) = 0. \quad (6.90)$$

We now look for solutions of (6.87) of the form $\theta^{(1)} \sim e^{i\omega S}$, which leads to the four roots

$$\omega_1^2 = a + \sqrt{a^2 - b^2}, \quad \omega_2^2 = a - \sqrt{a^2 - b^2}. \quad (6.91)$$

The condition $a = b$ gives the first bifurcation condition for the existence of oscillatory modes on an infinite domain. Explicitly, it reads

$$A^2(\gamma - 1)^2 - 4Ik\gamma = 0, \quad (6.92)$$

which leads, for a circular cross section of radius r , to the first condition

$$\gamma_1 = 1 + \frac{kr}{2\pi}(r + \sqrt{kr^2 + 4\pi}), \quad (6.93)$$

associated with a typical mode number $n = \sqrt{a}$; that is, a typical wavelength

$$\zeta = 2\pi/\omega_1 = 2\pi\gamma_1^{3/4} \left(\frac{I}{k}\right)^{1/4} = \frac{\pi^{5/4}}{\sqrt{2}}\gamma_1^{3/4}rk^{-1/4} \quad (6.94)$$

$$= r \frac{\pi^{1/4}}{\sqrt{2}} \left(\pi k^{-1/4} - \frac{\sqrt{\pi}}{4} k^{1/4} + \frac{1}{32} k^{3/4} \right) + \mathcal{O}(k^{5/4}). \quad (6.95)$$

In a finite domain with clamped boundary conditions, there is a delay at the bifurcation and the value of $\gamma_2 > \gamma_1$ for which the system is unstable can be found from the boundary conditions. Assuming $a > b$, the nontrivial solution, shown in Figure 6.14, reads

$$\theta^{(1)} = C_1 [\cos(\omega_1 S) - \cos(\omega_2 S)] + C_2 \sin(\omega_1 S) + C_3 \sin(\omega_2 S), \quad (6.96)$$

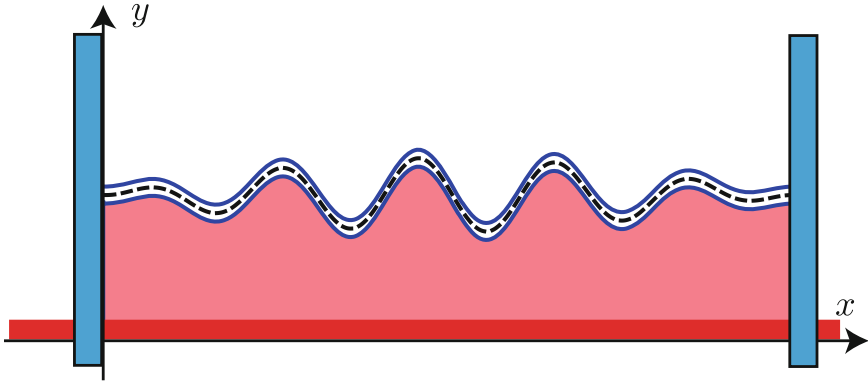


Figure 6.14 Buckling of a clamped growing rod on an elastic foundation. The rod is constrained to lie in the unit interval and clamped at the boundary (with $y_0 = 1/2$). Here $k = 1$, $r = 0.02$, and $\gamma_2 = 1.19934$. The amplitude is arbitrary and chosen to be $C_1 = -0.2$. The centerline is indicated by a dashed line.

where

$$C_2 = \frac{C_1 \omega_1 b (\cos(\gamma \omega_1) - \cos(\gamma \omega_2))}{(2a\omega_1 - \omega_1^3) \sin(\gamma \omega_2) + (\omega_2^3 - 2a\omega_2) \sin(\gamma \omega_1)}, \quad (6.97)$$

$$C_3 = \frac{C_1 \omega_2 b (\cos(\gamma \omega_2) - \cos(\gamma \omega_1))}{(2a\omega_1 - \omega_1^3) \sin(\gamma \omega_2) + (\omega_2^3 - 2a\omega_2) \sin(\gamma \omega_1)}, \quad (6.98)$$

with the condition

$$a \sin(\gamma \omega_1) \sin(\gamma \omega_2) + b \cos(\gamma \omega_1) \cos(\gamma \omega_2) - b = 0. \quad (6.99)$$

The first positive root of (6.99) is γ_1 , but it leads to the trivial solution $\theta^{(1)} = 0$. Therefore, the critical value of γ is the second root $\gamma_2 > \gamma_1$. However for $r \ll L_0$, the root γ_1 provides an excellent first approximation for the critical value γ_2 [720]. This linear analysis can be used as a starting point for a nonlinear analysis that predicts the amplitude of the buckled solution as a function of the load [764].

6.7 Application: Growing Vines

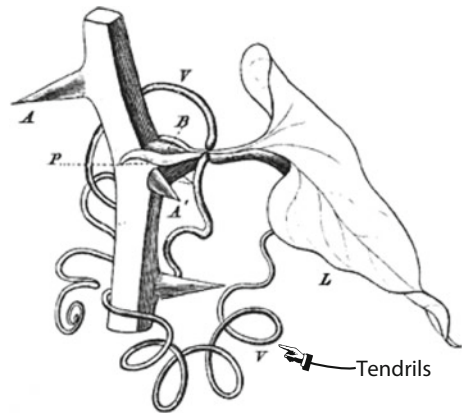
Climbing plants have developed a fascinating array of mechanical strategies to achieve vertical growth without being able to support themselves. Hookers, leaners, weavers, rooters, stickers, clingers, tendril-bearers, or twiners are just a few realizations of the thirty different ways vines manage to grow by taking advantage of their surroundings [869]. The growth process of climbing plants raises many interesting mechanical questions already noted by nineteenth century plant physiologists and further studied by Silk, Holbrook, and coworkers [838, 1124, 1155, 1160, 1162]. We now consider two problems in the growth of vines that can be modeled as morphoelastic rods.

6.7.1 Perversion in Tendrils

6.7.1.1 Background

As a first example, we consider the evolution of tendrils in plants, following [476, 853]. Among the many different mechanisms climbing plants use to climb along supports, the so-called “tendril-bearers” constitute an important class, e.g., the grapevine, the hop, the bean, the melon. A tendril is a modified leaf that can be found at the extremities of some climbing plants, and these are used to achieve vertical growth, as shown Figure 6.15. In the first stage of their development, tendrils are tender, soft, curly, and flexible organs originating from the stem. As they grow, the

Figure 6.15 Tendrils are modified leaves that are used by some climbing plants to attach themselves to a support [161].



tendrils *circumnutate* [772, 812]: The tip of the tendril describes large loops in space by completely rotating on itself until it touches a support, such as a trellis, pole, or branch. If the circumnutation does not result in contact, the tendrils eventually dry and fall off the stem, as illustrated in Figure 6.16. The tendrils which are in contact with a support enter another phase of their development; their tissues develop in such a way that they start to curl and tighten up, eventually becoming woody, robust, and tough [111]. This curling provides the plant with an elastic spring-like connection to the support, which enables it to resist high winds and loads.

Physically, a tendril is a filament under tension. Once a tendril has grasped a support, it starts to develop curvature by differential growth until it bifurcates into a shape made out of two or more helical structures with opposite handedness as shown in Figure 6.17. This shape can also be observed in telephone cords. If one completely untwists the helical structure of the telephone cord and pulls the ends, a straight cord can be obtained. Now, if one slowly releases the ends, the filament suddenly changes to a shape composed of two helical structures with *opposite handedness* and linked by a small inversion, as seen in Figure 6.18. Mechanically, this phenomenon is due to the fact that the original structure has no twist and neither end is allowed to rotate. The total twist remains zero at all times and the elastic energy is minimized by creating helices.

The German mathematician J. B. Listing [94, 793] refers to an inversion of chirality as a *perversion*. D'Arcy Thompson used the idea to characterize seashells: “*the one is a mirror-image of the other; and the passing from one to the other through the plane of symmetry (which has no “handedness”) is an operation which Listing called perversion*” [1230, p. 820]. Maxwell also uses the word perversion, in his “*Treatise on Electromagnetism*” published in 1881: “*They are geometrically alike in all respects, except that one is the perversion of the other, like its image in a looking glass*” [844]. The usage of the word *perversum* actually originated in the description of rare left-handed specimens of seashells from a species of overwhelmingly right-handed individuals. For instance, there are only six known left-handed specimens out of the millions of known *Cerion*, a West Indian land snail [491, 1089]. Accordingly,

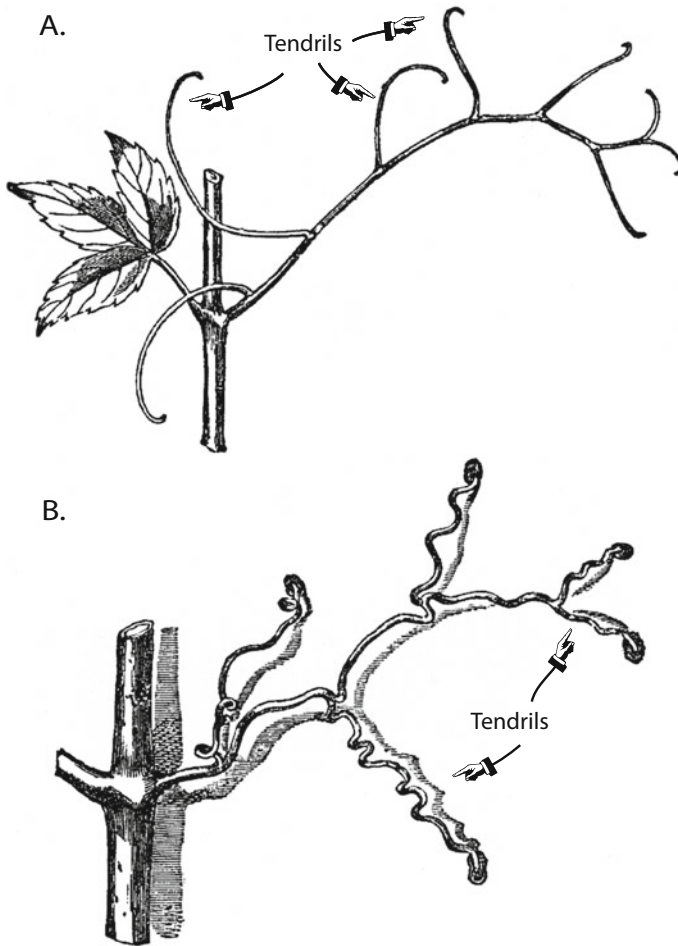


Figure 6.16 Growth and attachment of tendrils. A. In the first stage, the tendrils are *circumnutating* until they find an attachment. B. In the second stage, the tendrils are attached and *perversion* sets in. Adapted from Darwin [261].

following the terminology introduced in [477], we refer to any filamentary structure supporting both left- and right-handed helices as a *perversion*.

The phenomenon of perversion in climbing plants has a long interesting scientific history. Inversion of helicity in tendrils already appears in the illustration of Linnaei in “*Philosophia Botanica*” in 1751 [791] shown in Figure 6.19. However, according to De Candolle [161, 162], the first record of a scientific observation of perversion goes back to a letter of the French scientist Ampère to the French Academy of Sciences. Most major nineteenth century plant physiologists, such as Dutrochet in 1844 [316], von Mohl in 1852 [897], and Léon in 1858 [782, 783] have described the perversion found in tendrils.

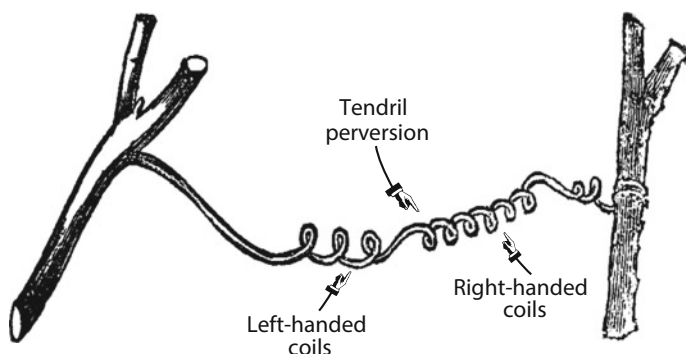


Figure 6.17 After attachment, the tendril of *Bryonia dioica* curls on itself to create a tendril perversion connecting coils of opposite handedness. Drawing adapted from Darwin [261].

It is Charles Darwin, inspired by the related studies of his friend, the American botanist, Asa Gray [495], who gave the first complete and truly scientific analysis of the growth of climbing plants in his delightful little book, “The Movements and Habits of Climbing Plants” [261], based on an essay presented at the Linnean Society in 1865. In this book, he devotes an entire chapter to the problem of tendril growth and gives the first qualitative explanation of the phenomenon: “*When a tendril has caught a support and is spirally contracted, there are always as many turns in one direction as in the other; so that the twisting of the axis in the one direction is exactly compensated by the twisting in the opposite direction... I cannot resist giving one other illustration, though superfluous: When a haberdasher winds up ribbon for a customer, he does not wind it into a single coil; for, if he did, the ribbon would twist itself as many times as there were coils; but he winds it into a figure of eight on his thumb and little finger, so that he alternately takes turns in opposite directions, and thus the ribbon is not twisted. So it is with tendrils, with this sole difference, that they take several consecutive turns in one direction and then the same number in an opposite direction; but in both cases the self-twisting is avoided.*” This situation is illustrated in Figure 6.17.

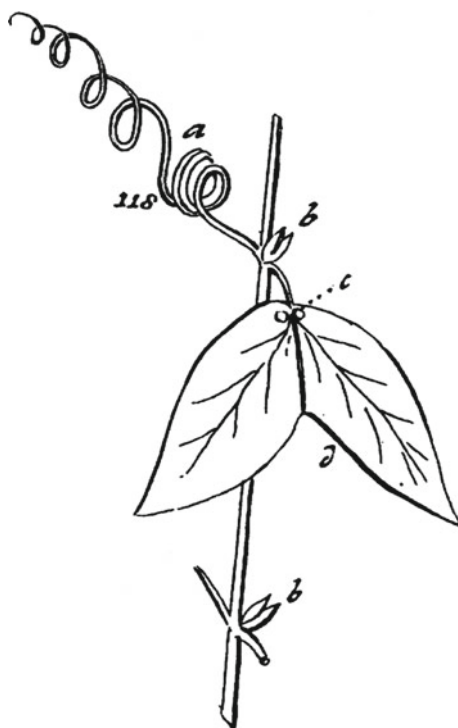
The onset of twisting is due to the development of intrinsic curvature in the filament. In physical systems, there are various mechanisms for creating intrinsic curvature in an initially straight unstressed filament. In the case of tendrils, *differential growth* takes place between the ventral and dorsal side of the sections as already explained by de Vries in 1877 and illustrated in Figure 6.20.

Another mechanism is *heat setting*, as used, for instance, in the textile industry, where it is known as the *false-twist technique* [556, 882]. In this process, an initially



Figure 6.18 Example of a telephone cord perversion.

Figure 6.19 Tendril perversion illustrated by Linnaeus in “*Philosophia Botanica*” [791].



straight filament is heated and shaped as a ring, or helix, and cooled down. This method is used to roughen yarns and is based on the creation of inversion along the fibers. Due to the thermoplasticity of many materials, the material conserves its new shape at lower temperatures. Finally, in a common experiment happening daily in hair salons, chemical unbonding and rebonding is performed on hair to artificially create curls. This process is based on the destruction of certain chemical bonds while setting the filament in the desired shape where the bonds are then recreated by both chemical and heat setting.

Another striking occurrence of perversion can be found in the structure of human umbilical cords. As seen in Figure 6.21, umbilical cords are generally made out of two

Figure 6.20 Transverse section through a tendril from “*Physiological Plant Anatomy*”, Haberlandt, 1884 and based on de Vries studies (1877). The ventral side is on top and the dorsal side at the bottom.

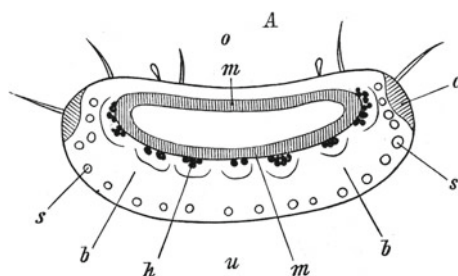




Figure 6.21 The umbilical cord of Zéphyr, the author's third son. An umbilical cord is composed of two arteries and a vein winding to form a left-handed triple helical structure.

arteries and one vein embedded in a compact gel-like structure known as *Wharton's jelly* [823]. The arteries are longer than the vein, which is itself longer than the jelly, and therefore the cord forms a triple helix. The handedness of this helix was already described in 1521 by Berengarius [322], fascinating medical doctors and scientists ever since [186].

The umbilical cord is, on average, 50–60 cm long with up to 40 helical turns, and helicity can be observed as early as 42 days' gestation [334]. Umbilical cords can be either left-handed, right-handed, straight or with mixed helicity. Strangely enough, the ratio of left-handed to right-handed cords is about 7 to 1, the usually accepted ratio of right-handed to left-handed adults. However, there is no statistical correlation between cord handedness and hand preference [747]. According to different statistical studies, inversion from left-handed to right-handed structures in umbilical cords, as shown in Figure 6.22, varies from 2% to 26% of all cases [186, 461, 1120]. This discrepancy comes from the fact that most studies have not focused on perverted umbilical cords and have classified some of them as predominantly right- or left-handed. To date, there is no model for the growth of umbilical cords that would explain the difference of handedness, its inversion or even the occurrence of helicity.

Both genetic and mechanical factors seem important as indicated by the correlation between umbilical cord helicity in monozygotic twins [322] and experiments on the effect of tension on fetal activity in laboratory rats [61, 894]. In light of the generic development of perversions in growing helical filaments, it is reasonable to assume

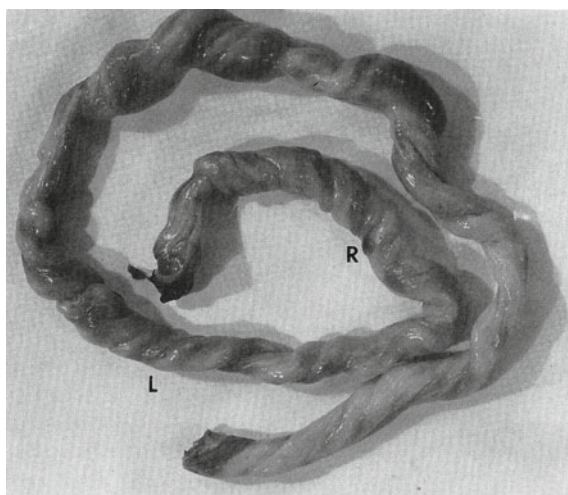


Figure 6.22 Example of umbilical perversion [85].

that the onset of umbilical perversion is the result of biased differential growth of the cord with external constraints, such as tension and the blockage of twist.

Inversion of helicity also appears in the microscopic world. For instance, cotton [1300] and cellulose fibrils [163] exhibit perversions, as seen in Figure 6.23. The flagella of some bacteria, such as *Salmonella* or *Escherichia coli*, have helical shapes [622, 679]. These flagella, which are about $4\ \mu\text{m}$ long, are composed of a few protofilaments made out of a single protein. Depending on the respective positions of the different protofilaments, the flagella can be, in their unstressed configuration, either right-handed or left-handed [174, 177, 817, 1348]. Flagella are attached to the cell body through a molecular rotary motor [88] and are observed to flip from a left- to a right-handed helix when the running motion is interrupted by a tumble motion where the flagella bundle disassembles [680, 1260]. This inversion of helicity plays a crucial role in the ability of the bacterium to change its direction of motion and it is performed by propagating a right-handed helix onto a left-handed helix, henceforth creating a perversion [452].

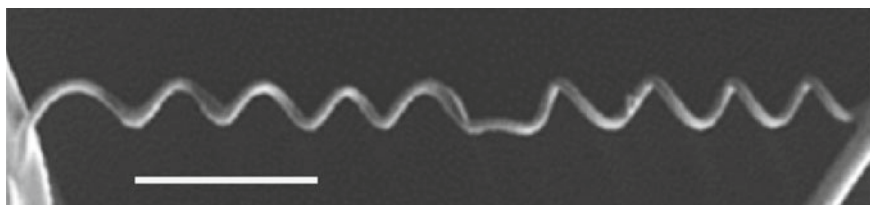


Figure 6.23 Example of cellulose perversions obtained by electrospinning from liquid crystalline solution [163] (Bar $100\ \mu\text{m}$).

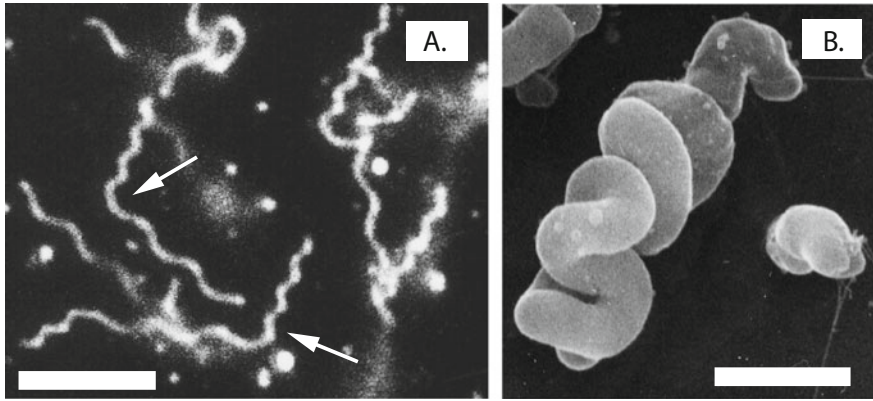


Figure 6.24 Perversion in bacteria. A. Flagella of *Salmonella*, with coexisting left- and right-handed helices (arrows) (picture courtesy of H. Hotani). B. Solenoidal form of *Bacillus subtilis* fiber, with coexisting helices (picture courtesy of M. Tilby). Scale bars: 5 and 2 μm , respectively.

Perversion can also be observed in a variety of other microscopic biological systems as shown in Figure 6.24: It is found in the shape of certain bacteria such as spirochetes [454], in some mutant forms of *Bacillus subtilis* [1232], in *Salmonella* flagella, and in the shape of miniature (1 to 2 mm long) seashells [1278]. Another example, orders of magnitude smaller, involves two distinct conformations of DNA. Experiments indicate stretches of left-handed Z-DNA spontaneously forming from right-handed B-DNA due to the stresses generated by twisting during the process of transcription [570].

6.7.1.2 The Model

The creation of these helical structures from a straight filament is the result of differential growth that, in the first instance, can be understood within our framework in terms of parameter variation. The tendril is modeled as an initially straight filament under tension. Due to faster growth on the dorsal side of the tendril, intrinsic curvature increases slowly so that the filament is in static equilibrium at all times. The problem reduces to exploring the possibility of a bifurcation from a straight solution to a solution asymptotically connecting two helical structures of opposite handedness.

We assume that the tendril is an inextensible, unshearable homogeneous rod with circular cross section and intrinsic curvature $\hat{\kappa}$, with no body load. Assuming that only static solutions are relevant for our problem, (5.79–5.80) read

$$\mathbf{n}' = \mathbf{0}, \quad (6.100)$$

$$\mathbf{m}' + \mathbf{r}' \times \mathbf{n} = \mathbf{0}, \quad (6.101)$$

with

$$\mathbf{m} = (u_1 - \hat{\kappa})\mathbf{d}_1 + u_2\mathbf{d}_2 + \Gamma u_3\mathbf{d}_3, \quad (6.102)$$

where we have rescaled the equations according to the scaling given in Section 5.4 and $\Gamma = K_3/K_1$, as given by (5.57).

This system of equations can be written as a six-dimensional autonomous dynamical system for the variable $\mathbf{X} = (\mathbf{n}_1, \mathbf{n}_2, \mathbf{n}_3, u_1, u_2, u_3)$ where

$$\mathbf{X}' = \mathbf{F}(\mathbf{X}; \hat{\kappa}). \quad (6.103)$$

The boundary conditions are given by a wrench, a pair of couple and force, (M, N) applied at both ends.

6.7.1.3 Analysis

The question of finding a perversion solution can now be cast into three parts. First, we identify possible asymptotic helical states with different handedness. Second, we find the critical bifurcation value for the parameter $\hat{\kappa}$ at which the straight filament becomes unstable. Third, we build a solution connecting the two asymptotic regimes after the bifurcation.

Following Section 5.7.2, the helical solutions of interest are twistless and have the form

$$\mathbf{u} = (0, \kappa, \tau), \quad (6.104)$$

where κ and τ are constant. This restriction leaves, as possible asymptotic states, a two-parameter family of solutions given by curvature and torsion. If we further restrict these solutions to those with no total twist, the set of possible asymptotic helices is given by (5.106) with $\hat{\tau} = 0$; that is,

$$\left(\kappa - \frac{\hat{\kappa}}{2}\right)^2 + \Gamma\tau^2 = \frac{\hat{\kappa}^2}{4}. \quad (6.105)$$

In the curvature–torsion plane, this set is an ellipse, as shown in Figure 6.25. For the dynamical system (6.103), a perversion is a *heteroclinic orbit*, an orbit asymptotically connecting two fixed points. The fixed points are all located on this ellipse and an inversion of handedness is obtained when a heteroclinic orbit connects fixed points with opposite torsion. We first consider an infinitely long filament maintained by a force $N = \mathbf{n} \cdot \mathbf{e}_3 > 0$ applied in opposite directions at $s = \pm\infty$ for which we have

$$N = \gamma\tau\delta, \quad (6.106)$$

where

$$\gamma = \left(\frac{\hat{\kappa}}{\kappa} - 1 + \Gamma\right), \quad \delta = \sqrt{\kappa^2 + \tau^2}. \quad (6.107)$$

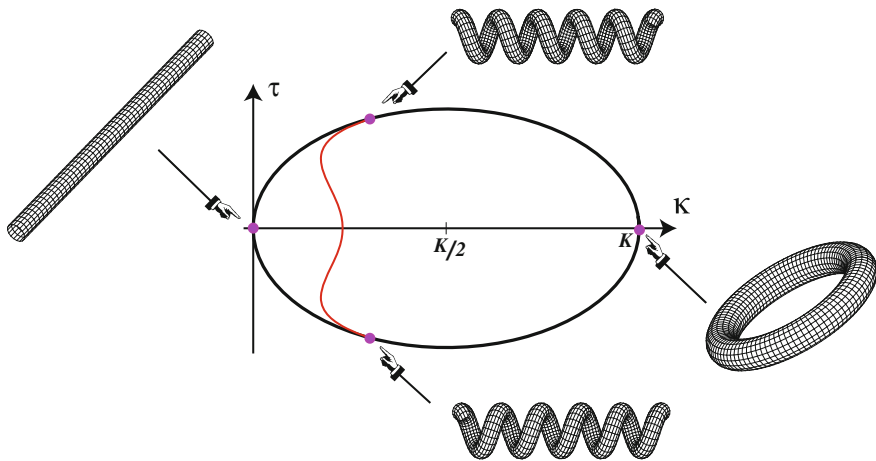


Figure 6.25 Each point in the curvature–torsion plane represents a helix. The set of helices that can connect asymptotically to another helix with opposite torsion forms an ellipse in the curvature–torsion plane.

For a given N , there is a single pair of asymptotic curvature and torsion $(\kappa, \pm\tau)$. Therefore, the moment and force at infinity are given by

$$\mathbf{m} = (\kappa - \hat{\kappa})\mathbf{d}_2 \pm \Gamma\tau\mathbf{d}_3, \quad (6.108)$$

$$\mathbf{n} = \gamma\tau\mathbf{u}. \quad (6.109)$$

Physically, when a rod is held straight and the tension is slowly released, a moment must be applied at the ends in order to keep them from rotating. The condition for a perversion solution is that the total twist is zero, which is equivalent to the condition that the ends do not rotate as the tension is released.

These infinite heteroclinic orbits are not physical solutions, as there is no infinite filament. However, the heteroclinic solution approaches the asymptotic helices exponentially fast (in arc length) so that a finite piece of a heteroclinic orbit symmetric with respect to torsion, is close to the limiting helical solutions such that the boundary conditions would be close to those of a finite rod. The normal form analysis performed in [853] confirms the existence of a family of periodic orbits with arbitrary period converging to the heteroclinic orbit. These solutions can be matched to specific symmetric boundary conditions for finite length perversion solutions.

The study of finite length solutions also reveals more complicated behavior with the possibility of multiple inversions on a finite domain [291] and a complex dynamics creating them past the bifurcation point [794].

Third, the linearized system for Equation (6.103) around the fixed point $\mathbf{X}^* = (0, 0, N, 0, 0, 0)$ representing a straight, untwisted rod under end force N , has linear eigenvalues

$$0, \pm\sqrt{N}, \text{ and } \pm\sqrt{N - \frac{\hat{\kappa}^2}{\Gamma}}. \quad (6.110)$$

At the critical tension, $N_c = \hat{\kappa}^2 / \Gamma$, two eigenvalues coalesce. This coalescence is known in dynamical systems as a Hamiltonian pitchfork bifurcation [828]. For $0 < N < N_c$, a perversion solution exists. A dynamical analysis of the Kirchhoff equations (5.79–5.80) was performed in [477], where it was revealed that for $N < N_c$, the straight filament with intrinsic curvature is unstable. We can therefore study the phenomenon of perversion near this critical value of the tension as a bifurcation problem. This is done by combining center manifold reduction with normal form expansion to obtain a reduced system that is valid close to the bifurcation point. This system can be solved explicitly and solutions to the asymptotic problem can be obtained as shown in [853]. These solutions together with numerical solutions obtained by direct simulation of the full system are shown in Figure 6.26.

6.7.1.4 A Twistless Spring

A tendril perversion is made out of two helices with opposite handedness connected by a small inversion. This structure has interesting properties compared to a regular spring. In tension, the total twist remains zero. Following [853], we call such a structure a *twistless spring*, i.e., a spring with zero total twist. To understand the properties of such a spring, we compare it to a *helical spring* and an *ideal spring*.

The ideal spring is characterized by a Hookean law $N = k z$, where N is the axial force, z is the displacement along the axis of the spring from its rest length, and k is its Hooke's constant.

The helical spring is made out of an inextensible helical rod with circular cross sections. The rod is subjected to a wrench as described in Section 5.7.2, consisting of an axial force N and axial moment M needed to prevent rotation of the ends. The response of a helical rod away from its intrinsic curvature vector $\hat{\mathbf{u}} = \hat{\kappa} \mathbf{d}_1 + \hat{\tau} \mathbf{d}_3$ is fully specified by the spring formula (5.102–5.103). As tension is applied, the helix deforms to a new helix with curvature κ and torsion τ .

Preventing the ends from rotating imposes the constraint that the total twist remains constant:

$$Tw = \int \mathbf{u}_3 ds = \int \hat{\tau} ds = \int \tau ds. \quad (6.111)$$

This condition constrains the torsion τ to remain constant; that is, $\tau = \hat{\tau}$. We calculate the length the spring is stretched by a tension T along the axis of the asymptotic helices. Consider two points on successive rings $\mathbf{P}_1$ and $\mathbf{P}_2$ as shown in Figure 6.27. When tension is applied the points separate. The twistless condition imposes a moment at the end and we can use the helix spring formulas (5.102–5.103) to compute the resultant force

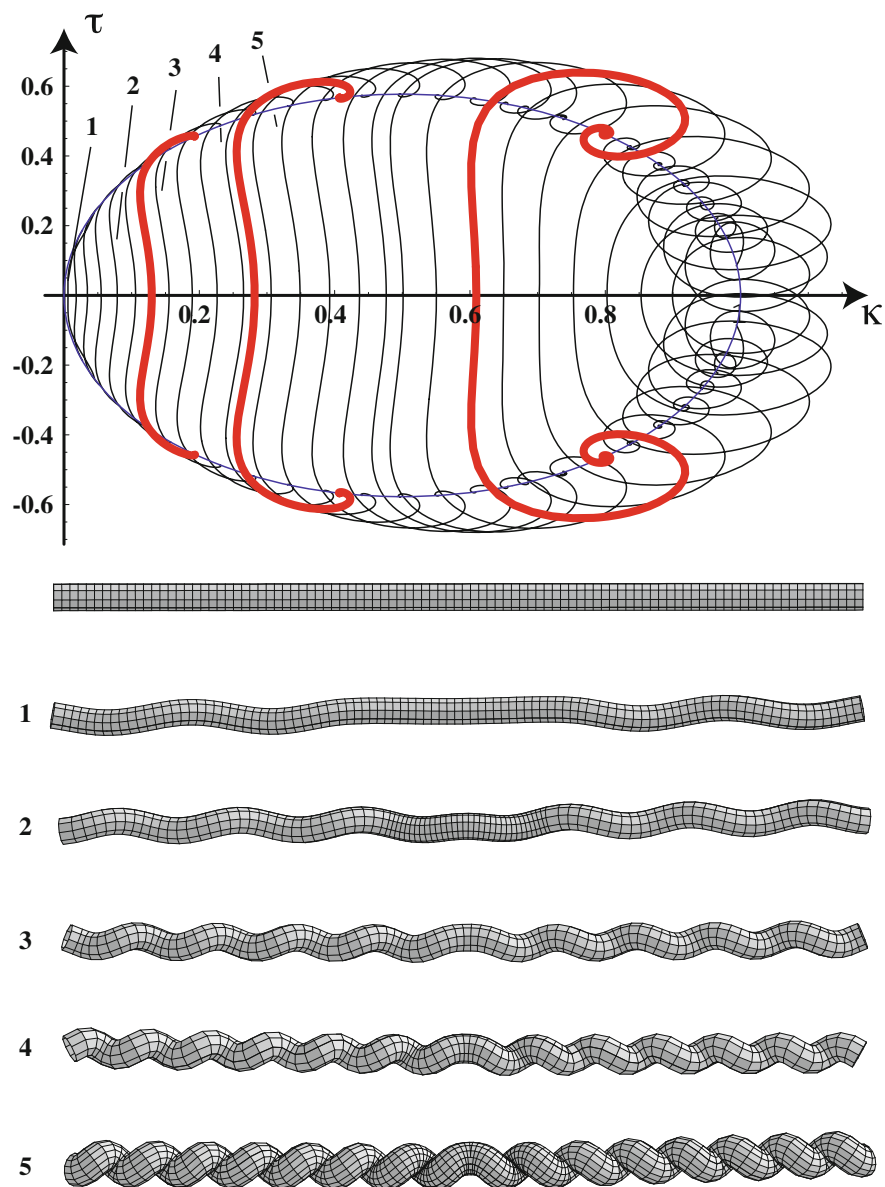
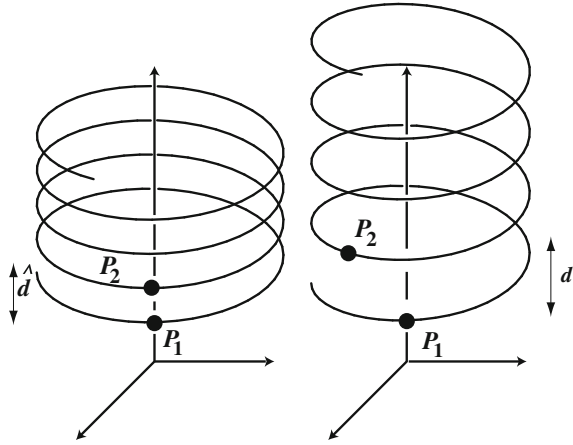


Figure 6.26 Family of heteroclinic orbits in the curvature–torsion plane together with the corresponding filament shapes ($\hat{\kappa} = 1$, $\Gamma = 3/4$) (reproduced from [853]).

Figure 6.27 Axial separation of two consecutive points on a helix provides a simple comparison with an ideal spring.



$$T = K_1 \left(\frac{\hat{\kappa} \tau}{\sqrt{1-d^2}} - \frac{\tau^2}{d} \right). \quad (6.112)$$

We define the distance d between the z -coordinates of $\mathbf{P}_1$ and $\mathbf{P}_2$. In the unstressed state, this distance is $d = \hat{d} = \hat{\tau}/\hat{\delta}$. We see that, as d varies from $\hat{d}$ to 1, the force N varies from 0 to ∞ . Writing $d = \hat{d} + z$, we have

$$T = kz + \mathcal{O}(z^2), \quad k = E I_1 4 \pi^2 \left(1 + 4 \pi^2 \frac{\hat{\tau}^2}{\hat{\kappa}^2} \right). \quad (6.113)$$

Next, we compute the response of a twistless spring made of two connected helices of opposite torsion in which the ends are held so that they do not rotate as the axial force is changed. As tension is applied the helix deforms to a new helix with curvature κ and torsion τ constrained to lie on the ellipse (6.105). The distance d is now $d = 2\pi\tau/\delta\hat{\kappa}$ and the axial force is

$$T = k \frac{d}{(1 - d^2(1 - \Gamma))^2}, \quad (6.114)$$

where $k = 4\pi^2\Gamma EI_1$. To third order in z , (6.114) reads

$$T = h z + 2 h z^3 (1 - \Gamma) + \mathcal{O}(z^5). \quad (6.115)$$

Since $0 \leq (1 - \Gamma) \leq 1/3$ and $0 \leq z \leq 1$, the deviation of this relation from Hooke's law is small for small z . However, as the rod is stretched to its full length, $d \rightarrow 1$, the cubic term dominates. The tension T varies from 0 to h/Γ^2 as d varies from 0 to 1, in contrast to the ideal spring in which the tension varies from 0 to h . Note that as $\Gamma \rightarrow 1$, the elastic properties of a perversion spring approach those of an ideal spring.

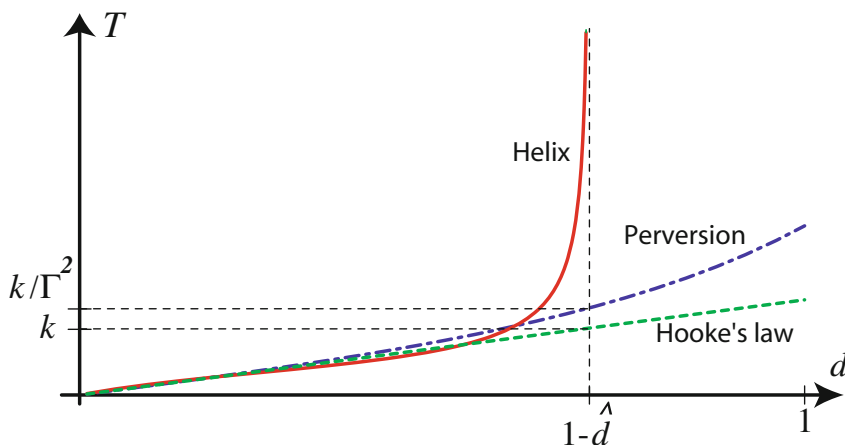


Figure 6.28 Comparison of different springs made of perversions and helices. The dash-dot curve is the plot of the tension T versus the distance d for a perversion. The solid curve is the plot for a helical spring. The dashed curve is the plot of the tension versus the displacement for an ideal spring given by Hooke's law.

In Figure 6.28, we compare the responses of the three springs. We see that the twistless spring is much closer to an ideal spring. Physically, as tension is applied to the ends of the twistless spring, it unwinds, relieving some of the torsional energy. Another advantage of the twistless spring is that it does not apply moments at the ends since moments are balanced in the middle of the spring.

Finally, we note another peculiar behavior of the twistless spring. We saw in Section 5.7.3 that springs under pure axial force tend to overwind first then unwind. Since a perversion is essentially made out of two helical springs under pure axial force, we expect, when pulling on such a structure, to see the inversion connecting the two asymptotic helices to first turn one way before changing its rotation. This behavior is readily observed by manipulating vine tendrils.

6.7.2 Twining Vines

6.7.2.1 Background

Next, we turn our attention to another class of climbing plants, the *twiners* as shown in Figure 6.29A. Twiners, such as garden peas, climbing jasmines, and morning glories, are perhaps the most studied of all vines [1049]. The growing tip waves around in a circular motion known as circumnutation until it finds an appropriate upright support. It then starts wrapping around it to extend itself upwards as seen in Figure 6.29B. The tip of the vine keeps nutating and the vine continues to climb by forming a spiral around the support.

Can a given twining plant climb around supports of different sizes? This question was first raised by Charles Darwin in his book “The Movements and Habits of

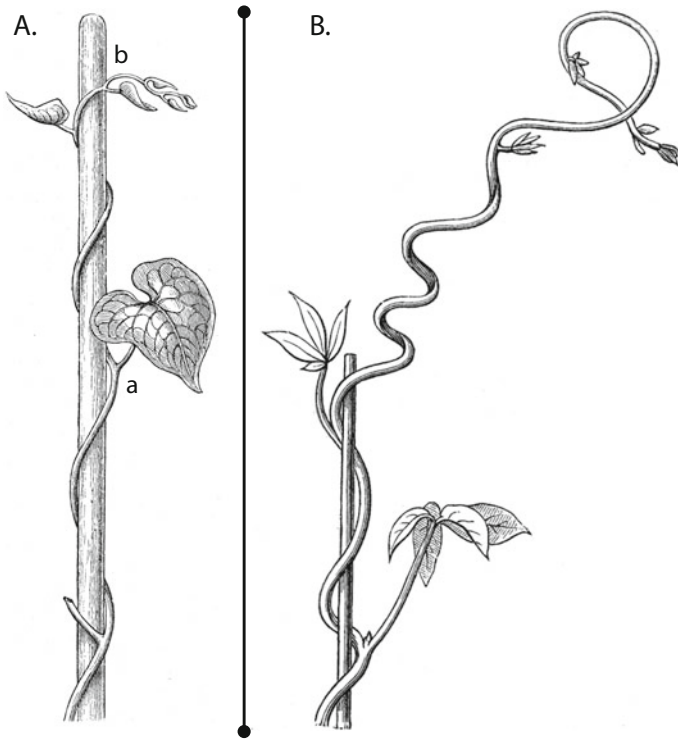


Figure 6.29 A. Purple morning glory (*Ipomoea purpurea*). B. Chocolate vine (*Akebia quinata*) (adapted from [1107]).

Climbing Plants” [261]. He comments: “Most twining plants are adapted to ascend supports of moderate though of different thicknesses. Our English twiners, as far as I have seen, never twine round trees... By what means certain twining plants are adapted to ascend only thin stems, whilst others can twine round thicker ones, I do not know.”

As an example, Darwin noted that *Solanum dulcamara* can twine around supports of 3 mm but not on supports of 5 or 6 mm (see many other examples in [1103]). The natural question is to determine the critical cylinder radius above which a plant is no longer able to twine.

In the process of establishing themselves on a pole, twining plants rely on friction [1049, 1160]. As noted by Julius von Sachs [1107], the vine may slide off “...if the surface of their vertical support is too smooth to furnish a strong mutual friction.” What is the effect of friction in the vine’s ability to grasp the pole? Similarly, what is the pressure generated by a plant on the pole? How does it change with its intrinsic properties and shape?

The stems of most plants, such as trees or flowers, are in compression. However, a peculiar feature of twining plants is that their stem is in tension [1162]. How is this tension generated? There is no applied load pulling the tip of the growing plant, gravity only increases compression and although the stem can build compressive

and tensile domains through differential growth, the net effect, once averaged over the cross section, vanishes. Therefore, a vine in continuous contact with a pole cannot generate tension. As we will see, tension is actually produced when the plant establishes discrete points of contact, known as *anchorage points* (see [470] for details).

Before lignification, the vine is a long, thin, flexible filament subject to twisting and bending. Due to the small lineal density of the vine and the large stresses developed through self-contact, the gravitational load on the vine has been experimentally found to be negligible by comparison to other forces involved in the problem. For instance the linear weight in *Pharbitis nil* (ivy morning glory) is about 0.4 mN cm^{-1} , but it can exert a contact force of 300 mN cm^{-1} [1162]. Therefore, the gravitational load will be omitted in the analysis of the grasping problem.

During circumnutation, the vine at the apex develops intrinsic curvature and torsion. We assume that these curvatures are constant and uniform. This assumption is also consistent with the vertical and lateral oscillations of the vine tip observed during growth. In Figure 6.29A, the shoot apex, the growing flexible part of the vine, spans from a to b . Below the point a , the vine is set and woody by lignification.

6.7.2.2 A Model

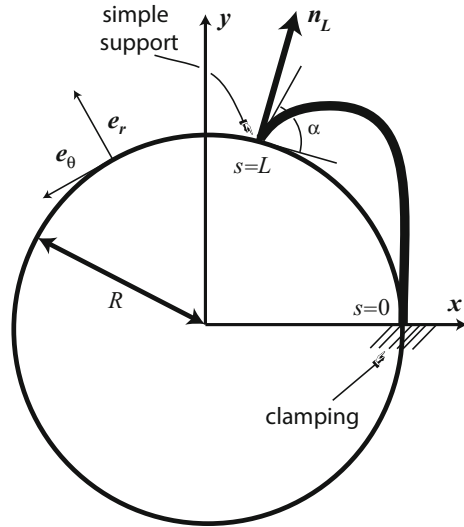
Viewed as a growth problem, we can study the possible equilibria of a rod with intrinsic curvature, torsion and increasing length, in contact with a cylinder. Therefore, the problem reduces to finding suitable solutions with the increasing length taken as our control parameter.

We model the growing vine as an inextensible, unshearable elastic Kirchhoff rod with intrinsic curvature and torsion. A further simplification of the problem is obtained by assuming that the rod is confined to the plane. In this case, the support is a rigid disk of radius R and the problem is to find equilibrium configurations of an elastic rod with intrinsic curvature $1/R_c$ in contact with the disk as illustrated in Figure 6.30. The filament is assumed to be strongly anchored at its base while its tip, located at $s = L$, is simply supported. These conditions imply that at the origin, we have $\mathbf{r}(0) = (R, 0)$, $\mathbf{r}'(0) = (0, 1)$ whereas at $s = L$, the rod lies on the disk and its curvature is equal to the intrinsic curvature; that is, $\kappa = 1/R_c$.

The Kirchhoff equations, together with the boundary conditions, completely specify the problem for any given values of L , R , R_c , and numerical continuation of equilibrium solutions of this boundary-value problem can be performed. In order to gain insight into the possible solutions, two series of equilibrium configurations for filaments with different intrinsic curvatures are shown in Figure 6.31. In both cases, the disc radius is kept constant while the length is increased. For the first series, presented in Figure 6.31A, a stable configuration develops and a continuous contact with the support is established.

Conversely, in the second series, shown in Figure 6.31B, no continuous contact configurations exist. Instead, past a certain length, the filament starts to wind outside the disc. Therefore, the limiting ratio R/R_c between climbing and non-climbing

Figure 6.30 A rod with intrinsic curvature is clamped on one end of a rigid disk and simply supported at the other end.



states is found to be in the interval $3 < R/R_c < 3.5$, as illustrated in Figure 6.32. A detailed bifurcation analysis [470] reveals that the critical ratio is $R/R_c \approx 3.31$.

The analysis so far has been restricted to the frictionless case. However, it has been emphasized by different authors [1049, 1160] that friction plays an important role in the ability of a climbing plant to support its weight. Here, friction is modeled by a tangential component of the disk reaction force on the tip of the anchor. To understand its effect, we first consider an equilibrium configuration obtained in the absence of friction. We then change the length of the filament without moving the tip. This is made possible by introducing a tangential component in the reaction force along e_θ at $s = L$ due to friction. As L increases, the tangential force component reaches a critical value equal to μp where $\mu < 0$ is the friction coefficient and p is the normal force exerted on the disk. Similarly, if L decreases, the tangential forces reach μp with $\mu < 0$. Past this value, the tip slips incrementally on the disk to find a new nearby equilibrium configuration where the tangential component equals the critical tangential value. Therefore, to identify the equilibrium configurations with friction, we increase the length and find configurations where the tangential force equals μp . For each friction coefficient μ we compute, as detailed above, the critical value $R_c = R_c(\mu)$ defining the bifurcation between filaments that can grow around the disk and filaments that leave the disk. The results in Figure 6.33 show that friction can have a crucial effect on the ability of a plant to remain on a large disk. Note that in the case of a twining plant, once the tip is in contact with the pole, friction prevents the plant from sliding back, therefore corresponding to positive values of μ .

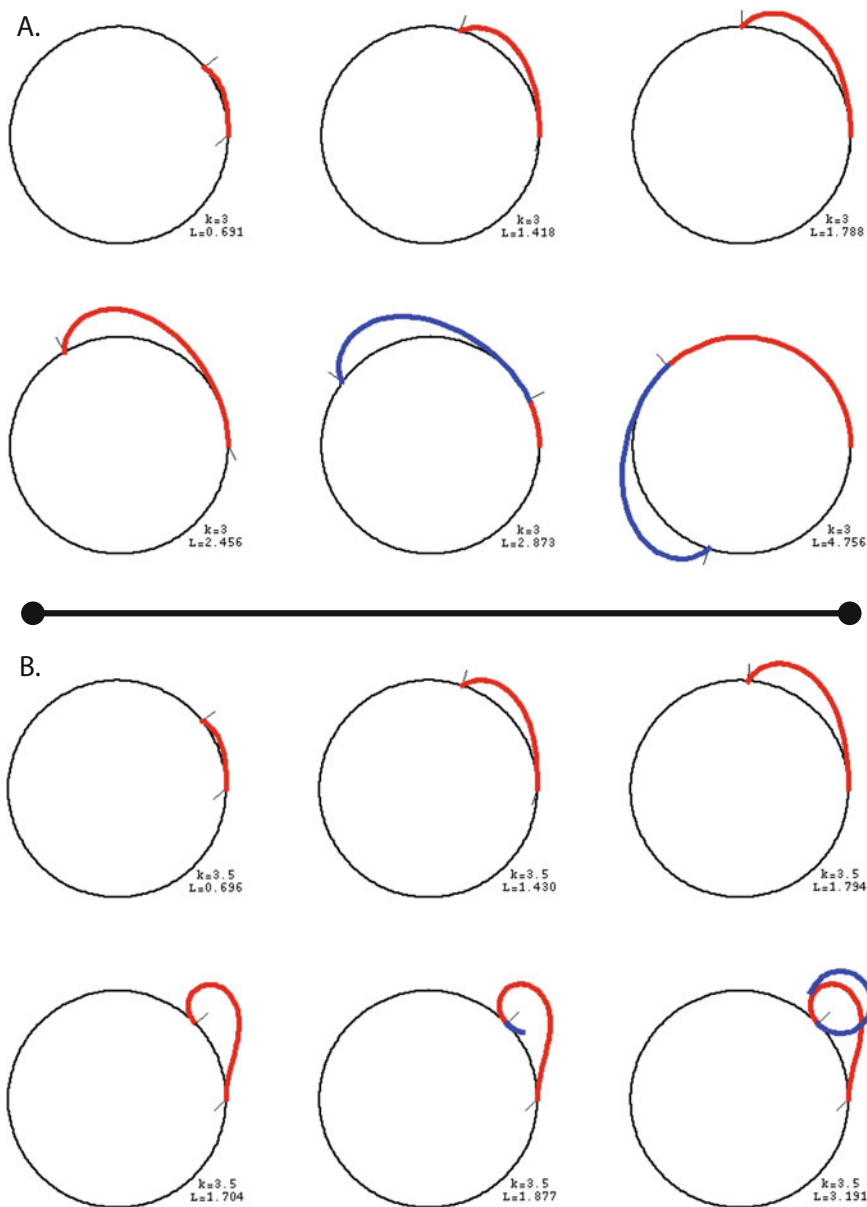


Figure 6.31 Equilibrium configurations for a naturally curved filament around a disk with A. $R/R_c = 3$ and B. $R/R_c = 3.5$. A. Configurations with continuous contact eventually develop. The vine is successfully attached to the pole. B. No configuration with continuous contact exists. The vine fails to grasp the pole. (Figure courtesy of Sébastien Neukirch).

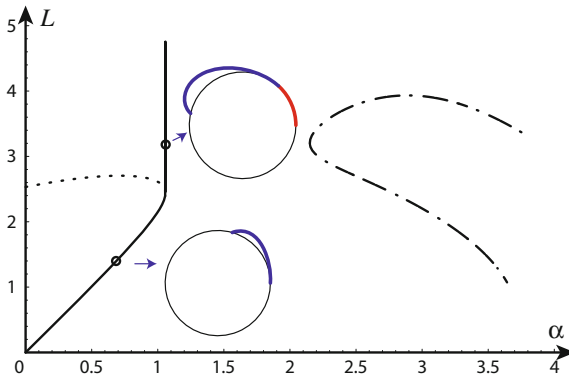


Figure 6.32 Bifurcation diagram corresponding to the equilibrium configurations of Figure 6.31B.

Intuitively, one can understand Darwin's problem as follows: For thin supports, the vine tip and the tangent of the support are almost parallel and the vine follows the support without curling back on itself. For thicker supports, in order to maintain its grip, the tip needs to touch the support surface at a larger angle α . If the support becomes too large, so too will the angle α , and the vine will curl back on itself. For increasing friction the contact angle needed for this to happen will be higher and, consequently, the plant can wind on thicker supports.

We now turn our attention to the three-dimensional case. The main properties found in the two-dimensional problem still hold; namely, discrete points of contact exist between the plant and support, tension is generated by these contact points, and attachment is possible only by the difference between intrinsic curvature and

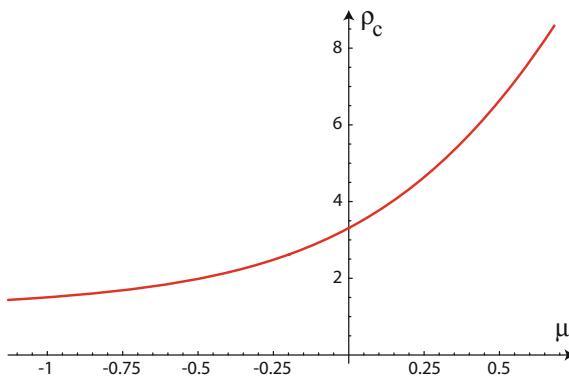


Figure 6.33 Change of critical radii ratio $\rho_c = R/R_c$ as a function of friction. Positive friction coefficients act when the tangential force prevents the filament from sliding back whereas negative friction coefficients correspond to situations where friction prevents the tip from slipping forward. Range of μ values are consistent with experimental data [1160]. The prediction of an upper bound of ρ_c around 8 is consistent with the observation of Bell [75] (reproduced from [470]).

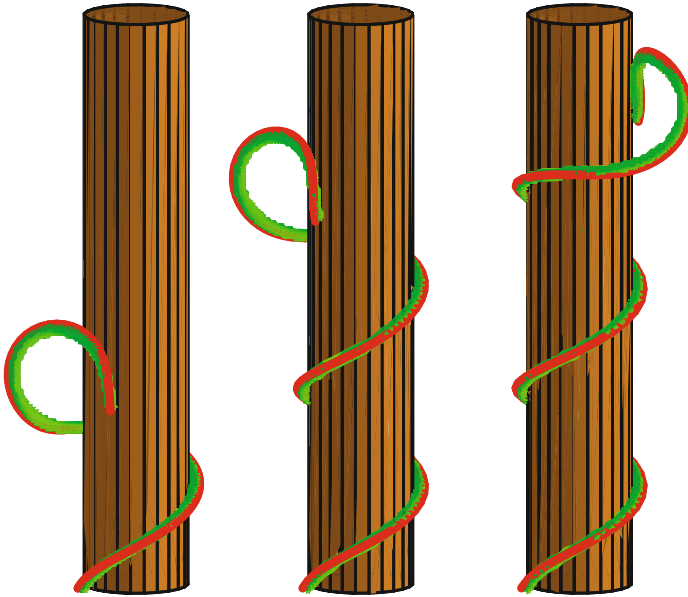


Figure 6.34 A sequence of three-dimensional solutions to the attachment problem. Note the continuous, almost helical, solution, followed by the anchor that provides tension in the filament (reproduced from [470]).

geometry of the support. An example of such solutions is given in Figure 6.34. Numerical studies suggest that the value of R_c obtained in the planar case provides an upper bound for the three-dimensional case.

The analysis of the growing vine shows that a model for a growing elastic rod in contact with a pole can provide a simple explanation for the limitation of twining plants to wind around thick supports, and for the role of friction to boost the plant's ability to achieve vertical growth. The model also explains how tension is generated and shows that both continuous and discrete contact points between stem and pole exist, a prediction consistent with experiments [655].

6.7.3 Application: The Growth of *Bacillus subtilis*

As an example of the effects of a local growth law, we consider the evolution of length and twist in a model for growing *Bacillus subtilis*.

6.7.3.1 Background

The individual cells of the bacterial strain *Bacillus subtilis* are rod-shaped and typically of length $3\text{--}4\ \mu\text{m}$ and diameter $0.8\ \mu\text{m}$. Under certain circumstances, they are found to grow into filaments consisting of the cells linked in tandem due to the failure of daughter cells, produced by growth and division, to separate. As they elongate, these filaments, which are immersed in a liquid environment whose temperature and viscosity can be controlled, are observed to twist at a uniform rate. The degree of twist and handedness can be controlled experimentally and a wide range of states, from left-handed to right-handed forms, can be produced. The actual twist state of the cells seems to be related to properties of the polymers which are inserted into the cell wall during growth.

Eventually, the filaments are observed to writhe and deform into double-helical structures. These structures continue to grow and periodic repetition of this process results in macroscopic fibers termed *macrofibers*, with a specific twist state and handedness as shown in Figure 6.35. Two different schematic looping mechanisms of *Bacillus subtilis* are given in Figure 6.36.

A striking feature of this iterated process is that at every stage of the self-assembly, the handedness of the new helical structures that are created is the *same*, e.g., a right-handed double helix gives rise to a right-handed four-strand helix and so on. The nature of the environment does, however, influence certain aspects of the self-assembly. In a viscous environment, the basic writhing instability leads to an instability at the middle of the filament with the formation of a tight central loop; this is followed by a helical windup which starts at the base of this loop (Figure 6.36B).

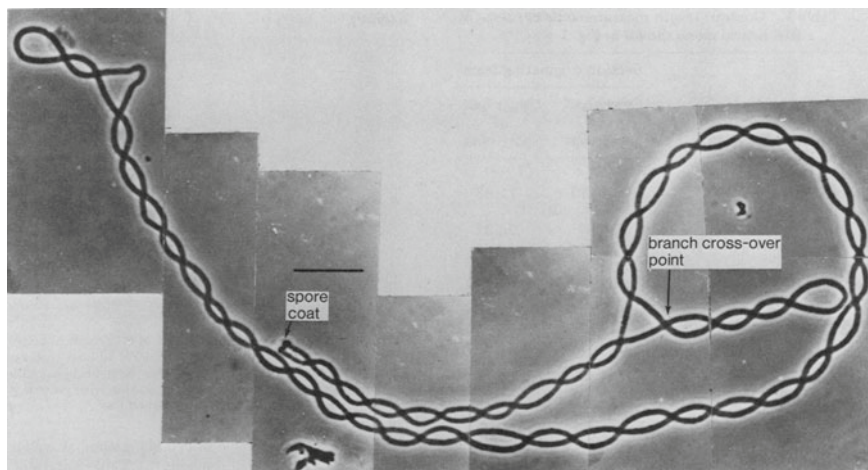


Figure 6.35 Macrofibers of *Bacillus subtilis* (picture courtesy of Neil Mendelson).

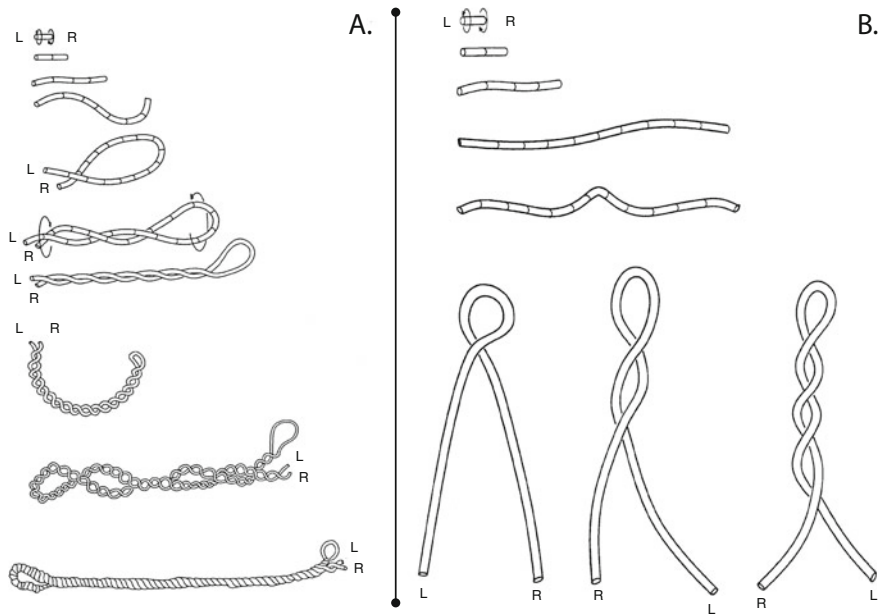


Figure 6.36 The two basic looping mechanisms of *Bacillus subtilis*. A. In nonviscous medium. B. In viscous medium (picture courtesy of Neil Mendelson).

By contrast, in a nonviscous medium, the instability causes the filament to fold over into a large loop closed by contact between the ends of the filament. This closure is then followed by a helical windup starting at the instability point (Figure 6.36A). In both cases, this self-assembly conserves handedness and usually continues over long periods until macrofibers, several millimeters long, are formed.

The dynamics of the self-assembly and the mechanical properties of the bacterial threads have been studied in great detail, by Mendelson and coworkers [866–868]. In addition to the fascinating questions of growth and form raised by this process, the macrofibers themselves offer the prospect of unusual biomaterials that can be mineralized and packed in ways that are of practical biomedical and biotechnical use.

6.7.3.2 A Model

First, we propose a simple qualitative explanation of the observation that, in *Bacillus subtilis*, the twisting and supercoiling are of the *same* handedness. The key to this transition is the buildup in time of an intrinsic twist, described in the Kirchhoff model by a nonvanishing parameter $\hat{u}_3$. We assume that in *Bacillus subtilis* each bacterial cell possesses an intrinsic twist. Reproductive growth of all the cells in the bacterial filament results in an exponential growth of its length accompanied

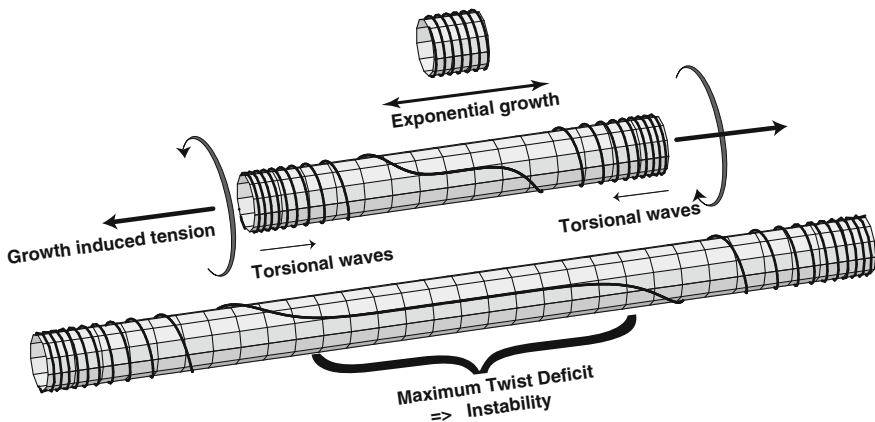


Figure 6.37 Exponential growth and linear torsional wave competition. As the filament grows exponentially, the linear twist wave propagating from the end does not reach the middle of the filament where the twist deficit is maximal.

by a reduction of twist density. Consider a file of such cells making a filament with right-handed intrinsic twist, represented by drawing marker lines with a right-handed helical pitch, as shown in Figure 6.37. One end is twisted in the opposite direction until they are approximately straight. The twist density of the filament now appears to vanish whereas its natural state is one of nonzero twist density—as indicated by the original helical marker lines. Thus we now have a twist deficit, given that $\hat{u}_3 \neq 0$. To return to its natural state, the filament must make up for this deficit by restoring twist. This can be achieved in two different ways. If one end is free, the tube winds sending a twist wave down the rod. Alternatively, if the ends are held but brought toward each other, the tube will relax by supercoiling with the *same* handedness as the intrinsic twist. This is the behavior observed in *Bacillus subtilis*.

To obtain a full picture of the dynamics of *Bacillus subtilis*, we can use the Kirchhoff equations with uniform growth and model the viscous environment as a local drag force, as done in a series of computer simulations by Isaac Klapper [700, 701, 1337]. Among other things, the model gives quantitative predictions about the self-assembly geometry, such as the way the loop size scales with environmental conditions. The computer simulation of growing rods with intrinsic twist predicts the formation of looping in filaments remarkably similar to the ones found in the experiments as seen in Figure 6.38. A great deal of experimentation has shown that the twist state and helix handedness of *Bacillus subtilis* macrofibers stem from the individual cell from which the fiber is derived. The information required to control macrofiber morphogenesis appears to reside in the growth plan of this cell and all its

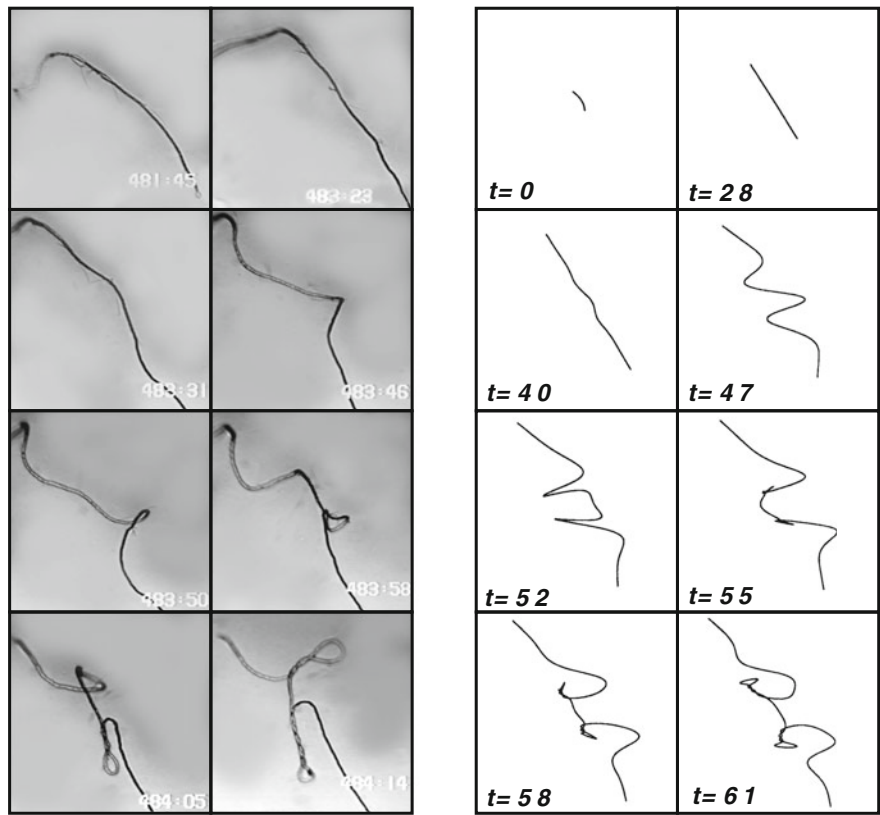


Figure 6.38 Writhing dynamics of *Bacillus subtilis*. Left: Experiments (courtesy of N. Mendelson). Right: Simulation of Kirchhoff rods with growth (courtesy of I. Klapper [700, 701]).

descendants. Intrinsic twist, a key feature of the dynamic model described here, is a logical candidate for the mechanical information in the growth plan that dictates all subsequent growth and form.

Part III

Surface Growth: A Two-Dimensional Theory

*And then the justice,
In fair round belly, with a good capon lin'd,
With eyes severe, and beard of formal cut,
Full of wise saws, and modern instances,
And so he plays his part. . .*

Chapter 7

Accretive Growth



We now consider the growth of biological structures that can be modeled as two-dimensional objects; that is, three-dimensional bodies that have a transverse length scale much smaller than the other two typical length scales. In developing useful models for the growth of surfaces, it is important to distinguish between hard and soft surfaces.

Seashells, horns, antlers, and teeth can be modeled as hard surfaces that cannot be easily deformed. In these structures, *accretive growth* takes place by adding mass locally on the boundary of the structure since there is no possibility of deforming the material in the bulk in order to add mass. From a continuum mechanics perspective, surface growth poses a particularly interesting challenge. Since new material points are continually deposited on the surface of the body, the domain on which all physical quantities are defined also evolves in time, so there is no fixed reference configuration. Therefore, incorporating accretive growth within classic continuum mechanics requires particular care [421]. There is significant interest in this topic from a fundamental mechanical standpoint as well, and several theories and continuum balance laws have been proposed to address the issue [338, 579].

Other biological structures can be modeled as two-dimensional soft surfaces, such as leaves, pollen tubes, and flowers. In these systems, there is a fair amount of elastic deformation. In contrast to the previous case, growth is typically distributed over

the entire area. The shape is the result of a competition between the local addition of mass and the bending and stretching properties of the surface. By analogy with the general three-dimensional case, we refer to this type of surface growth as *area growth*.

We start with a geometric description of accretive growth in simple hard structures for which elastic deformations are negligible. We assume that as the object grows it remains mostly two-dimensional. Historically, there have been two different approaches to the growth of hard surfaces. The first approach is to consider the problem from a mechanistic rather than a descriptive point of view. Here accretion takes place at the boundary of the surface and is characterized by a certain deposition rate in a given spatial direction that is fixed by the intrinsic geometry of the surface [914, 915, 1077, 1173]. The second approach is mostly descriptive, that is, one tries to characterize the object by a parameterized surface with a few parameters that can be obtained from direct measurements. Along these lines, the description of seashells is the most developed theory [861], and due to its historical importance and intrinsic beauty, we use seashells as a paradigm for accretive growth. We start with the mechanistic description and, later, compare this approach with the classic description of seashells by surface parameterization.

7.1 Intrinsic Accretive Growth

We adopt a local constructive view for the general problem of growth of hard bodies through surface accretion following the theory of Moulton and coworkers [914, 915]. We consider the growth of a surface starting with a generating curve. At time $t = 0$, the curve is assumed to be a twice continuously differentiable curve $\mathbf{R}(S) = \mathbf{r}(S, 0) \in \mathbb{R}^3$ defined by its arc length $S \in [0, L]$. Accretion is modeled by the evolution of this initial curve by defining at each point S on this curve a growth vector $\mathbf{q}(S, 0)$ representing the local evolution of material points during growth as illustrated in Figure 7.1. This vector field is the initial growth velocity of the material point located at S . At any time t , we specify a growth field $\mathbf{q}(S, t)$ defining the growth velocity of a material point S at time t so that the problem is to integrate this velocity field in time to obtain a curve $\mathbf{r}(S, t)$.

Since the velocity vector describes a process of accretive growth, this curve can be thought of as a *cell track*, initially at position $\mathbf{R}(S)$ on the surface $\mathbf{r}(S, t)$, i.e., the track that would be left by the cell depositing the new material over time. Since the direction and amplitude of the accretion process determined by the velocity vector is a local process, it is reasonable to assume that the velocity vector is a function of the local coordinate system, as well as any physical; chemical; or biological field, such as rate of accretion, morphogen gradient, temperature, pH, etc.

Following our discussion of curves in Chapter 6, we attach a general frame to the curve $\mathbf{r}(S, t)$:

$$\mathbf{D} = [\mathbf{d}_1 \ \mathbf{d}_2 \ \mathbf{d}_3], \quad (7.1)$$

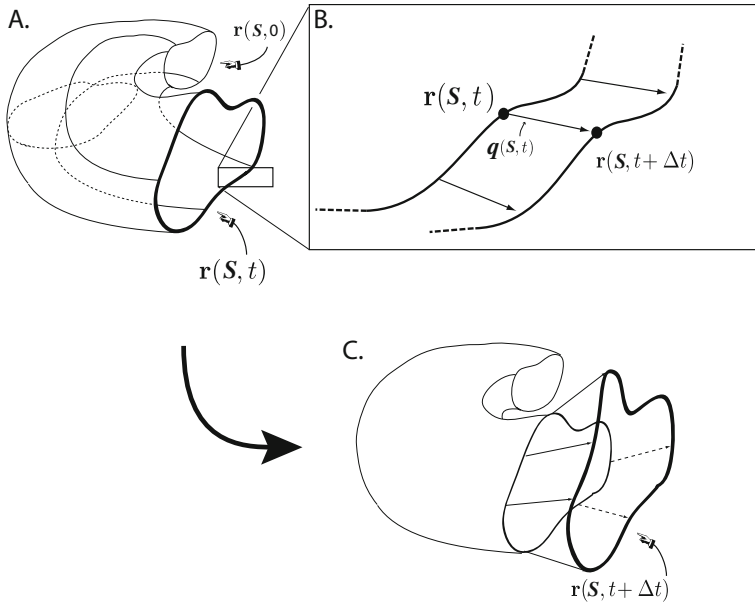


Figure 7.1 Creation of a surface from an initial generating curve. A. At time t an initial curve is given. This curve evolves in time by the specification of a local velocity field attached to the outer edge of the surface. B. In the incremental process of growth, at any time t , a curve is given together with a velocity field $\mathbf{q}$. C. The new curve at $t + \Delta t$ is obtained by moving the original curve by $\Delta t \mathbf{q}$. The curve created by the accretive process is the new generating curve for subsequent accretive processes.

where $\mathbf{d}_3$ is the unit tangent vector to $\mathbf{r}(S, t)$ and is given by

$$\mathbf{r}' = \mathbf{v} = v_3 \mathbf{d}_3 = \lambda \mathbf{d}_3, \quad (7.2)$$

where $(\cdot)' \equiv \partial_S(\cdot)$ and $\lambda = v_3$ is a coefficient that describes the stretch of the curve with respect to the initial arc length S .

The general frame $\{\mathbf{d}_1, \mathbf{d}_2, \mathbf{d}_3\}$ forms an orthonormal basis for all S and t , that is, $\mathbf{D}$ is an orthonormal matrix:

$$\mathbf{D}^T \mathbf{D} = \mathbf{D} \mathbf{D}^T = \mathbf{1}, \quad (7.3)$$

which implies

$$\mathbf{D}' \equiv \partial_S \mathbf{D} = \mathbf{D} \mathbf{U}, \quad (7.4)$$

$$\dot{\mathbf{D}} \equiv \partial_t \mathbf{D} = \mathbf{D} \mathbf{W}, \quad (7.5)$$

where $\mathbf{U}$ is the Darboux matrix, a skew-symmetric matrix describing the rotation of the local basis at a given time t along the curve and $\mathbf{W}$ is the spin matrix, a skew-symmetric matrix describing the rotation of the local basis at a point S as time

evolves. As discussed in Section 5.1.2, these matrices read

$$\mathbf{U} = \begin{bmatrix} 0 & -u_3 & u_2 \\ u_3 & 0 & -u_1 \\ -u_2 & u_1 & 0 \end{bmatrix}, \quad \mathbf{W} = \begin{bmatrix} 0 & -w_3 & w_2 \\ w_3 & 0 & -w_1 \\ -w_2 & w_1 & 0 \end{bmatrix}, \quad (7.6)$$

with the associated axial vectors $\mathbf{u} = (u_1, u_2, u_3)$, and $\mathbf{w} = (w_1, w_2, w_3)$ in the general frame. Following the convention of Chapter 5, a vector $\mathbf{a}$ in a fixed basis $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$:

$$\mathbf{a} = a_1 \mathbf{e}_1 + a_2 \mathbf{e}_2 + a_3 \mathbf{e}_3, \quad (7.7)$$

can be written in the general frame as $\mathbf{a} = \mathbf{D}\mathbf{a} = a_1 \mathbf{d}_1 + a_2 \mathbf{d}_2 + a_3 \mathbf{d}_3$. The general basis $\mathbf{D}$ of a curve of class C^3 is determined up to an arbitrary choice of angle between the vector normal to the curve and the vector $\mathbf{d}_1$ as explained in Section 5.1.3, and the elements of $\mathbf{U}$, which are related to the usual notion of curvature and torsion.

Recalling that the time t represents the evolution of growth, at any point on a curve $\mathbf{r}(S, t)$ we attach a growth velocity vector $\mathbf{q}(S, t)$ so that

$$\dot{\mathbf{r}}(S, t) = \mathbf{q}(S, t) = \mathbf{D}\mathbf{q}, \quad (7.8)$$

where $(\dot{\cdot}) \equiv \partial_t(\cdot)$. Note again that $\mathbf{q} = (q_1, q_2, q_3)$ are the components of the velocity vector $\mathbf{q}$ expressed in the local frame $\mathbf{D}$ as opposed to (q_1, q_2, q_3) , the components of the velocity vector $\mathbf{q}$ in the fixed reference frame.

We assume that growth is controlled locally, that is the information about growth is contained in the local components of the growth vector. Therefore, we restrict our attention on the vector of components $\mathbf{q}$.

Assuming that the curve $\mathbf{r}$ is at least twice differentiable in t and S , the symmetry of second derivatives provides two sets of compatibility conditions

$$\frac{\partial}{\partial S} \left(\frac{\partial}{\partial t} \mathbf{r} \right) = \frac{\partial}{\partial t} \left(\frac{\partial}{\partial S} \mathbf{r} \right), \quad (7.9)$$

$$\frac{\partial}{\partial S} \left(\frac{\partial}{\partial t} \mathbf{D} \right) = \frac{\partial}{\partial t} \left(\frac{\partial}{\partial S} \mathbf{D} \right). \quad (7.10)$$

Using again the orthonormality constraint $\mathbf{D}\mathbf{D}^T = \mathbf{1}$, we obtain, after simplification

$$\mathbf{q}' - \dot{\mathbf{v}} = \mathbf{W}\mathbf{v} - \mathbf{U}\mathbf{q}, \quad (7.11)$$

$$\mathbf{W}' - \dot{\mathbf{U}} = \mathbf{U}\mathbf{W} - \mathbf{W}\mathbf{U}, \quad (7.12)$$

where $\mathbf{v}$ is the stretch vector defined in (7.2). In components, these two equations read

$$q'_1 + u_2 q_3 - u_3 q_2 = \lambda w_2, \quad (7.13)$$

$$q'_2 + u_3 q_1 - u_1 q_3 = -\lambda w_1, \quad (7.14)$$

$$\mathbf{q}'_3 + u_1 \mathbf{q}_2 - u_2 \mathbf{q}_1 = \dot{\lambda}, \quad (7.15)$$

$$\dot{\mathbf{u}}_1 - \mathbf{w}'_1 = u_2 \mathbf{w}_3 - u_3 \mathbf{w}_2, \quad (7.16)$$

$$\dot{\mathbf{u}}_2 - \mathbf{w}'_2 = u_3 \mathbf{w}_1 - u_1 \mathbf{w}_3, \quad (7.17)$$

$$\dot{\mathbf{u}}_3 - \mathbf{w}'_3 = u_1 \mathbf{w}_2 - u_2 \mathbf{w}_1. \quad (7.18)$$

For a given growth vector $\mathbf{q}$, these equations form a set of six nonlinear first order partial differential equations for the seven dependent variables $\{\mathbf{u}, \mathbf{w}, \lambda\}$. The extra degree of freedom is given by the extra degree of freedom in the choice of the general basis. If we assume that the curve is at least three times differentiable, then we can use the Frenet frame, and $\{\mathbf{d}_1, \mathbf{d}_2, \mathbf{d}_3\} = \{\mathbf{v}, \boldsymbol{\beta}, \boldsymbol{\tau}\}$ are the normal, binormal, and tangent vectors, respectively. Then, the Darboux matrix $\mathbf{U}$ takes the simple form

$$\mathbf{U} = \lambda \begin{bmatrix} 0 & -\tau & \kappa \\ \tau & 0 & 0 \\ -\kappa & 0 & 0 \end{bmatrix}, \quad (7.19)$$

where $\kappa \geq 0$ and τ are the usual geometric curvature and torsion as given by (5.4) and (5.7). This choice implies $u_1 = 0$ thus reducing the system to a set of six equations for six unknowns which can be solved for an initial profile and growth field. Once $\mathbf{u}(S, t)$ and λ are known, the surface built through the accretive process is obtained by integrating the system of twelve nonlinear ODEs given by

$$\frac{\partial}{\partial S} \mathbf{D} = \mathbf{D} \mathbf{U}, \quad \text{and} \quad \frac{\partial}{\partial S} \mathbf{r} = \lambda \mathbf{d}_3. \quad (7.20)$$

To understand the computational steps involved in solving this system of equations, we consider a few simple solutions.

7.1.1 Simple Examples

7.1.1.1 Cylinders, Cones, and Tori

We first consider the case of a growing cylinder. We work in the Frenet frame and take the generating curve C_0 to be a circle of radius 1, $\mathbf{r}(S, 0) = (\cos(S), \sin(S), 0)$. We choose a constant growth velocity field along the binormal, that is, $\mathbf{q} = (0, 1, 0)$. In this simple case, the compatibility equations and frame evolution are trivial, and the surface is found by integrating (7.8):

$$\mathbf{r}(S, t) = \int_0^t \mathbf{q} \, dt + \mathbf{r}(S, 0) = (\cos(S), \sin(S), t), \quad (7.21)$$

producing, as shown in Figure 7.2A, a parameterization of a cylinder.

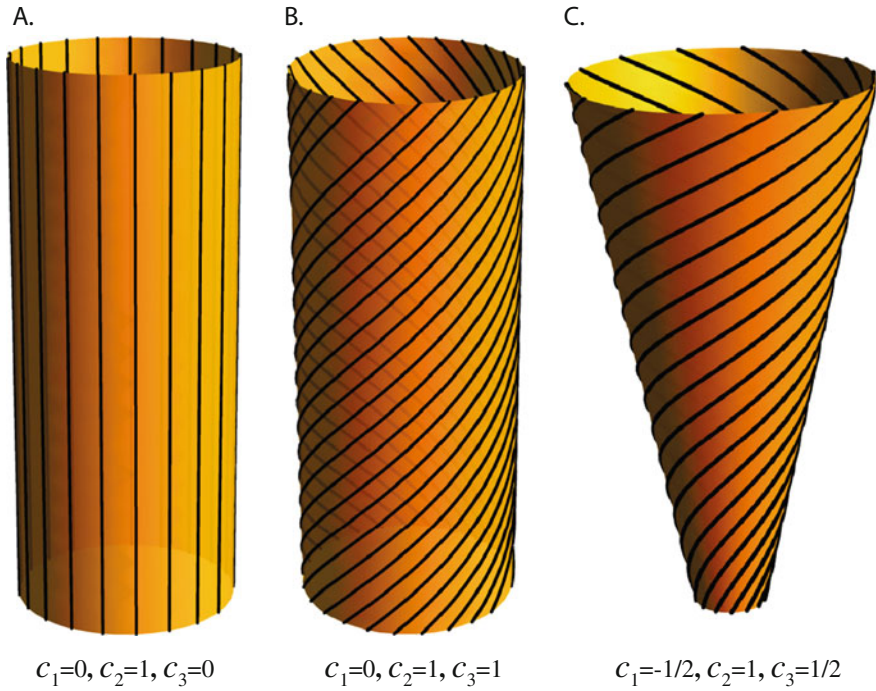


Figure 7.2 A. A straight cylinder. B. A twisted cylinder. C. A twisted cone.

If we add a constant velocity component in the tangential and normal directions to the generating curve by assuming that the growth velocity field is $\mathbf{q} = (0, c_2, c_3)$ with $c_2 c_3 \neq 0$, we obtain

$$\mathbf{r}(S, t) = (\cos(S + c_3 t), \sin(S + c_3 t), c_2 t), \quad (7.22)$$

which is a parameterization of a twisted cylinder, as shown in Figure 7.2B, and different from (7.21). The difference between the two cylinders can be understood in terms of cell track motions. In an accretive growth process, a cell in Figure 7.2A deposits new material directly in the binormal direction to the ring whereas a cell in Figure 7.2B has an additional tangential component.

Next, we add a normal velocity component, so that $\mathbf{q} = (c_1, c_2, c_3)$ with $c_1 c_2 c_3 \neq 0$. In this case, the frame evolution is the same as the twisted cylinder case, but since $\dot{\lambda} = -c_1$ from (7.15), the surface parameterization is

$$\mathbf{r}(S, t) = ((1 - c_1 t) \cos(S + c_3 t), (1 - c_1 t) \sin(S + c_3 t), c_2 t), \quad (7.23)$$

and the resulting surface is a cone with twisted cell tracks, as depicted in Figure 7.2C.

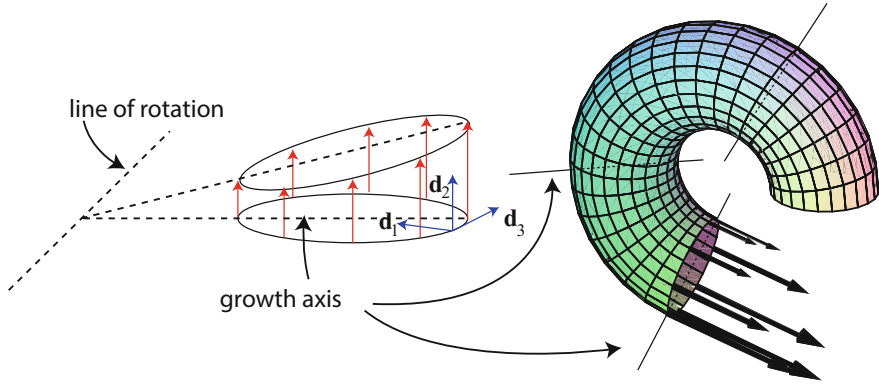


Figure 7.3 Growth of a torus. On the left is a schematic illustrating the linear growth along the growth axis. On the right is a growing torus along with growth velocity field on the generating curve ($b_1 = 2$, $b_2 = 1$).

More interesting shapes are obtained if the local growth vector is not constant. Taking again a unit circle as an initial curve, coiling is achieved by taking q_2 to be a linear function along a *growth axis* in the plane of the generating curve

$$q_2 = b_1 + b_2 \cos(S), \quad (7.24)$$

where b_1 and b_2 are constants. We show in Section 7.1.2 that the generating curve remains circular for all time. We can obtain a torus from (7.24) by choosing $q_1 = q_3 = 0$ and integrating the governing equations (7.13–7.18):

$$\mathbf{r}(S, t) = \left(\frac{1}{b_2} (\cos(b_2 t) q_2 - b_1), \sin(S), \frac{q_2}{b_2} \sin(b_2 t) \right), \quad (7.25)$$

an example of which is given in Figure 7.3.

7.1.1.2 Planar Horns and Shells

We extend this construction to generate more complex surfaces by adding a constant normal component to the growth vector defined by (7.24). There are three different velocity profiles that can produce normal growth in this context:

$$q_1 = -c, \quad q_2 = b_1 + b_2 \cos(S), \quad q_3 = 0, \quad (7.26)$$

$$q_1 = -c, \quad q_2 = \lambda(b_1 + b_2 \cos(S)), \quad q_3 = 0, \quad (7.27)$$

$$q_1 = -c, \quad q_2 = b_1 + b_2 \lambda \cos(S), \quad q_3 = 0. \quad (7.28)$$

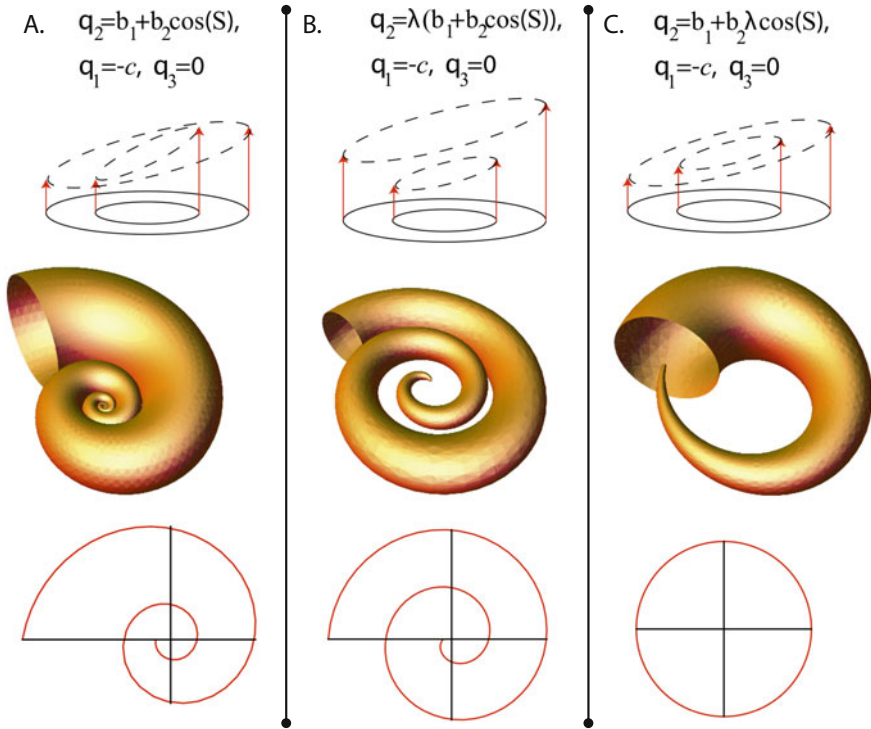


Figure 7.4 Three primary forms of growth with a linearly expanding circular generating curve. For each case, we show from top to bottom: the local velocity, a schematic illustrating the binormal growth gradient as the radius changes, a sample structure, and the curve traced by the center of the generating curve [914].

These three different choices lead to surfaces with expanding generating curves as shown in Figure 7.4.

7.1.1.3 Three-Dimensional Structures

We note that in the examples given so far, each point of the generating curve follows a path in time that is either linear or planar. For more complex structures such as seashells, we need to consider nonplanar growth. For simplicity, we keep a circular generating curve. We consider two different methods of growth that produce similar surfaces, yet have distinct and important differences from a biological viewpoint.

- **Rotating growth axis:** To create out-of-plane growth, we can rotate the growth axis in time. For the binormal velocity $q_2 = b_1 + b_2 \cos(S)$, the growth axis is always on a line contained in the x - z plane, and thus the rotation remains in this plane. If this growth axis locally rotates during the evolution, the direction

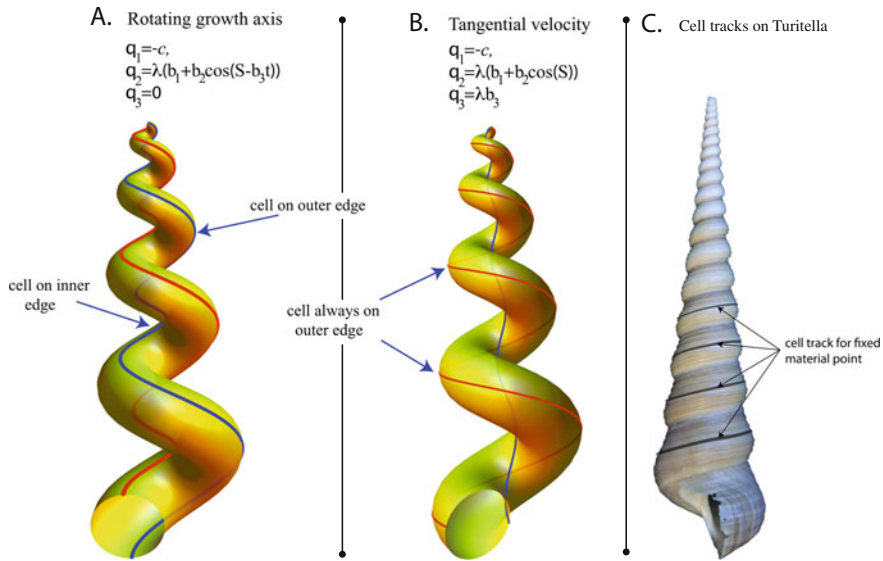


Figure 7.5 A. and B. Comparison of two primary forms of local velocity for out-of-plane growth giving rise to the same shape. The plotted surfaces are identical, but with different parameterizations, reflecting the distinct difference in cell tracks. The parameters are $c = 0.12$, $b_1 = 1.6$, $b_2 = 1$, $b_3 = 0.55$ for each surface. C. The cell tracks of a Turitella shell can be seen by tracing the small antimarginal ribs. A particular track has been highlighted. The tracks stay in the same relative position on the shell aperture during growth (reproduced from [915]).

of rotation will also vary and growth will be nonplanar. To illustrate this effect, consider the growth velocity field

$$q_1 = -c, \quad q_2 = b_1 + b_2 \cos(S - b_3 t), \quad q_3 = 0, \quad b_2 > 0. \quad (7.29)$$

Maximal growth occurs at material point $S = b_3 t$, thus the parameter b_3 dictates the rotation rate of the growth axis. An example is shown in Figure 7.5A.

- **Tangential velocity:** An alternative form to rotating the growth axis is to add a tangential velocity component, so that

$$q_1 = -c, \quad q_2 = b_1 + b_2 \cos(S), \quad q_3 = b_3, \quad b_2 > 0. \quad (7.30)$$

Maximal growth always occurs at a fixed material point, the point $S = 0$, and this point moves in the tangential direction with time, hence rotating the growth axis around the generating curve as illustrated in Figure 7.5B.

While these two forms can produce the exact same surface by using the same parameter values, there is a subtle but important biological difference between these two models. In (7.29), there is no tangential motion and the material points remain in

the same location on the generating curve, but the growth rate for any given material point on the generating curve varies with time. Hence the location where growth is maximal also varies. This idea is illustrated in Figure 7.5, in which surfaces are plotted using a rotating growth axis and a tangential velocity component. Note that the forms are slightly different from Equations (7.29) and (7.30) as the scale factor λ has been included in the velocities. Included on each surface are curves representing a cell track for the particular value $S = 0$. In the case of the rotating growth axis, shown in Figure 7.5A, the binormal velocity of the cell varies with time, and the cell track oscillates between the inner and outer edge of the global structure. By comparison in the tangential velocity case, shown in Figure 7.5B, $S = 0$ always corresponds to the point of maximal growth, and the cell track follows the outer edge of the global structure.

From a biological perspective, either form could be achieved *a priori*. They can only be differentiated by following cell tracks. For example, in Turitella shown in Figure 7.5C, one can trace the cell tracks by following the locations of the small antimarginal ribs. We observe that the cell tracks take the form of Figure 7.5B, suggesting that out-of-plane growth was produced by a growth velocity field of the form (7.30).

Next, we derive conditions that the local growth velocity fields have to satisfy to guarantee universal shape properties. In particular, we identify conditions so that the generating curve remains either planar or similar, up to a global dilation.

7.1.2 Shape Planarity

Consider an arbitrary planar curve $\mathbf{r}(S, t)$. Suppose, without loss of generality, that the curve is initially parameterized by its arc length, so that $|\mathbf{r}'(S, 0)| = \lambda_0 = 1$. What are the general constraints on the growth velocity field so that the curve remains planar at all time? Planarity implies that at any given time the curve can be expressed as

$$\mathbf{r}(S, t) = \mathbf{p}(t) + x(S, t)\hat{\mathbf{X}} + y(S, t)\hat{\mathbf{Y}}, \quad (7.31)$$

where $\mathbf{p}$ is the position vector of a point in the plane of the curve and the unit vectors $\hat{\mathbf{X}}, \hat{\mathbf{Y}}$ form a basis for the plane of the curve. This construction is illustrated in Figure 7.6. In this representation, the quantities λ and κ take the form

$$\lambda = \sqrt{x'^2 + y'^2}, \quad \kappa = \frac{x'y'' - x''y'}{(x'^2 + y'^2)^{3/2}}. \quad (7.32)$$

In order for the generating curve to remain planar during its evolution, its torsion must vanish identically, i.e., $u_3 = \dot{u}_3 = 0$. Using this condition in (7.13–7.18) leads to the following equation for $\mathbf{q}_2$:

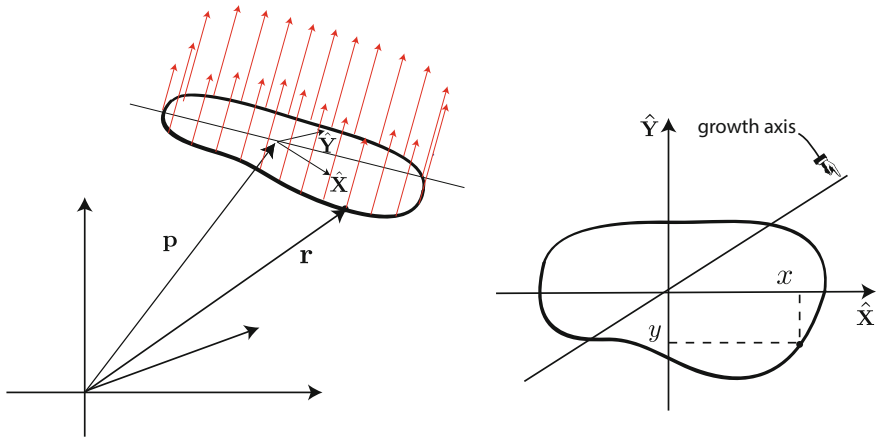


Figure 7.6 A planar curve is represented by a position vector $\mathbf{p}$ and the unit vectors $\hat{\mathbf{X}}$ and $\hat{\mathbf{Y}}$, which form a basis for the plane of the curve. The growth axis in this figure is given by $\hat{\mathbf{Y}} = -b_2/b_3 \hat{\mathbf{X}}$.

$$q_2''' - q_2'' \left(\frac{2\lambda}{\lambda} + \frac{u_2'}{u_2} \right) + q_2' \left(u_2^2 + \frac{2\lambda'^2}{\lambda^2} - \frac{\lambda''}{\lambda} + \frac{u_2' \lambda'}{u_2 \lambda} \right) = 0, \quad (7.33)$$

the general solution of which is

$$q_2 = b_1(t) + b_2(t)x(S, t) + b_3(t)y(S, t). \quad (7.34)$$

The form (7.34) implies a remarkable universal feature of growth. Namely, if the generating curve remains planar, then there exists a distinguished axis along the vector $b_2 \hat{\mathbf{X}} + b_3 \hat{\mathbf{Y}}$ such that the binormal growth on the generating curve is a linear function when projected onto this axis. This axis is the *growth axis* that we defined in the case of a circular generating curve. In particular, for the initial curve $\mathbf{r}(S, 0) = (\cos(S), \sin(S), 0)$, the form is $q_2 = b_1 + b_2 \cos(S) + b_3 \sin(S)$. Taking $b_3 = 0$ sets the x -axis of the initial plane to be the growth axis, and we recover the growth law for the torus given by (7.24) and shown in Figure 7.3.

7.1.3 Shape Invariance

We further restrict the growth velocity field so that the planar shape of the generating curve remains similar, that is, identical to the original curve up to a global dilation. This constraint implies that the curve can only undergo translation, rotation, and dilation. Therefore, we look for conditions on q_1 and q_3 so that the shape of the generating curve does not change as the curve evolves. Shape invariance implies that at any time t , $|\mathbf{r}'| = \lambda = \lambda(t)$, and that the curvature $\kappa(S, t)$ is the initial curvature scaled by the dilation factor λ , so that

$$\kappa(S, t) = \lambda^{-1} \kappa(S, 0). \quad (7.35)$$

Working in the Frenet frame, the shape variables are then given by

$$\mathbf{u}_1 = \mathbf{u}_3 = 0, \quad \mathbf{u}_2 = \lambda \kappa = \kappa(S, 0). \quad (7.36)$$

Therefore, we conclude that to ensure shape planarity, two conditions must be satisfied:

$$\dot{\mathbf{u}}_2 = 0 \quad (7.37)$$

$$\mathbf{q}_1'' + \mathbf{u}_2 \mathbf{q}_3 + \mathbf{u}_2^2 \mathbf{q}_1 + \mathbf{u}_2 \dot{\lambda} - \lambda' \mathbf{w}_2 = 0. \quad (7.38)$$

Motivated by the notion that the allowable transformation of the cross section should consist of dilation, rotation, and translation, we find that in global coordinates, the solution is of the form

$$\mathbf{q} = c_1(t) \mathbf{r} + c_2(t) \mathbf{r}_\perp + \mathbf{a}(t), \quad (7.39)$$

where $\mathbf{r}_\perp$ is a vector perpendicular to the position vector $\mathbf{r}$ with the same magnitude. The first term describes a growth velocity in the radial direction and accounts for dilation of the curve. The second term gives a growth velocity in the circumferential direction and accounts for rotation. The arbitrary vector, $\mathbf{a}(t)$, in the third term characterizes a rigid translation. To see that the form (7.39) satisfies (7.38) and to determine the explicit form of c_1 and c_2 , we express $\mathbf{q}$ in the local coordinates. This is achieved by writing

$$\mathbf{r} = \beta_1 \mathbf{d}_1 + \beta_3 \mathbf{d}_3, \quad \mathbf{r}_\perp = \beta_3 \mathbf{d}_1 - \beta_1 \mathbf{d}_3, \quad \mathbf{a} = \alpha_1 \mathbf{d}_1 + \alpha_3 \mathbf{d}_3. \quad (7.40)$$

The local velocities are then

$$\mathbf{q}_1 = c_1 \beta_1 + c_2 \beta_3 + \alpha_1, \quad \mathbf{q}_3 = c_1 \beta_3 - c_2 \beta_1 + \alpha_3. \quad (7.41)$$

Recalling that $\mathbf{r}' = \lambda \mathbf{d}_3$ and using the Frenet equations $\mathbf{d}_1' = -\mathbf{u}_2 \mathbf{d}_3$, $\mathbf{d}_3' = \mathbf{u}_2 \mathbf{d}_1$, we have

$$\beta_1' = -\mathbf{u}_2 \beta_3, \quad \beta_3' = \lambda + \mathbf{u}_2 \beta_1, \quad (7.42)$$

$$\alpha_1' = -\mathbf{u}_2 \alpha_3, \quad \alpha_3' = \mathbf{u}_2 \alpha_1. \quad (7.43)$$

Then, by inserting (7.41) into (7.38), we find that this latter relation is satisfied if

$$c_1(t) = \frac{\dot{\lambda}}{\lambda}, \quad c_2(t) = \mathbf{w}_2(t), \quad (7.44)$$

which highlights the relationship between the dilation factors c_1 and $\dot{\lambda}$ as well as the equivalence between the rotation factor c_2 and the frame rotation component $\mathbf{w}_2$.

7.1.4 Self-Similarity

A remarkable feature of many seashells is the property of scale invariance also known as *self-similarity*. Self-similarity is a global property of an object. Globally, we may define self-similarity in space as the requirement that the ratio of the distance between successive landmark points is constant. For instance, the ratio of the distance between successive whorls in a logarithmic spiral shell is constant [226], as shown in the next section. The question is now to define self-similarity at a local level: Which local growth velocity fields ensure global self-similarity? The key property for scale invariance is that, for each material point, the local direction of the growth vector does not vary in time. In the case of $q_3 = 0$, this is expressed by the requirement

$$\partial_t \left(\arctan \left(\frac{q_2}{q_1} \right) \right) = 0. \quad (7.45)$$

Property (7.45) is required for a surface to be scale invariant. However, it does not imply an invariance in growth *rate*, only in the growth *direction*. To enforce invariance in time, we further require that at each point the ratio of the magnitude of the growth vector to the size of the generating curve (i.e., radius of the circular cross section under consideration) should not vary in time. Note that if the initial radius is 1, then the radius at time t is $\lambda(t)$, and the requirement is

$$\partial_t \left(\frac{|\mathbf{q}|}{\lambda} \right) = 0, \quad (7.46)$$

where $|\mathbf{q}| = \sqrt{\mathbf{q} \cdot \mathbf{q}}$ is the magnitude of the growth vector. This condition motivates the growth law:

$$q_1 = -\lambda(t)c, \quad q_2 = \lambda(t)(b_1 + b_2 \cos(S)), \quad q_3 = 0. \quad (7.47)$$

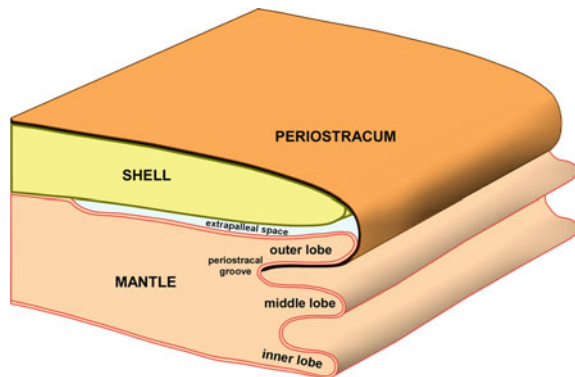
The difference with (7.26) is that here each velocity component is scaled by the stretch factor $\lambda(t)$. The direction of the growth vector is still time independent, i.e., the ratio q_2/q_1 is fixed for each S . This growth law produces a structure similar to Figure 7.4A with the difference that the magnitude of its growth rate is also scale invariant, i.e. (7.46) is also satisfied.

7.2 Application: The Growth of Seashells

7.2.1 Background

By their beauty and simplicity, seashells have captured the imagination of mankind for centuries. They have been used as currencies, jewelry, ornaments, tools, and are the favorites of many insatiable collectors. Most seashells are the hard mineralized

Figure 7.7 Organization of the generative zone in most modern mollusks. The mantle is part of the living animal and the periostracum is a thin organic layer of the shell that acts as a promoter of deposition for the mineralized shell [916].



shells of gastropod mollusks. More precisely, the shells of mollusks are microlaminate composite bioceramics made of minerals and biopolymers arranged in layers of prismatic calcite crystals or brick wall aragonite crystals [824]. The regular and complex arrangements of these layers, which account for up to 98% of the total mass of the animal, provide the shell with a strength that exceeds that of the mineral itself [38, 1176]. The shell of most modern mollusks is the result of a repeated secretion process generated by the mantle, a thin soft tissue of the mollusk that extends out of the shell to wrap around its edge to cover the *periostracum*, a thin outer organic layer [1164] shown in Figure 7.7.

During growth, the mantle moves forward slightly beyond the calcified shell edge whilst secreting the periostracum, which isolates the extrapallial fluid from which the calcified shell is precipitated [1114]. The periostracum is secreted in the periostracal groove, between the outer and middle mantle lobes, and is extruded between the two mantle lobes, whereby a stiffening process of sclerotization takes place [1288]. It is subsequently turned inside out around the outer mantle lobe and reaches its external position where no further thickening occurs.

When calcification occurs, the periostracum becomes fixed on the outer shell surface. The unfixed periostracum surrounds the outer mantle lobe and is attached at both extremities along the calcified shell edge and inside the periostracal groove. The shape of the generative zone, namely the stiff periostracum surrounding the softer outer mantle lobe, is therefore incrementally set in the calcified shell during growth. In turn, the calcified shell edge acts as a template for the new growth increment.

Strikingly, despite the fact that gastropod mollusks are a diverse group of metazoans with over 100,000 extant and fossils known, their external shells seem to follow a remarkably simple design based on an expanding spiral [533, 1077] that closely matches the logarithmic spiral [539], identified as the key feature of seashells by Moseley in 1838 [908].

This morphological regularity has long been recognized and appreciated, and has inspired a large body of research. In particular, D'Arcy Thompson described the elegance and simplicity of the spiral coils of the molluscan shell in mathematical and geometric terms [1230], as shown in Figure 7.8. Following the work of Raup

[1061, 1062], who triggered the field of research termed “theoretical morphology,” many models and approaches have been devised [274, 1199]. While most of the early works were descriptive, focusing on the form and shape of shells, research has shifted in recent decades to questions of biology and evolution [1077], understanding pigmentation patterns [108, 381, 862, 863], and the growth process underlying shell form [532]. Nevertheless, even in the case of the molluscan shell, which has been reproduced mathematically numerous times, a full understanding of *how* growth occurs, e.g., the biomechanical basis for coiling, remains elusive.

7.2.2 Geometric Description

Mathematically, the ideal form of these seashells can be described with the general framework of curves and rods of Chapter 5. The central axis of the seashell is a logarithmic spiral and the radius of the rod increases with arc length. A convenient way to represent the surface of a seashell is to consider a centerline curve $\mathbf{p} = \mathbf{p}(t)$ where

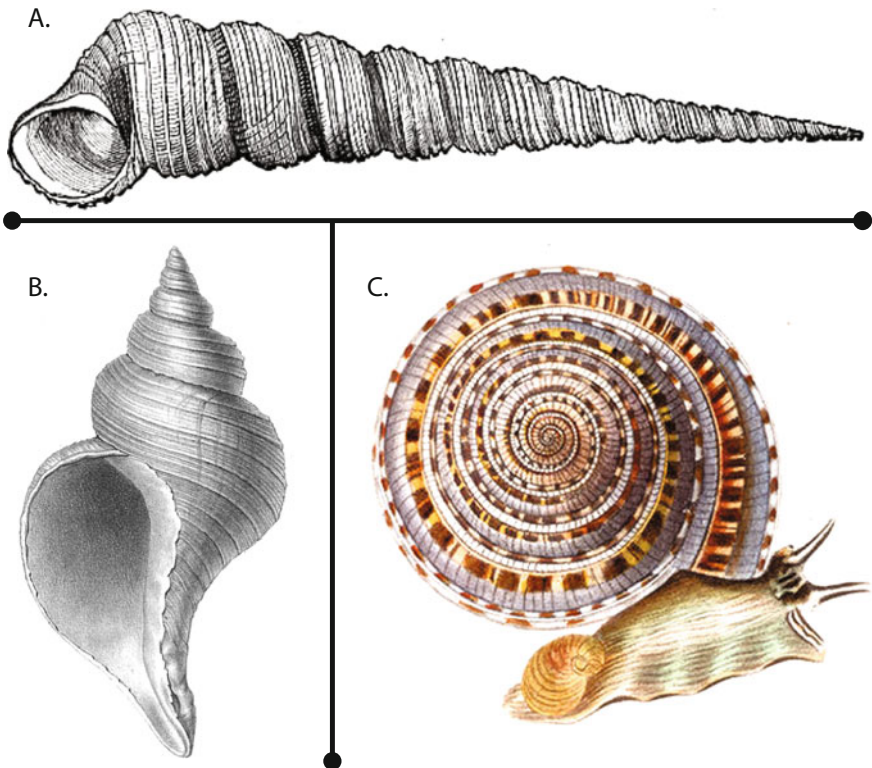


Figure 7.8 Example of shells in mollusks. A. *Turritella terebra*. B. *Neptunea angulata* (drawing by P.H. Nyst, 1878 [970]). C. *Architectonica perspectiva* (clear sundial snails, drawing by L.C. Kiener, 1880 [689]).

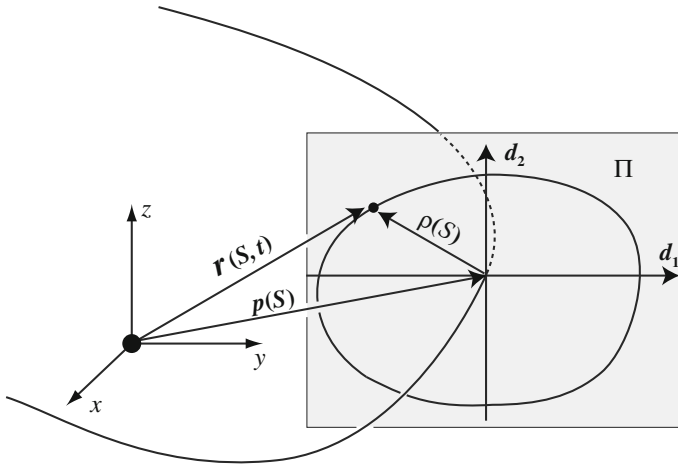


Figure 7.9 The generating curve $\mathcal{C}$ defining the cross section of the seashell.

t is a parameter. As before, at each point on this curve we attach three orthonormal vectors $\mathbf{d}_1(s)$, $\mathbf{d}_2(s)$, and $\mathbf{d}_3(s)$ such that $\mathbf{d}_3(s) \cdot \mathbf{p}' \neq 0$. We define for each t , a generating curve $\mathcal{C}$ in the plane spanned by the first two directors of a simple curve:

$$\boldsymbol{\rho}(S, t) = r_1(S, t)\mathbf{d}_1(t) + r_2(S, t)\mathbf{d}_2(t), \quad (7.48)$$

such that $\boldsymbol{\rho}(S, t)$ is a periodic and twice differentiable function in S and t . The surface of the seashell is then given by

$$\mathbf{r}(S, t) = \mathbf{p}(t) + \boldsymbol{\rho}(S, t). \quad (7.49)$$

With appropriate guesswork and proper choice of functions $\mathbf{p}$ and $\boldsymbol{\rho}$ most seashells can be represented within this framework.

Here, we focus on a particular set of surfaces whose central curve $\mathbf{p}$ is given by a logarithmic spiral and whose generating curve $\mathcal{C}$ is a circle as shown in Figure 7.9. These simplifying assumptions lead to a family of curves with three parameters whose geometry can be easily explored.

The central curve is taken to be a *logarithmic spiral* in 3 dimensions, that is,

$$\mathbf{p}(t) \equiv (x, y, z) = Ae^{\alpha t}(\sin \beta \cos t, -\sin \beta \sin t, \cos \beta), \quad (7.50)$$

where A , α , and β are real parameters. This curve, sketched in Figure 7.10, is constructed as follows: It is an *equiangular* (or *logarithmic*) *spiral* in the horizontal $x - y$ plane. An equiangular spiral is defined by the property that the angle between a line from the center to any point on the curve and the tangent at the same point makes a constant angle. If the parameter t is chosen to be the angle θ in the $x - y$ plane, then the radial line makes an angle $\gamma = \text{arccot}(\alpha)$ with the tangent vector at

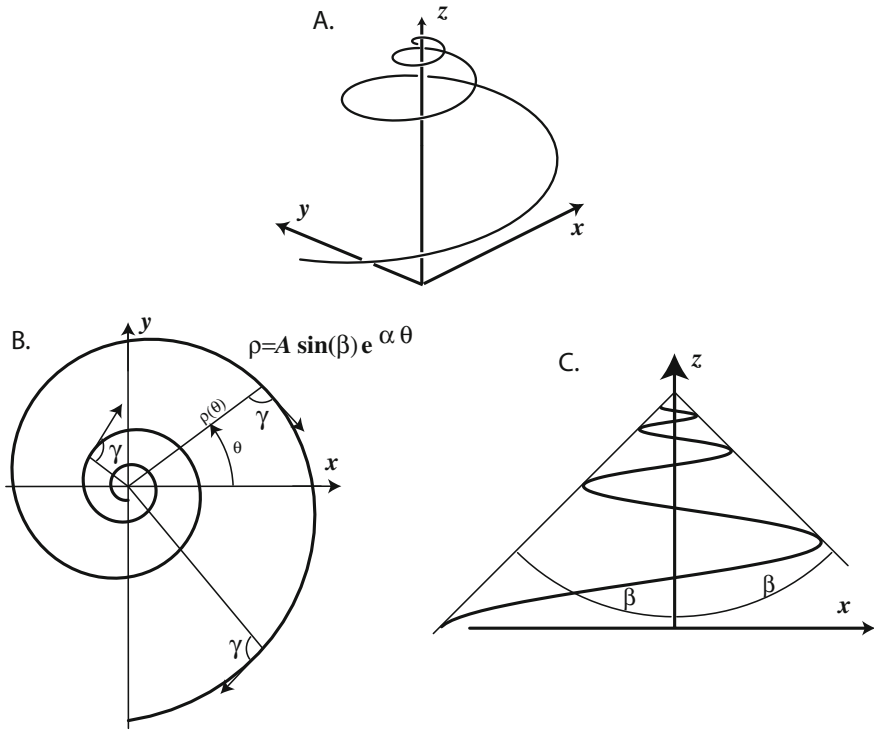


Figure 7.10 A. The logarithmic spiral. B. In the x - y plane, the logarithmic spiral is an equiangular spiral. The angle between the radial line at a point and the tangent vector is constant and is equal to $\gamma = \text{arccot}(\alpha)$ (three different points shown). C. In the x - z plane, the curve is tangent to two lines. These lines have an opening angle 2β .

this point. In the $x - z$ plane, and in any plane containing the z -axis, the projection of the curve is a sine function modulated by a linear function, so that the curve in space lies on a cone of opening 2β .

The logarithmic spirals are self-similar in the sense that given n points $\{\mathbf{p}_i = \mathbf{p}(t_0 + 2i\pi), i = 1, \dots, n\}$, the distance ratios between three successive points,

$$\frac{d(\mathbf{p}_{i-1}, \mathbf{p}_i)}{d(\mathbf{p}_i, \mathbf{p}_{i+1})}, \quad (7.51)$$

is independent of the choice of i . The computation of this ratio also gives access to the value of α . For instance, from the z -distance between successive coils, we find

$$\alpha = \frac{1}{2} \log \left(\frac{z_i - z_{i+1}}{z_{i-1} - z_i} \right). \quad (7.52)$$

Conversely, we can test the self-similarity of a given seashell by measuring the ratio of similar points and by checking that this ratio remains close to a constant. It is a

remarkable fact of nature that many seashells are actually extremely close to perfect self-similar shapes [539].

We can now build the actual seashell surface by considering a generating curve $\mathcal{C}$ around the centerline and scaling its size with the same exponential function. Here, for simplicity, we take $\mathcal{C}$ to be a circle whose radius expands exponentially with t ; that is,

$$\rho(S, t) = Be^{\alpha t} (\cos(S)\mathbf{d}_1(t) + \sin(S)\mathbf{d}_2(t)), \quad S = 0, \dots, 2\pi. \quad (7.53)$$

We still have to define the orientation of the plane Π with respect to the logarithmic spiral. Historically, two different parameterizations of seashells have been considered. The first one consists in choosing the plane Π so that it contains the z -axis. This constraint is satisfied by taking $\mathbf{d}_2 = \mathbf{e}_z$ and $\mathbf{d}_1$ to be perpendicular to the curve. In this case, we have

$$\mathbf{r}(S, t) = e^{\alpha t} (\cos t (A \sin \beta + B \sin S), -\sin t (A \sin \beta + B \sin S), -A \cos \beta + \cos S). \quad (7.54)$$

This original description of seashells found in the work of Moseley in 1838 is still widely used. Models of this type are almost exclusively descriptive, since a fixed reference frame is an artificial construction disconnected from any actual growth process and the existence of a fixed axis in space does not allow for any variation away from the logarithmic spiral. However, this representation is particularly easy to implement and provides an explicit form for the surface [643, 644, 813, 1061, 1062, 1122].

There are, however, some clear disadvantages to identify the plane Π with a vertical plane: The plane Π is defined with respect to the axis and is not perpendicular to the tangent vectors. Therefore, this representation is closely linked to the particular choice of a logarithmic spiral as a central curve. For other choices of central curves, this representation cannot be generalized. Thus, it is natural and mathematically appealing to define Π to be the normal plane to the curve at every point. This choice was originally proposed by Okamoto [981, 982] and subsequently adopted by multiple authors [381, 653, 813]. In this case, we identify the directors $\mathbf{d}_1$ and $\mathbf{d}_2$ with, respectively, the normal and binormal vectors which, together with the unit tangent vector $\mathbf{d}_3$ define the Frenet frame:

$$\mathbf{d}_3 = \frac{\partial_t \mathbf{p}}{|\partial_t \mathbf{p}|}, \quad \mathbf{d}_1 = \frac{\partial_t \mathbf{d}_3}{|\partial_t \mathbf{d}_3|}, \quad \mathbf{d}_2 = \mathbf{d}_3 \times \mathbf{d}_1. \quad (7.55)$$

In the case of a logarithmic spiral, a straightforward computation leads to

$$\mathbf{d}_1 = \left(-\frac{\cos t + \alpha \sin t}{\delta_1}, \frac{\sin t - \alpha \cos t}{\delta_1}, 0 \right), \quad (7.56)$$

$$\mathbf{d}_2 = \left(-\frac{\alpha (\sin t - \alpha \cos t) \cos \beta}{\delta_1 \delta_2}, \frac{\alpha (\cos t + \alpha \sin t) \cos \beta}{\delta_1 \delta_2}, -\frac{\delta_1}{\delta_2} \sin \beta \right), \quad (7.57)$$

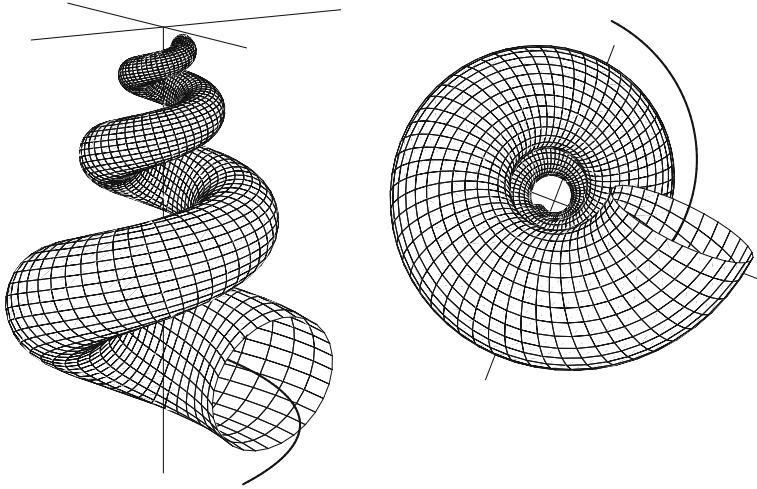


Figure 7.11 An example of a seashell surface produced by Equations (7.59–7.61) with $A = 1$, $\rho = 0.17$, $\alpha = 0.1$, $\beta = 0.3$. Note that the solid curves on the surface are either at a constant angle in the normal plane or in the normal plane (circular cross section). The inclination of the normal planes clearly indicates that the circular aperture is not in a plane containing the z -axis.

$$\mathbf{d}_3 = \left(\frac{(-\sin t + \alpha \cos t) \sin \beta}{\delta_2}, -\frac{(\cos t + \alpha \sin t) \sin \beta}{\delta_2}, -\frac{\alpha}{\delta_2} \cos \beta \right), \quad (7.58)$$

where $\delta_1 = \sqrt{\alpha^2 + 1}$ and $\delta_2 = \sqrt{\alpha^2 + \sin^2 \beta}$. The surface of the shell is then given by

$$x(S, t) = e^{\alpha t} [A \sin \beta \cos t + \rho (d_{1x} \sin S + d_{2x} \cos S)], \quad (7.59)$$

$$y(S, t) = e^{\alpha t} [-A \sin \beta \sin t + \rho (d_{1y} \sin S + d_{2y} \cos S)], \quad (7.60)$$

$$z(S, t) = e^{\alpha t} [-A \cos \beta + \rho (d_{1z} \sin S + d_{2z} \cos S)], \quad (7.61)$$

where $d_{1x} = \mathbf{d}_1 \cdot \mathbf{e}_x$ and so on. We define the variables $S \in [0, 2\pi]$ and $t \in [0, 2n\pi]$ where n is the number of coils. The above parameterization defines a 4-parameter family of surfaces. However, we can set, without loss of generality, the distance of the central curve at $t = 0$ to the z -axis to be $A = 1$ and measure all lengths with respect to this distance. Doing so, we obtain a 3-parameter family of shapes parameterized by α, β, ρ . The parameter ρ is the distance from the central curve to the opening at time $t = 0$. An example of such a seashell surface is given in Figure 7.11.

7.2.3 Accretive Growth of Seashells

The previous representation of seashells is purely geometric as it describes shapes from an external viewpoint. We now compare this approach to an intrinsic local view of

seashells by describing growth as a local accretion process. To do so, we first relate the local rate of growth to the growth velocities and the evolution of the growth axis.

First, we impose shape invariance, shape planarity, and self-similarity in space as defined in Section 7.1. These three conditions lead to two possible growth laws for linear or planar growth given by (7.26) and (7.47); that is,

$$\mathbf{q}_1 = -c, \quad \mathbf{q}_2 = b_1 + b_2 \cos(S), \quad \mathbf{q}_3 = 0, \quad (7.62)$$

$$\mathbf{q}_1 = -\lambda(t)c, \quad \mathbf{q}_2 = \lambda(t)(b_1 + b_2 \cos(S)), \quad \mathbf{q}_3 = 0. \quad (7.63)$$

These two laws produce identical structures, and only the time evolution can distinguish between the different growth processes as noted in [1077, 1267]. Note that (7.62) is not time invariant and so the *coiling rate*, i.e. the time necessary to complete one full whorl in the terminology of seashells, is not fixed. The time to coil increases exponentially while the aperture size increases linearly.

For the process (7.63), the time to complete one coil is fixed, independent of size or time, hence the material deposition rates must increase exponentially. This growth process appears to be inconsistent with the observation that shell growth rates decrease with increasing octogenetic age [104, 652, 1130]. We can directly relate the area growth rate to the deposition velocity. We define the material rate $\dot{m}$ as the rate of increase of surface area, as follows

$$\dot{m}(t) = \int_C |\mathbf{q}| \, ds = \int_C (\mathbf{q}_1^2 + \mathbf{q}_2^2 + \mathbf{q}_3^2)^{1/2} \, ds. \quad (7.64)$$

If we assume that the material rate, $\dot{m}$ is constant in time, we obtain the self-similar form

$$\mathbf{q}_1 = -\frac{c}{\lambda}, \quad \mathbf{q}_2 = \frac{b_1 + b_2 \cos(S)}{\lambda}, \quad \mathbf{q}_3 = 0. \quad (7.65)$$

This form has a coiling rate *logarithmic* in time while the radius increases as $t^{1/2}$. Therefore, assuming a constant growth rate, the existence of a self-similar accreted structure, generated by a circular opening, implies that the growth velocity must follow (7.65). Further assumptions on the growth rate can match either microscopic models of accretion or data on growth.

7.2.4 Other Accreted Structures

Once the key ingredients of the local accretion model are understood, it is fairly easy to understand the balance between the different components of the growth vector to reproduce different shapes observed in nature. For instance, several horns and seashells are shown in Figure 7.12 with their associated growth vectors.

Another example with a noncircular generating curve is the bivalve shell shown in Figure 7.13. This shape was obtained by using a simple initial curve and binormal growth that is linear along a given direction with time varying coiling rate.

A.

$$\begin{aligned} \mathbf{q}_1 &= -(c + k \sin(S)), \\ \mathbf{q}_2 &= b_1 + b_2 \cos(S) \\ \mathbf{q}_3 &= k \cos(S) \end{aligned}$$



Turitella seashell



B.

$$\begin{aligned} \mathbf{q}_1 &= -(c + k(t) \sin(S)), \\ \mathbf{q}_2 &= b_1 + \lambda b_2 \cos(S) \\ \mathbf{q}_3 &= k(t) \cos(S), \\ \text{with } k &= k_1 + k_2 t \end{aligned}$$



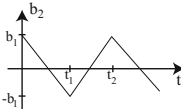
Antelope horns



C.

$$\mathbf{q}_2 = b_1 + b_2(t) \cos(S)$$

with b_2 of form:



plus global velocity:

$$\mathbf{q}_g = \begin{cases} k_1 \mathbf{e}_y & t < t_1 \\ k_2 \mathbf{e}_x & t_1 < t < t_2 \\ -k_3 \mathbf{e}_y & t > t_2 \end{cases}$$

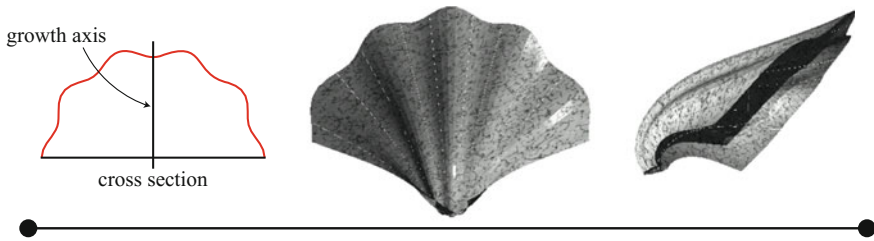


Nipponite shell



Figure 7.12 Examples of surfaces generated by accretive growth. A. A *Turritella* shell. B. Antelope horns. C. A *Nipponite* shell. The form of the growth velocity field and a sample structure are shown. In each case, an explicit solution for the curve evolution can be obtained. Parameters: for A: $b_1 = 1$, $b_2 = 10$, $c = -0.025$, $k = 0.32$, and initial radius 0.1; for B: $b_1 = 0.75$, $b_2 = 0.3$, $c = -0.04$, $k_1 = 0.25$, $k_2 = 0.02$, and initial radius 0.1; for C: $t_1 = 12$, $t_2 = 20.4$, $k_1 = 0.8$, $k_2 = 0.73$, $k_3 = 1.2$, and radius 1 (adapted from [914]).

A.



B.

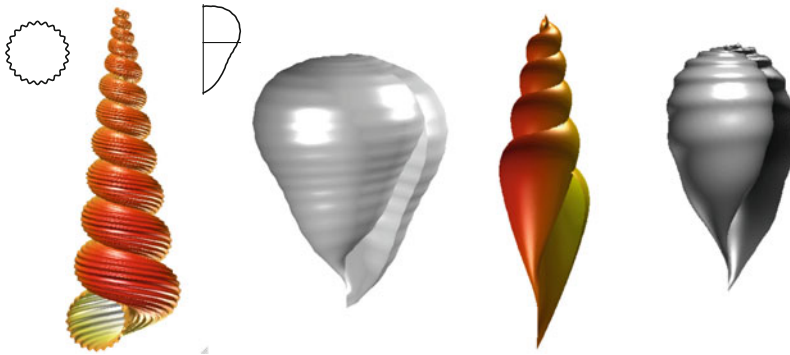


Figure 7.13 Noncircular apertures. A. Growth of a bivalve shell using an initial curve $\mathbf{r}_0 = (R \cos(S), R \sin(S), 0)$ with $R = 1 + 0.05 \cos(10S)$ and velocity $\mathbf{q}_1 = -c(\mathbf{r}_0 \cdot \mathbf{d}_1(S, 0))$, $\mathbf{q}_2 = b_1 + b_2(t)R \cos(S)$, $\mathbf{q}_3 = -c(\mathbf{r}_0 \cdot \mathbf{d}_3(S, 0))$ (with $c = 3$, $b_1 = 0.1$, $b_2 = 5 - 0.5t$). B. Various seashells obtained from different initial aperture profiles (explicit values of the parameters can be found in [915]).

7.2.5 The Role of Mechanics in Morphological Patterns

The kinematic analysis of accreted growth in the previous section reveals that the logarithmic spiral structure of seashells is controlled by simple local laws. It also reveals the existence of a growth gradient along the aperture. How this growth gradient is established and maintained through distant points so that the shell recognizes the growth direction remains a mystery and to-date there is no model or even a qualitative explanation for this basic property.

Nevertheless, we can use this basic growth structure as the underlying evolution of the shell shape and focus our attention on the morphological patterns appearing on top of the basic coiled shape. There are two basic morphological patterns superimposed on the self-similar structures: commarginal or antimarginal ornamentations.

Commarginal ornamentation or transverse ribbing is a common feature of a number of mollusk shells. It is characterized by an oscillatory component to the dilation in the aperture as shown in Figure 7.14. The generating curve remains similar up to a global dilation factor.



Figure 7.14 Commarginal ornamentation in *Dictomosphinctes*. (picture courtesy of Régis Chirat).

Antimarginal ornamentation are patterns that are orthogonal to the aperture. Therefore, they are a modification of the shape of the generating curve different from a simple dilation. This includes antimarginal ribs as well as more complex patterning such as the spines shown in Figure 7.15 and fractal-like structures.

These morphological patterns are created through the interaction of the soft mantle and the hard shell. At each accretion step, the mantle, a soft tissue growing with its own timescale, may not take the exact shape of the aperture. This potential mismatch in growth between accretion and soft tissue growth is responsible for the patterns observed empirically by a number of authors [189–191, 1193] and has been proposed as a theoretical mechanism to explain pattern formation in [531, 905, 906]. Following this idea, Moulton and coauthors developed a mathematical model based on the complex interaction between accretion and soft mantle growth to explain various known morphological patterns [202, 914–916].

7.2.5.1 Commarginal Ornamentation

Commarginal ornamentation is particularly apparent in some species of ammonites. Ammonites are an iconic group of extinct cephalopods that are characterized by nearly perfect logarithmic spiral shells with regular ribbing patterns. This pattern is almost

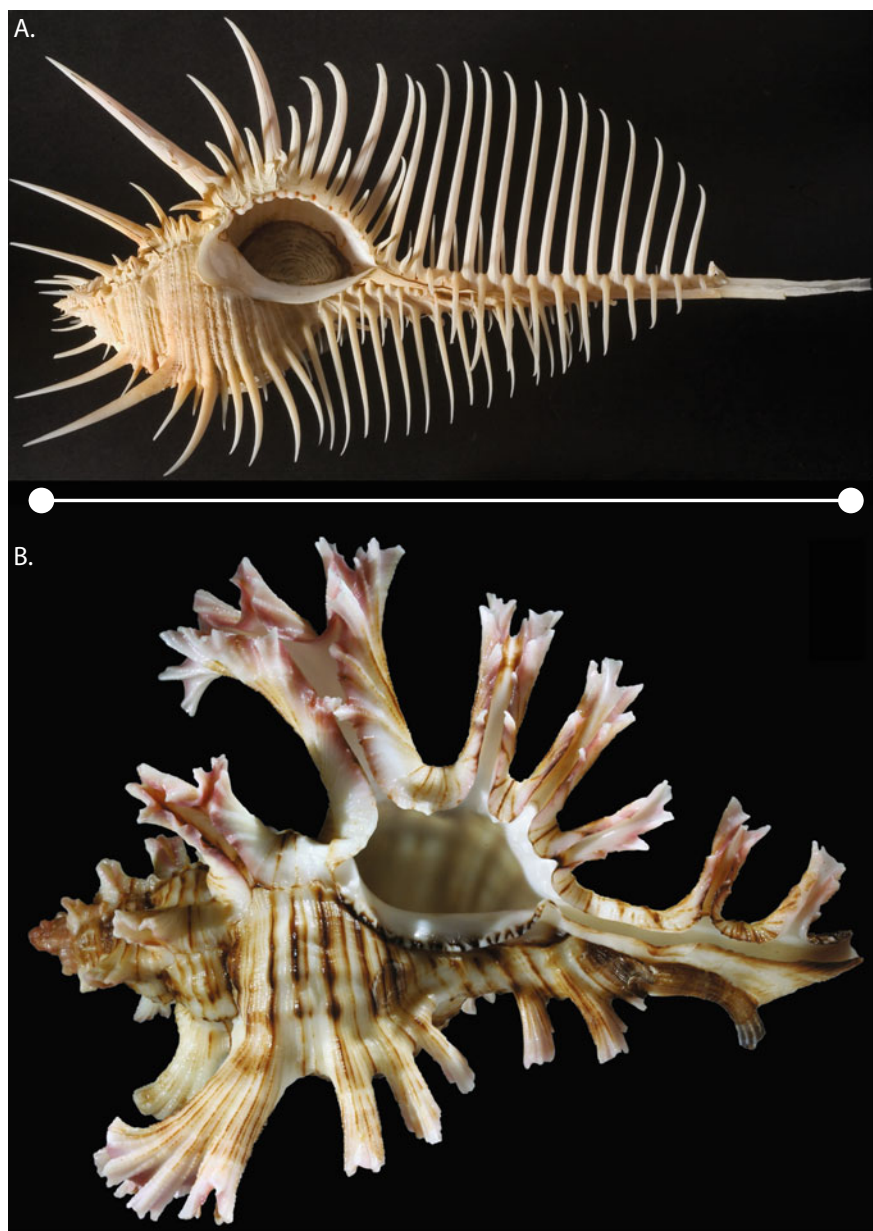


Figure 7.15 Antimarginal ornamentation: Spines in A. *Murex pecten* and B. *Chicoreus (Triplex) palmarosae*. (pictures courtesy of Régis Chirat).

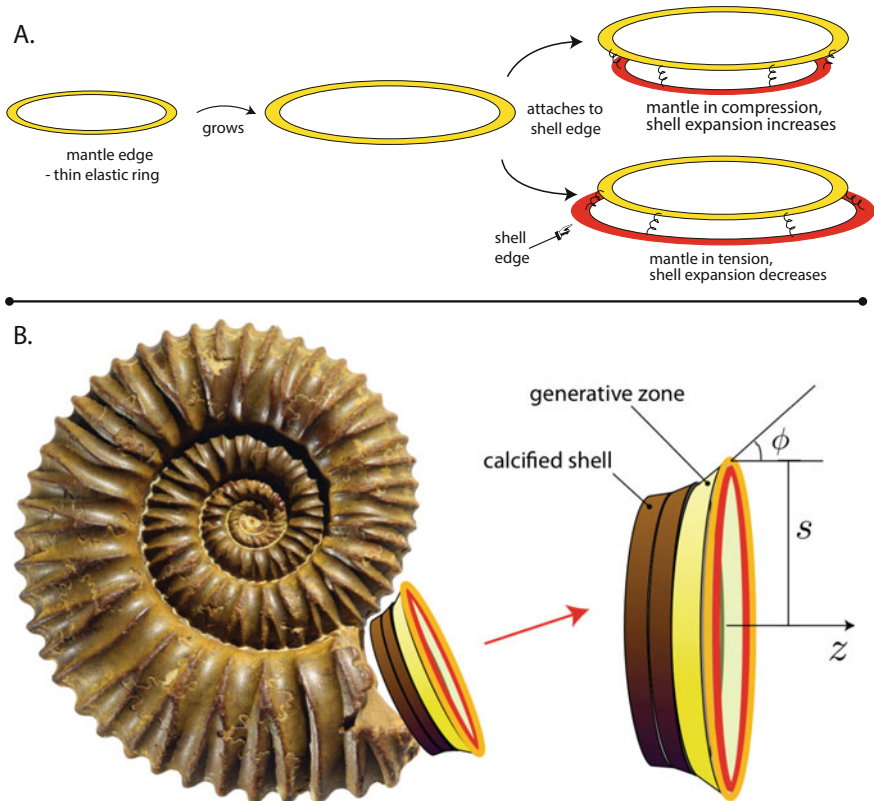


Figure 7.16 Model of commarginal ornamentation. A. Model of growth showing the mantle and the shell layer, and the attachment forces acting between them [915]. B. Commarginal ribs in *Peltoceras schroederi* and primary variables for the model. The shell has radius s and orientation angle ϕ with respect to the growth axis z [916].

universally present in ammonites and forms along the direction of the accreted shell, appearing as an oscillation in the expansion of the shell cross section as illustrated in Figure 7.14.

We model the mantle as a circular growing elastic ring with a given growth rate as shown in Figure 7.16A. When the mantle adheres to the current shell edge, it is subject to both a compression/stretching force and an attachment force. We assume that the compressive force acting on the mantle is sufficiently small so that it remains circular and that the equilibrium diameter is a balance between these two forces.

At equilibrium, the mantle is not in a stress-free state, and we assume that the deposition of new layers is controlled by the level of stress through an adjustment of the angle of deposition, as shown in Figure 7.16A. If the mantle is in compression, it increases the angle of deposition as to increase the radius of the new aperture and therefore relieve its stress. Conversely, if the mantle is in tension, the angle is decreased and so is the rate of increase of the aperture radius. This simple law naturally creates

oscillation of the radial profile as a function of time due to a mismatch between accretion and growth.

Let k_g be the constant growth rate, so that in a time Δt , $k_g \Delta t$ is the length of material added to the shell. The angle of material deposition is denoted by ϕ . Denoting r_s as the shell radius, it follows that

$$\dot{r}_s = k_g \cos \theta \sin \phi, \quad (7.66)$$

where θ is the fixed angle of the growth vector between the normal and tangent direction. The key assumption is that the mantle can change the angle ϕ based on its stress level. Let n_3 be the axial stress in the mantle edge; note that $n_3 > 0$ if the mantle is in tension and $n_3 < 0$ if the mantle is in compression. This axial stress n_3 depends on the shell radius r_s as well as the diameter of the mantle edge in the unstressed state, determined by the growth function γ . The feedback between the deposition angle and the tension in the mantle is modeled by

$$\dot{\phi} = \frac{k_\phi}{r_s} \left(1 - e^{Kn_3} \right). \quad (7.67)$$

The system of ordinary differential equations (7.66–7.67) can be solved numerically once the tension is computed from either rod theory or three-dimensional elasticity, as shown in [915]. An example of a three-dimensional structure combining the kinematic of an expanding logarithmic seashell with an oscillating radii provided by this model is shown in Figure 7.17B where the typical ribbing pattern is obtained through this feedback process. A detailed analysis of ammonite ribbing leads to an excellent match with known forms as shown in Figure 7.17. This model provides a mechanistic explanation for most of the trends and patterns observed in fossil records [916].

7.2.5.2 Antimarginal Ornamentation

We model the formation of antimarginal ribs by assuming that the mantle is a circular growing inextensible elastic ring with a given growth rate attached to the aperture. We further assume that the aperture at the next accretion step depends on the shape of the mantle since it creates a template for the next accretion cycle. Since the growing mantle will exhibit an excess of length compared to the previous growth increment, it will be subject to buckling upon adhering to the aperture, as shown in Figure 7.18. The new deposited layer of shell material takes the deformed shape set by the next foundation upon mineralization. Therefore, the mechanical deformation of the mantle dictates the evolution of the shape of the aperture.

The theory of growing rings developed in Chapter 6 can be directly coupled to an evolving foundation. The centerline of the mantle is the curve ρ with total length l , and the centerline of the aperture is $\hat{\mathbf{r}}$ with arc length $\hat{l}$. We assume that $\hat{l} > l$ to account for growth of the mantle, and that the connection provided by the periostracum acts as a linear foundation for the mantle. Note that in this configuration the mantle induces both a body force and a body couple as sketched in Figure 7.19.

Following the notation of Section 5.1.3, we write the normal and binormal vectors

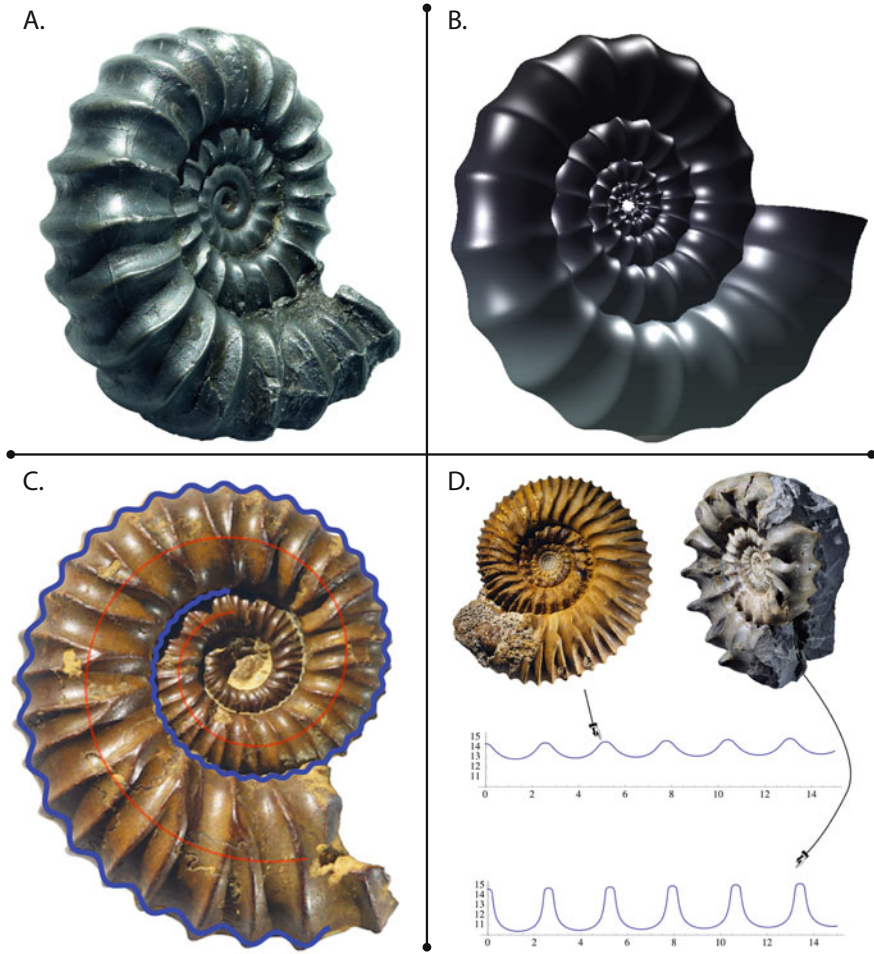


Figure 7.17 Commarginal ornamentation. A. Ammonite *Promicroceras*. B. Simulated ammonite. Stress in the mantle governs the dilation of the shell edge and is combined with a fixed rule for coiling (AB from [914]). C. Theoretical rib profile overlaid on a shell of *Peltoceras schroederi*. D. Asymmetric ribbing profiles produced by a model with bimodal elastic response in tension and compression. Left: *Stephanoceras*, Right: *Xipheroceras* (CD from [916]).

$$\mathbf{v} = -\cos(S/\gamma)\mathbf{e}_x - \sin(S/\gamma)\mathbf{e}_y, \quad \boldsymbol{\beta} = \mathbf{e}_z. \quad (7.68)$$

The angle of rotation of the cross section due to the applied couple is a nonzero register angle, φ , that is used to define the director basis for the unperturbed system:

$$\mathbf{d}_1^{(0)} = \mathbf{v} \cos \varphi + \boldsymbol{\beta} \sin \varphi, \quad (7.69)$$

$$\mathbf{d}_2^{(0)} = -\mathbf{v} \sin \varphi + \boldsymbol{\beta} \cos \varphi. \quad (7.70)$$

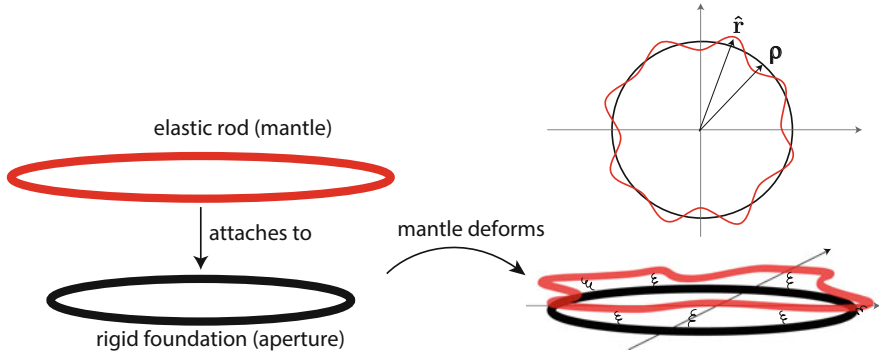


Figure 7.18 Mantle buckling model. The shape of the deformed mantle, described by the curve $\hat{\mathbf{r}}$, is found as the minimizer of the sum of bending energy and spring energy due to attachment to the foundation given by the curve $\boldsymbol{\rho}$.

According to (5.23), the components of the Darboux vector are

$$\left(u_1^{(0)}, u_2^{(0)}, u_3^{(0)}\right) = (\gamma^{-1} \sin \varphi, \gamma^{-1} \cos \varphi, 0). \quad (7.71)$$

The foundation is assumed to be a circle of radius 1 located in the x - y plane, i.e., $\boldsymbol{\rho} = -\mathbf{v}$. Therefore, the foundation force is of the form

$$\mathbf{f} = k(\boldsymbol{\rho} - \mathbf{r}_A), \quad (7.72)$$

with $\mathbf{r}_A = \mathbf{r} - a\boldsymbol{\beta}$ and a is the radius of the rod. We are interested in computing the first bifurcation to a noncircular solution. Before bifurcation, the rod's centerline is a circle of radius $\gamma = L/2\pi$, located in the plane $z = h$. Mechanical equilibrium is satisfied if the plane of the ring satisfies $h = a \cos \varphi$, and the register angle solves

$$EI\gamma^{-1} \sin \varphi + ka \cos \varphi (a \sin \varphi - \gamma + 1) = 0, \quad (7.73)$$

where EI is the bending stiffness of the mantle.

The critical length of the mantle at which the first bifurcation occurs is computed by following the general method given in Section 6.5. In Figure 7.19, γ^* is plotted against the foundation stiffness. We note that within this context, modes 2 and 3 do not exist for all values of k , and mode 2 has a minimum value.

Next, we can apply this basic idea to compute the growth of a bivalve clam shell. The initial foundation is taken to be a semicircle with a fixed linear increase in length occurring at each increment of mantle growth. Fixed rates of coiling, dilation, and translation are imposed with the shape change. Figure 7.20 shows the evolution of the fixed plane curve as well as the full surface produced when mechanics is coupled with kinematics. It can be noted that the folds of the aperture deepen over time through the incremental mantle deformation process.

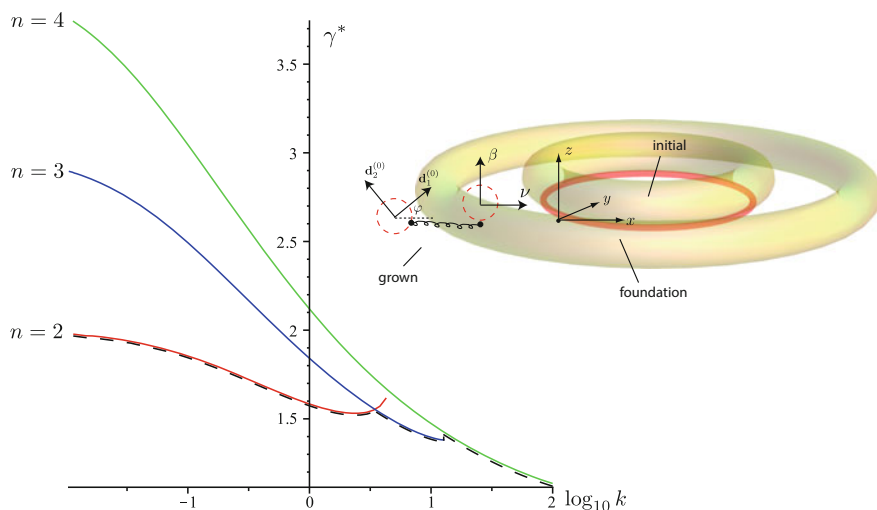


Figure 7.19 Left: Critical buckling growth in the case of the foundation underneath the initial ring. The dashed line is the envelope of the critical growth—it is not monotonic, and suffers a discontinuous jump in the transition from mode 3 to mode 4. Right: Growing ring with foundation underneath.

7.2.5.3 Spine Formation

Spines are also antimarginal ornamentation since they change the shape of the generating curve. However, in distinction with the previous example, they emerge during phases where there are large excesses of length in the mantle as shown in Figure 7.21. The formation of spines can be understood in terms of the changing morphology of the shell edge, driven by the growth and elastic response of the mantle. The basic idea is to predict the form that is incrementally generated by the edge of the thin elastic mantle with an excess of length relative to the previously formed and fixed configuration. The mantle edge is modeled as an inextensible elastic rod and is assumed to grow at a fixed rate. At each growth increment, the mantle adheres to the current shell edge through the elastic periostracum. As the mantle has grown since the last secretion, it is longer than the shell edge and deforms upon adhering. The shape of the deformed mantle is the elastic equilibrium shape obtained as a balance of two components: the bending moment of the mantle dependent upon the geometric curvature of the mantle edge, and an attachment force between the mantle and the shell edge (the template that serves as a mechanical rigid foundation).

The development of the shell proceeds by first incrementally increasing the length of the mantle edge; second, determining the mantle shape through mechanical equilibrium, and, lastly, by updating the shell edge as the shape of the deformed mantle. The emergent form is governed by the length dimensions and elastic properties of the mantle edge, the strength of adhesion, and the marginal growth rate, i.e., the excess of length as

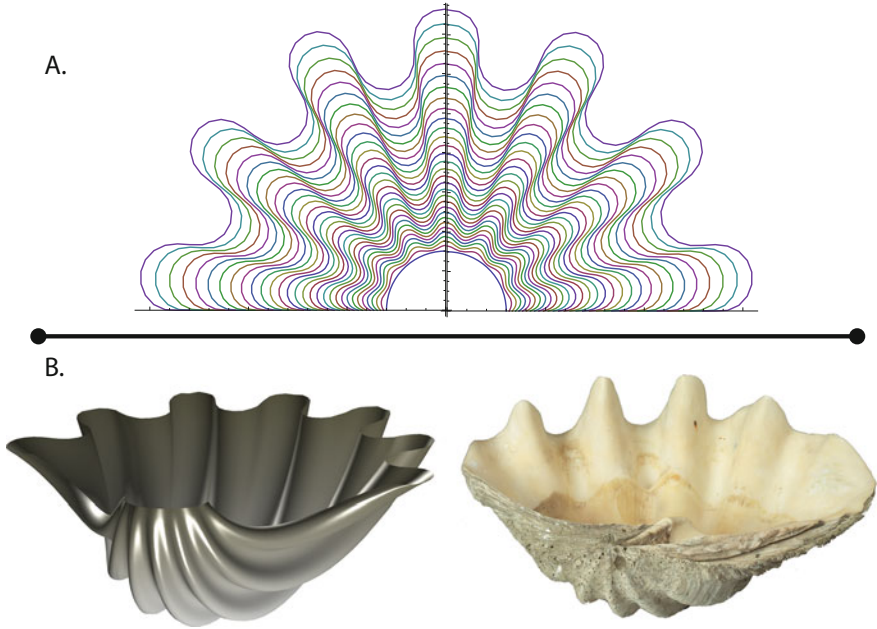


Figure 7.20 Growth of a giant clam shell (*Tridacna gigas*). A. Mechanical deformation of the mantle dictates the evolution of the aperture shape. B. Combined with an overall logarithmic growth to simulate a three-dimensional shell [914].

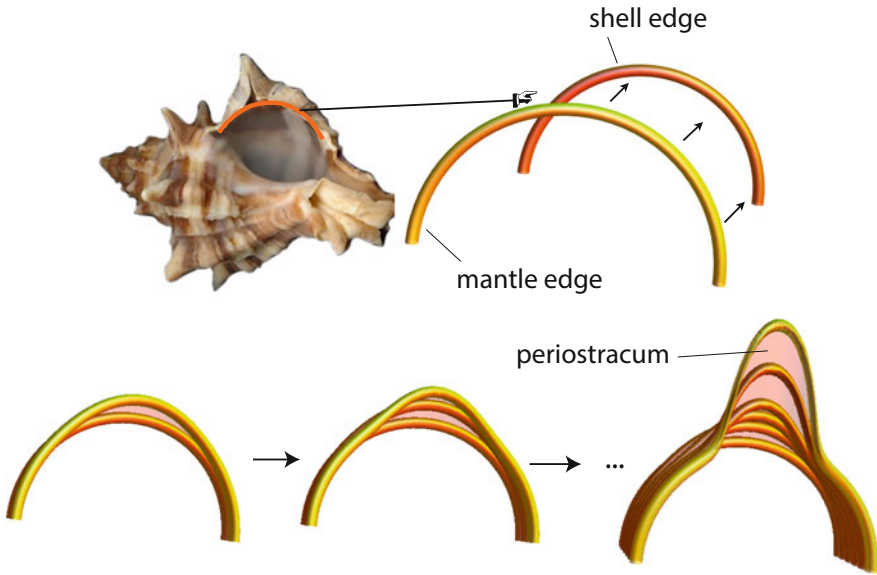


Figure 7.21 Modeling spine formation. The elastic mantle edge, showing an excess of length compared to the previous and fixed shell edge, deforms and then secretes new material in the deformed shape [202].

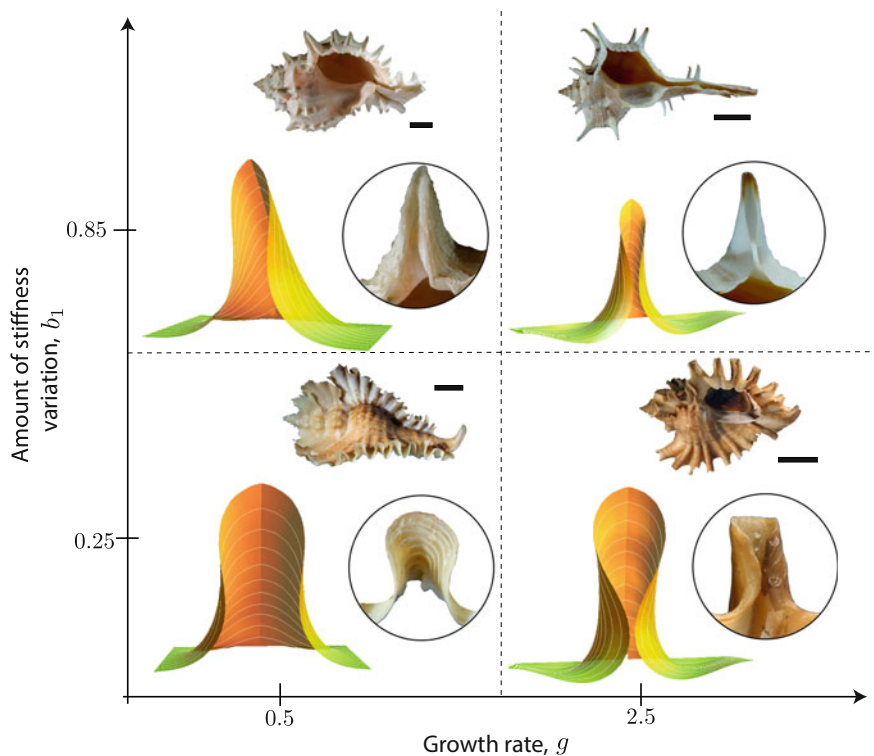


Figure 7.22 Phase diagram showing the effect of the growth rate and the degree of stiffness variation on the evolving spine. Variations in spine morphology among species of the same family, *Muricidae*, are shown for comparison: A. *Hexaplex erythrostomus*, B. *Bolinus brandaris*, C. *Pterynotus phyllopterus*, D. *Ceratostoma burnetti*. Scale bar is 10 mm. Reproduced from [202].

compared to the previous growth increment. Examples of these processes are given in Figure 7.22.

Chapter 8

Membranes and Shells



The two-dimensional structures described in the previous sections were grown from hard materials whose kinematics was either prescribed or derived from the interaction with a soft organism. We now turn our attention to two-dimensional biological structures that are soft and best described as either morphoelastic membranes, plates, or shells. We start with a discussion of the elastic response of axisymmetric membranes and shells.

Our main motivating example will be the description of tip growth in filamentous cells such as fungi, actinomycetes, root hairs, and pollen tubes introduced in Section 1.1.1. Although there are many fundamental differences in the structure, life cycles, size, and function of these diverse organisms, the overall pattern of growth appears to share certain fundamental features; most notably, in these systems the hyphal growth is apical, i.e., the growth and incorporation of new cell wall material is concentrated at the tip of the cell. The fact that filamentary cells grow with this general morphology reflects an interplay between the anisotropy of the cell wall, the mechanical stresses, and the growth process. We will explore this inhomogeneous morphoelastic process in Section 9.2.

Since we are interested in the fundamental problem of tip growth we further focus our attention on the case where the surface remains axisymmetric at all times. This constraint limits the possible deformations to those that respect this particular symmetry, but it allows for the derivation of a full mechanical theory based on simple fundamental principles.

Before proceeding, we comment on various terminology. Depending on the field of study, the word “membrane” has different meanings. In biology, it is used to characterize a thin layer separating two compartments with no precise physical properties. It is sometimes equivalent to the term used in biophysics and sometimes equivalent to the term used in mechanics. In mechanics, precise definitions are available: A *membrane* is a two-dimensional elastic structure in a three-dimensional space that can resist tension but not compression or bending. A *plate* is an initially flat structure that resists bending, tension, and compression. It can be unshearable or shearable depending on the theory. A *shell* is an initially curved surface that resists bending, tension, and compression. It can be unshearable or shearable. In biophysics, a lipid bilayer is also called a membrane, but it is modeled as a *fluid membrane*, that is, a shearless structure that is fluid along the surface. Some biophysical membranes can resist bending and stretching, whereas others support stretching but not bending. Technically, fluid membranes are elastic shells or elastic membranes with a special material symmetry group. They can be derived from standard rational mechanics arguments within the theory of *one-director Cosserat surfaces* or a *Kirchhoff–Love shell* with constraints [278, 279, 1188].

8.1 Elastic Membranes

We begin by considering an extensible axisymmetric elastic membrane filled with an incompressible viscous fluid under pressure, whilst neglecting shear and bending resistance. This type of formulation has been used successfully to describe the shape of red blood cells and other biomembranes [1135, 1174] and we adapt it to include the effects of pressure induced stretch, growth, bending, and geometry-dependent elastic properties of both membranes and shells based on the derivations in [353, 479, 480, 1340]. First, we give a full derivation of the equations describing an elastic membrane under loads from basic principles. As usual in the derivation of an elastic theory, we proceed in three key steps by considering kinematics, mechanics, and constitutive laws.

8.1.1 Kinematics

As shown in Figure 8.1, the axisymmetric membrane surface S is defined by revolving a planar curve C around the z -axis. The planar curve C is parameterized by the material coordinate S counted from the intersection $\mathcal{O}$ of the surface with the z -axis. At any given time t , the *current configuration* is characterized by the curve C :

$$\mathbf{r}(S, t) = r(S, t)\mathbf{e}_r + z(S, t)\mathbf{e}_z, \quad S \in [0, L], \quad (8.1)$$

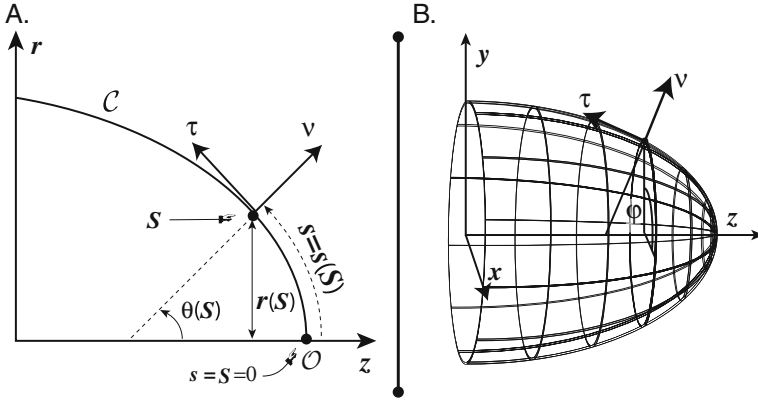


Figure 8.1 Basic membrane and shell geometry. A material point S is measured by its arc length, $s(S)$ from the apex of the shell and its position $r(S)$ on a curve $\mathcal{C}$. Here, ν and τ denote the normal and tangent vectors at that point. The angle $\theta(S)$ is the angle between the normal direction and the z -axis. The surface is assumed to be axisymmetric with an azimuthal angle φ .

where the vectors $\mathbf{e}_r$ and $\mathbf{e}_z$ are the canonical basis vectors in the $r - z$ plane. It is convenient to parameterize the curve $\mathcal{C}$ by the pair of functions $(r(S, t), \theta(S, t))$ where $\theta(S, t)$ is the angle between the normal to $\mathcal{C}$ at S and the z -axis. The arc length, measured from $\mathcal{O}$, is $s = s(S, t)$. Before an elastic deformation and keeping with the general formalism used so far, the material parameter S is identified with the arc length in a stress-free configuration, so that $S = s(S, 0)$. The initial stress-free shell configuration is referred to as the *reference configuration* and its shape is fully specified by $R(s) = r(S, 0)$.

The geometric variables satisfy the equations

$$\frac{\partial r}{\partial s} = \cos \theta, \quad \frac{\partial z}{\partial s} = -\sin \theta, \quad (8.2)$$

from which we define the local unit tangent, τ and normal vectors ν :

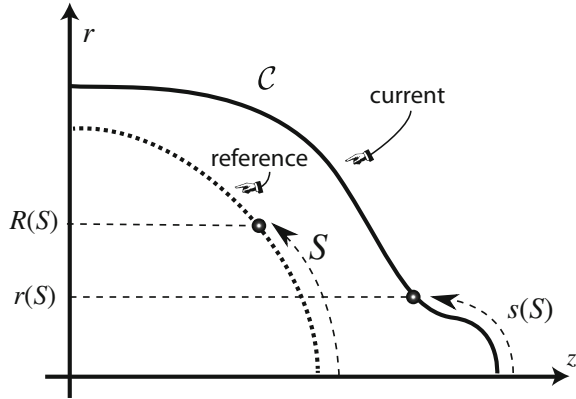
$$\tau = \cos \theta \mathbf{e}_r - \sin \theta \mathbf{e}_z, \quad (8.3)$$

$$\nu = \sin \theta \mathbf{e}_r + \cos \theta \mathbf{e}_z. \quad (8.4)$$

Two other important measures of the geometry of the surface are the principal curvatures [169, 496] which are given by

$$\kappa_s = \frac{\partial \theta}{\partial s}, \quad \kappa_\varphi = \frac{\sin \theta}{r}. \quad (8.5)$$

Figure 8.2 Deformation of an axisymmetric surface. The initial configuration (dashed) parameterized by $R(S)$ is mapped to the current configuration (solid) parameterized by $r(S)$. A material point in the reference configuration with material coordinate S is mapped to a new point with arc length $s(S)$. The radial stretch is the ratio $\alpha_\varphi = r/R$.



Next, we consider axisymmetric deformations of the surface from the reference to the current configuration as shown in Figure 8.2. These deformations are specified by two variables, the radial stretch and the tangential stretch. The *radial stretch*

$$\alpha_\varphi(S, t) = \frac{r(S, t)}{R(S)}, \quad (8.6)$$

at a given material point is the ratio of the new radius r to the original radius R at that material point S . The *tangential stretch*, or just *stretch* for short,

$$\alpha_s(S, t) = \frac{\partial s(S, t)}{\partial S}, \quad (8.7)$$

is the amount of stretching of the body coordinates with respect to the reference arc length. These two stretches (α_φ , α_s) completely define the deformation of the initial axisymmetric surface.

A physical membrane also has thickness. During deformation, the thickness varies from its initial value H to its current value $h(S, t)$ and has an associated *normal stretch*, $\alpha_n = h(S, t)/H$, measuring changes in the normal thickness of the shell. Depending on the constitutive assumptions, the change of thickness during deformation can take different forms. If we assume that the membrane is made out of an incompressible elastic material, α_n , is simply related to α_s and α_φ by the incompressibility condition $\alpha_s \alpha_\varphi \alpha_n = 1$. If, however, we model a lipid bilayer, the material cannot be modeled as a three-dimensional elastic material; a convenient choice to describe a *fluid membrane* [403] is to choose both $\alpha_n = 1$ and $\alpha_s \alpha_\varphi = 1$, denoting area incompressibility [545].

8.1.2 Mechanics

We now define the tensions acting on the membrane surface. Let t_s be the line tension on the surface along the tangent τ , in the direction of increasing arc length. The line tension t_s has the dimensions of a force per unit length. Similarly, we define t_φ as the line tension along the binormal vector $\beta = \nu \times \tau$, normal to τ in a plane tangent to S , and in the hoop direction. That is, the direction of increasing azimuthal angle φ in Figure 8.3. We consider an infinitesimal piece of this surface as seen in Figure 8.4 subject to an external body stress $\mathbf{f} = \tau_c \tau + P\nu$. The shear stress τ_c can be taken to represent the drag forces exerted by the surrounding medium on the membrane and the pressure P is the pressure difference across the membrane.

Next, we balance the total force acting over that surface element of area $r ds d\varphi$, that is,

$$[(t_s \tau r)|_{s+ds} - (t_s \tau r)|_s] d\varphi + [(t_\varphi \beta)|_{\varphi+d\varphi} - (t_\varphi \beta)|_\varphi] ds + \mathbf{f} r ds d\varphi = \mathbf{0}. \quad (8.8)$$

In the limit $ds \rightarrow 0$ and $d\varphi \rightarrow 0$, we obtain

$$\frac{\partial}{\partial s}(r t_s \tau) + \frac{\partial}{\partial \varphi}(t_\varphi \beta) + r \mathbf{f} = \mathbf{0}. \quad (8.9)$$

Using the fact that $\partial_s \tau = -\theta' \nu$ and $\partial_\varphi \beta = \tau \cos \theta + \nu \sin \theta$, we find three scalar equations

$$\frac{\partial t_\varphi}{\partial \varphi} = 0, \quad (8.10)$$

$$\theta' r t_s + t_\varphi \sin \theta - r P = 0, \quad (8.11)$$

$$\frac{\partial}{\partial s}(r t_s) - t_\varphi \cos \theta + r \tau_c = 0. \quad (8.12)$$

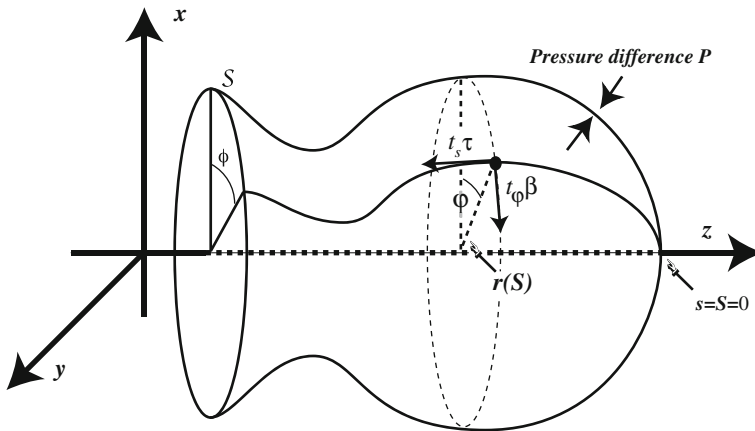


Figure 8.3 The surface S with the two principal tensions (t_s, t_φ) along the vectors τ and β .

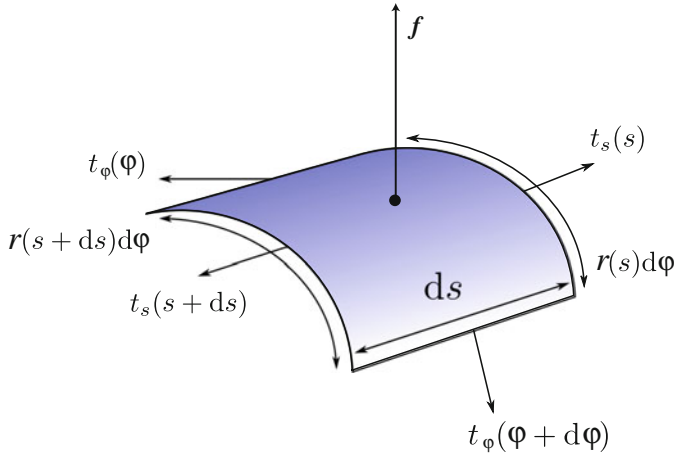


Figure 8.4 An infinitesimal surface element is subject to an external body force $\mathbf{f}$ as well as contact forces resulting from the rest of the surface.

The first equation expresses the fact that the force in the hoop direction remains constant along that direction as to maintain the axisymmetry. Using definition (8.5), the remaining two equations can be written as

$$P = \kappa_s t_s + \kappa_\varphi t_\varphi, \quad (8.13)$$

$$\frac{\partial(r t_s)}{\partial s} - t_\varphi \frac{\partial r}{\partial s} + r \tau_c = 0. \quad (8.14)$$

Equation (8.13) is a generalized version of the celebrated *Laplace's equation*, sometimes called *Young's equation* or *Young–Laplace's equation* in biophysics [1223]. It expresses the fundamental balance between the pressure across a surface, the curvatures, and the line tensions acting on a surface.

In many problems involving surface tension in liquids, we have $t_\varphi = t_s = \sigma$ [266]. In this case, Laplace's equations reduces simply to the traditional form

$$P = (\kappa_s + \kappa_\varphi) \sigma. \quad (8.15)$$

Furthermore, if the surface is locally spherical, $\kappa_s = \kappa_\varphi = 1/R$, and (8.15) specializes to $P = 2\sigma/R$.

We further investigate Equations (8.13–8.14) in the absence of shear stress. In the case of a constant pressure P we now show that there is a first integral, that is, a function of the variables that remains constant along the curve $\mathcal{C}$, given by [1038]

$$C = r^2 (2t_s \kappa_\varphi - P). \quad (8.16)$$

In particular, for all solutions $(r(s), \theta(s))$ crossing the z -axis, we have $C = 0$.

8.1.2.1 Derivation of the Constant

In order to derive the constant (8.16) it is convenient to collect together the governing equations in the form

$$P = k_s t_s + k_\varphi t_\varphi, \quad (8.17)$$

$$\frac{\partial(rt_s)}{\partial s} = t_\varphi \cos \theta, \quad (8.18)$$

$$\frac{\partial r}{\partial s} = \cos \theta, \quad (8.19)$$

where k_s , k_φ are given in (8.5). From (8.5) we easily see the purely geometric relationship

$$\frac{\partial(rk_\varphi)}{\partial s} = k_s \frac{\partial r}{\partial s}. \quad (8.20)$$

On multiplying both sides of (8.17) by $\partial r / \partial s$ and using (8.20) it follows that

$$t_s \frac{\partial(rk_\varphi)}{\partial s} + k_\varphi t_\varphi \frac{\partial r}{\partial s} = P \frac{\partial r}{\partial s}. \quad (8.21)$$

From (8.18) and (8.19) we observe that

$$\frac{\partial(rt_s)}{\partial s} = t_\varphi \cos \theta = t_\varphi \frac{\partial r}{\partial s}, \quad (8.22)$$

and hence

$$k_\varphi t_\varphi \frac{\partial r}{\partial s} = k_\varphi \frac{\partial(rt_s)}{\partial s}. \quad (8.23)$$

Equation (8.21) can now be written as

$$t_s \frac{\partial(rk_\varphi)}{\partial s} + k_\varphi \frac{\partial(rt_s)}{\partial s} = P \frac{\partial r}{\partial s}, \quad (8.24)$$

and on multiplying both sides by r this last relation can be re-expressed in the form

$$\frac{\partial(r^2 t_s k_\varphi)}{\partial s} = Pr \frac{\partial r}{\partial s}. \quad (8.25)$$

Integrating both sides with respect to s gives

$$r^2 t_s k_\varphi = \int Pr dr + \frac{C}{2}, \quad (8.26)$$

where C is an integration constant. Thus, for constant pressure $P = P_0$ we have

$$C = r^2(2t_s k_\varphi - P_0). \quad (8.27)$$

As noted, this first integral is particularly useful in problems where the pressure is constant and the axisymmetric surface intersects the z -axis.

8.1.3 Constitutive Laws

8.1.3.1 Linear Laws

We now relate stresses to strains by introducing a constitutive relationship that expresses the elastic response of the membrane under load. To start, we consider a simple law for isotropic incompressible membranes in small deformations and relate the components of the material strain tensor to the extension ratios [353, 1174]

$$e_s = \frac{1}{2}(\alpha_s^2 - 1), \quad (8.28)$$

$$e_\varphi = \frac{1}{2}(\alpha_\varphi^2 - 1). \quad (8.29)$$

For small deformations, where both e_s and e_φ are small, a first order expansion of the general nonlinear stress–strain relation for isotropic membrane (presented in the next section) leads to the simplified law

$$t_s = A(e_{ss} + 2e_{\varphi\varphi}), \quad (8.30)$$

$$t_\varphi = A(e_{\varphi\varphi} + 2e_{ss}), \quad (8.31)$$

where $A = EH/3$ characterizes the elastic property of the membrane, with E the Young's modulus and H the membrane thickness. Note that A can be a function of the material parameter S . In terms of the extension ratios the stress–strain relation can be written as:

$$t_s = A(2\alpha_s^2 + \alpha_\varphi^2 - 3), \quad (8.32)$$

$$t_\varphi = A(\alpha_s^2 + 2\alpha_\varphi^2 - 3). \quad (8.33)$$

8.1.4 A Complete Set of Equations

Using the linear constitutive law and the definition for the curvatures (8.5), the equations for mechanical equilibrium, in the absence of shear stress, reduce to a system

for the membrane variables for a given initial profile $R = R(S)$

$$\frac{\partial s}{\partial S} = \alpha_s, \quad (8.34)$$

$$\frac{\partial z}{\partial S} = -\alpha_s \sin \theta, \quad (8.35)$$

$$\frac{\partial r}{\partial S} = \alpha_s \cos \theta, \quad (8.36)$$

$$\frac{\partial \theta}{\partial S} = \frac{\alpha_s [\sin(\theta) (r^2 + R^2(S)(2\alpha_s^2 - 3)) - prR^2(S)]}{r[2r^2 - 3R(S)^2 + \alpha_s^2 R^2(S)]}, \quad (8.37)$$

where we have introduced $p = P/A$ as the inverse of a characteristic length that measures the relative effect of the pressure with respect to the stiffness modulus A .

This system is closed by expressing α_s as a function of the other variables through the first integral (8.16),

$$C = 2Ar \sin(\theta) \left(\alpha_s^2 + 2 \frac{r^2}{R^2(S)} - 3 \right) - r^2 P. \quad (8.38)$$

If we further assume that there is a point on the membrane such that $r = 0$, we have $C = 0$, which leads to

$$\alpha_s^2 = 3 - 2 \frac{r^2}{R^2(S)} + p \frac{r}{2 \sin \theta}. \quad (8.39)$$

8.1.4.1 Simple Examples

As a first example, it is straightforward to verify that the inflation of a sphere of radius R_0 into another sphere of radius R_1 by a pressure p , is a solution of these equations. We do this by choosing $R = R_0 \sin(S/R_0)$, $\theta = S/R_0$, $r = R_1 \sin(S/R_0)$, which leads to

$$\begin{aligned} R_1 &= \frac{R_0}{12} \left(pR_0 + \sqrt{p^2 R_0^2 + 144} \right) \\ &= R_0 \left(1 + \frac{pR_0}{12} + \frac{p^2 R_0^2}{288} + \mathcal{O}(p^3 R_0^3) \right). \end{aligned} \quad (8.40)$$

As a second example, we consider an infinite cylinder whose axis coincides with the z -axis. In this case, we have $\theta = \pi/2$, $\alpha_s = 1$, $R = R_0$, and $r = R_1$. In this case, we have

$$R_1 = \frac{1}{2} \left(\sqrt{p^2 R_0^4 + 4R_0^2} + pR_0^2 \right) \quad (8.41)$$

$$= R_0 \left(1 + \frac{pR_0}{2} + \frac{p^2 R_0^2}{8} + \mathcal{O}(p^3 R_0^3) \right). \quad (8.42)$$

In tip growth, the shape of a tip can be approximated as a spherical cap connected to a long cylindrical support. The two simple solutions for the sphere and cylinder show that in order to have a membrane that connects a cylinder to a sphere, there must be a steep change in the parameter p which, to a first approximation, needs to decrease by a factor six from the sphere to the cylinder. Hence, there must be a corresponding increase in the elastic parameter A . This simple analysis demonstrates that in order to have a tip shape supported by an elastic membrane, there must be a significant change of stiffness close to the tip.

8.1.4.2 Boundary Conditions

Depending on the specific problem, different sets of boundary conditions can be imposed. If the pressure remains constant and the surface crosses the z -axis, (8.39) can be used in the system (8.34–8.37). These equations form a system of four equations for the four unknowns (r, z, θ, s) . Choosing $S = 0$ at one intersection with the axis, we always have $s(0) = 0$. Without loss of generality, we can fix the translation along the axis by setting $z(L) = z_0$ where $S = L$ denotes a reference material point taken as the end point of the membrane, and z_0 is arbitrary. Then, depending on the nature of the attachment we can set either $r(L) = R_L$ (fixed radius at the boundary) or $\theta(L) = \theta_L$ (fixed angle at the boundary), or any combination of these two conditions. There remains one condition to be fixed at $\sigma = 0$. The condition is simply $r(0) = 0$, but since $R(0) = 0$, Equation (8.37) has a geometric removable singularity that leads to computational difficulties. This problem is easily dealt with by considering the boundary conditions at $\sigma = \epsilon$ where $\epsilon \ll 1$ and expanding all variables in power of ϵ . The lowest nonzero contribution will dictate the choice of the last boundary condition.

Finally, if we fix the volume to be a constant rather than the pressure, then the pressure becomes a Lagrange multiplier that enforces the volume constraint. Computationally, a solution with a given volume can be obtained starting from a guess pressure and varying the pressure up to the desired volume.

8.1.5 Application: The Shape of Sea Urchins

It was D’Arcy Thompson who first realized the similarity between the shape of urchins and the shape of sessile drops of liquid sitting on a table [1230, p. 944]: “*The full mathematical investigation of the forms of a drop is not easy, and we can scarcely hope that the systematic study of the Echinodermata will ever be conducted by methods based on Laplace’s differential equation; but we have little difficulty in seeing that the various forms represented in a series of sea urchin shells are no other than those which we may easily and perfectly imitate in drops.*”

The problem of determining the shape of a sessile liquid drop is a classic problem going back to Laplace [65, 771] and for which many details and properties have

Figure 8.5 A sessile water drop on a substrate.



been established [363, 364, 1311]. The shape, shown in Figure 8.5 is the result of a mechanical balance between a pressure gradient induced by gravity and surface tension. Similarly, it has been argued that the shape of an urchin is the result of a balance of forces generated by the *coelomic pressure* (the internal pressure that invertebrates develop in their body cavity), the *podia* (the tubed feet), and self-weight.

The skeleton of sea urchins, also known as a *test*, is made of a number of calcite plates that are loosely attached together at their sutures through collagen threads. During growth, new plates are inserted at the apex and each plate expands by a number of accretion, shrinkage, and fitting processes at the edge not dissimilar to the process described in the previous chapter for seashells [328, 1361]. It has been argued that despite their rigid shell-like structure, the great number of plates and their loose attachment during growth provide a flexibility that allows them to deform and relax through the action of competing forces of gravity and pressure, such that it is best described by the action of forces on an elastic membrane [668].

Therefore, we follow here the original idea of D'Arcy Thompson as well as the models of Barons [60] and Ellers [328, 329] to determine the basic shape of sea urchins as an application of the axisymmetric elastic membrane model. The basic assumption in this model is that growth takes place so that the line tension t_s and t_φ are equal at all points as to maximize strength. In that case, this problem is exactly the problem first described by Timoshenko of determining the optimal shape of a water tank [1233, p. 385]. Since the line tensions are assumed to be equal, it follows directly from (8.37) that t_s is constant at all points on the surface. Therefore, to compute such a shape we assume that the urchin sits flat so that the pressure increases linearly with gravity $P = \rho gz$. We are then left with (8.37) and (8.2) which can be written

$$\theta' = az - \frac{\sin \theta}{r}, \quad (8.43)$$

$$r' = \cos \theta, \quad (8.44)$$

$$z' = \sin \theta, \quad (8.45)$$

where we have flipped the z -axis so that increasing z corresponds to increasing pressure. The parameter $a = \rho g/t_s$ is the inverse of the square of the *capillary length*, the characteristic length at which both tension forces acting on the membrane and gravitational forces are of the same magnitude.

The boundary condition at the apex are $\theta(0) = 0$, $r(0) = 0$ and $z(0) = 2b$ where the length $2b$ sets the pressure at the apex. Without loss of generality, we set $b = 1$ and the urchin shapes are defined by a single parameter a up to a dilation.

To solve this system numerically, we consider a first order expansion of the boundary conditions around $s = 0$ so that

$$\theta(\epsilon) = a\epsilon, \quad r(\epsilon) = \epsilon, \quad z(\epsilon) = 2, \quad \epsilon \ll 1. \quad (8.46)$$

Equations (8.43–8.45) with conditions (8.46) reduces to a simple initial value problem that can be integrated up to the point $S = L$ at which $\theta(L) = \pi$, assuming that, unlike a drop, the angle between the flat interface and the curve is exactly π .

As expected, for large values a , the shape tends to become spherical and, as a decreases it becomes increasingly flat, since the extent to which gravity plays a role decreases with respect to the size of the urchin. This computation leads to a one-dimensional *morphospace*. A morphospace is a space of shapes parameterized by several parameters that can be matched to actual shapes found in nature. In our case, we have a single parameter a , and the morphospace reduces to a morpholine. The match against various species is actually surprisingly good considering that we have a one-parameter family and that the assumptions are only vaguely connected to biological reality. An example of such a fit is shown in Figure 8.6.

The key assumption on the equality of the line tensions that gives rise to this drop-like solution is particularly difficult to justify as these shapes cannot be obtained by starting from a spherical elastic membrane filled with water, in contradiction to D'Arcy Thompson's claim. Indeed, if the tensions are equal, they are constant and so are the stretches. In particular α_φ is constant which implies that $r(S) = \alpha_s R(S)$. Therefore, the shape obtained must be realized from a stress-free membrane with

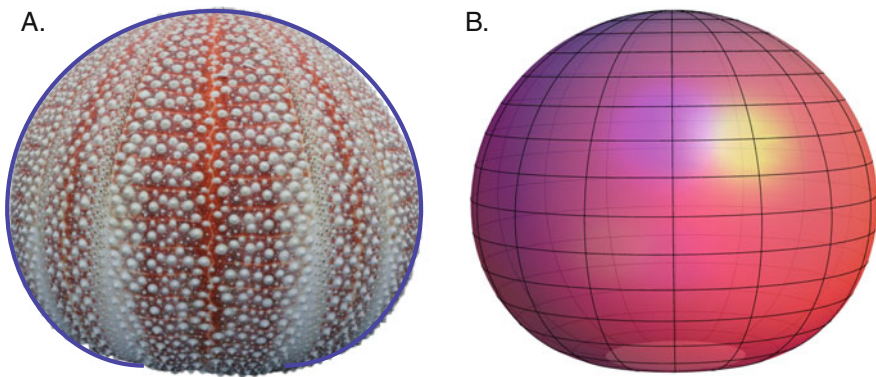


Figure 8.6 A. An urchin test together with a fit obtained for $a = 3.98$. B. The full shape obtained by integration of the model.

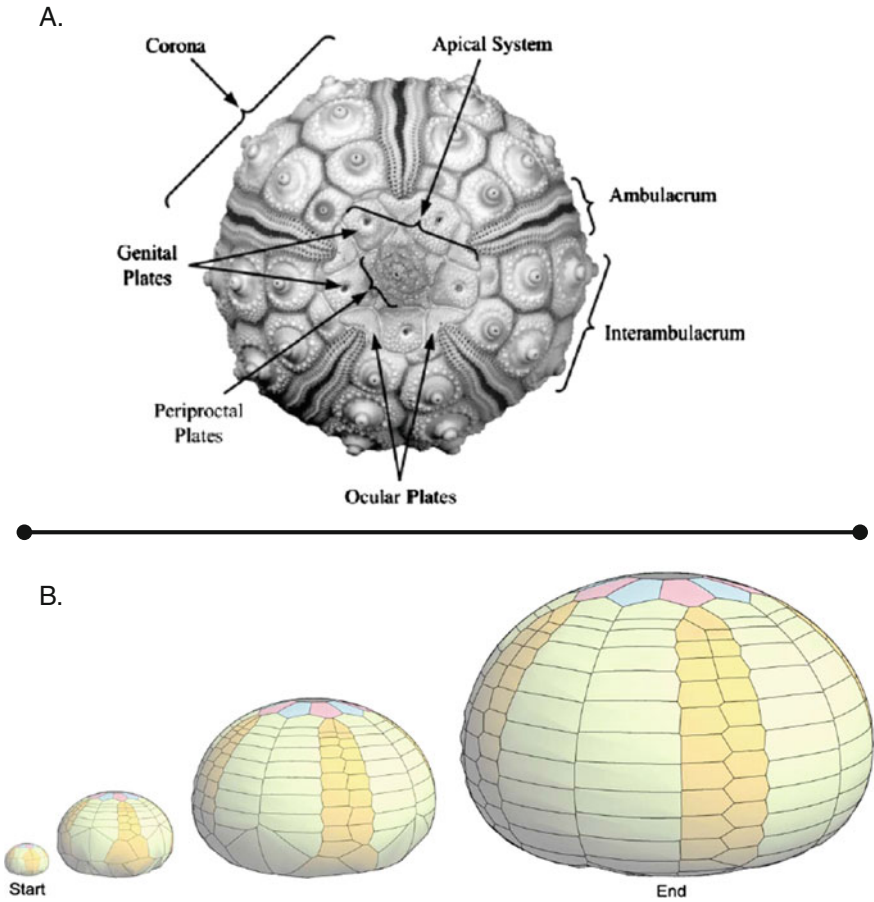


Figure 8.7 A computational model for a sea-urchin taking into account the creation, accretion, and fitting of plates. From Zachos [1361].

the same shape. Therefore, if the drop solution is indeed a valid representation of the skeleton shape in urchins, there must be both a relaxation process that constantly evolves the reference shape to the current shape, and a growth process that balances the deposition of new material in order to equilibrate the line tensions. How line tensions are being sensed and how the process is maintained and controlled during the growth of urchins remains a mystery, but one that could be partially elucidated by looking at plausible models of growth.

Finally, we mention an interesting computational model by Zachos [1361] who looked at the creation and evolution of plates developing from the apex. Some of the model results are shown in Figure 8.7. Note, however, that there is no mechanics in this specific model and the drop-like shape is obtained by mapping a tessellated spherical solution to the drop solution shown above.

8.2 Nonlinearly Elastic Shells

Next, we consider axisymmetric shells, that is, elastic objects that can be represented by a surface, support bending, and have a non-flat unstressed shape. At the level of kinematics, there is no difference in the geometric description of the deformations. Therefore, we adopt the same notations and move directly to mechanics.

8.2.1 Mechanics

The equations for mechanical equilibrium, including bending moments can be obtained by balancing linear and angular momenta on a small surface element. Long and tedious force and couple balances that are better done in the privacy of one's office lead to a system of three equations [353, 695]

$$\frac{d(rq_s)}{ds} = rq_n - r(\kappa_s t_s + \kappa_\varphi t_\varphi), \quad (8.47)$$

$$\frac{d(rt_s)}{ds} = t_\varphi \cos \theta + r\kappa_s q_s - r\tau_s, \quad (8.48)$$

$$\frac{d(rm_s)}{ds} = m_\varphi \cos \theta - rq_s, \quad (8.49)$$

where t_s and t_φ are, respectively, the meridional and azimuthal stresses; m_s and m_φ are the bending moments; and q_s is the shear stress normal to the surface. In (8.47), which represents the balance of normal stresses, q_n represents the total *normal* stress exerted on the shell. If the problem is pressure driven then $q_n = P$, namely the pressure difference across the shell; and if it is a combination of pressure and active forces, represented by some function τ_n , then $q_n = P + \tau_n$. In (8.48), which represents the balance of tangential stresses, τ_s is the external tangential shear stress acting on the shell and will be used here to represent the friction between the deformed shell and its environment.

8.2.1.1 Constitutive Relationship

In order to close the system of mechanical and geometric, equations constitutive relations must be introduced. These are developed through the introduction of an elastic strain-energy density function W . Assuming material isotropy, it can be shown that such a strain-energy function, specified as energy per unit volume, can only depend on the stretches $(\alpha_s, \alpha_\varphi, \alpha_n)$. In Section 11.3, we will present a full theory of constitutive relationships. For our purpose here, it is sufficient to state that a convenient way of writing the dependence of the strain-energy density function is to introduce three strain functions, the so-called *strain invariants*:

$$I_1 = \alpha_s^2 + \alpha_\varphi^2 + \alpha_n^2, \quad (8.50)$$

$$I_2 = \alpha_s^2 \alpha_\varphi^2 + \alpha_s^2 \alpha_n^2 + \alpha_\varphi^2 \alpha_n^2, \quad (8.51)$$

$$I_3 = \alpha_s^2 \alpha_\varphi^2 \alpha_n^2. \quad (8.52)$$

Then, the strain-energy density function is

$$W = W(I_1, I_2, I_3), \quad (8.53)$$

Assuming that the shell is incompressible, we have

$$\alpha_n = \frac{1}{\alpha_s \alpha_\varphi}, \quad \frac{\partial W}{\partial I_3} = 0, \quad I_3 = 1. \quad (8.54)$$

Once a function W is given, the constitutive equations relating line tensions to stretches can be obtained by differentiation of W with respect to its invariants. In our case, the line tensions are given by the relations

$$t_s = 2H\alpha_n(\alpha_s^2 - \alpha_n^2) \left(\frac{\partial W}{\partial I_1} + \alpha_\varphi^2 \frac{\partial W}{\partial I_2} \right), \quad (8.55)$$

$$t_\varphi = 2H\alpha_n(\alpha_\varphi^2 - \alpha_n^2) \left(\frac{\partial W}{\partial I_1} + \alpha_s^2 \frac{\partial W}{\partial I_2} \right), \quad (8.56)$$

where H is the shell thickness, and the factor $H\alpha_n$ is the wall thickness in the current configuration [1087]. Using these formulas we note that

$$t_s - t_\varphi = 2H\alpha_n(\alpha_s^2 - \alpha_\varphi^2) \left(\frac{\partial W}{\partial I_1} + \alpha_n^2 \frac{\partial W}{\partial I_2} \right). \quad (8.57)$$

The choice of W depends on the problem at hand. A popular choice for elastomers is the *Mooney–Rivlin model*,

$$W_{\text{mr}} = C_1(I_1 - 3) + C_2(I_2 - 3), \quad (8.58)$$

where C_1 and C_2 are certain elastic moduli. When $C_2 = 0$, (8.58) reduces to the so-called *neo-Hookean model* $W_{\text{nh}} = C_1(I_1 - 3)$ and, for small deformations, C_1 is related to the Young's modulus, E , by $E = 6C_1$. We note that despite its linearity in the invariants, the Mooney–Rivlin potential is still capable of describing finite deformations and is a highly nonlinear function of the stretches.

A variety of nonlinear material responses can be captured by considering other functional forms of W (See Section 11.7.2, e.g., for soft tissue the *Fung model* [408],

$$W_{\text{fu}} = \frac{C_1}{\gamma} (e^{\gamma(I_1 - 3)} - 1), \quad (8.59)$$

is often used. The parameter γ is used to describe *strain-stiffening*, that is, the increase of stiffness as the deformation increases. In the limit $\gamma \rightarrow 0$, the Fung model reduces to the Neo-Hookean model W_{nh} . Given any model, we write the constitutive relationships (8.55–8.56) in the form

$$t_s = Af_s(\alpha_s, \alpha_\varphi), \quad t_\varphi = Af_\varphi(\alpha_s, \alpha_\varphi), \quad (8.60)$$

where f_s, f_φ are dimensionless functions and A provides the dimensional factor appropriate for the scaling of the equilibrium equations. For the neo-Hookean and Mooney–Rivlin models, $A = 2C_1H = EH/3$.

In the limit of small deformations, the neo-Hookean, Fung, and Mooney–Rivlin models, all give the linear constitutive relations introduced in Section 8.1.3.1. Finally, we need to specify constitutive relationships for the bending moments. The bending moments are assumed to be isotropic and proportional to the change in the surface's mean curvature, so that we have

$$m_\varphi = m_s = B(\kappa_s + \kappa_\varphi - 2K_0), \quad (8.61)$$

where K_0 is the initial mean curvature and B is the bending modulus [353, 712].

8.2.1.2 The Complete Shell Equations and the Membrane Limit

The geometric and mechanical equations can be combined to give a closed system. It is convenient to express all the derivatives in terms of the material coordinate, S , leading to

$$\frac{dz}{dS} = -\alpha_s \sin(\theta), \quad (8.62)$$

$$\frac{dr}{dS} = \alpha_s \cos(\theta), \quad (8.63)$$

$$\frac{d\theta}{dS} = \alpha_s \kappa_s, \quad (8.64)$$

$$\frac{d\kappa_s}{dS} = \alpha_s \left[\frac{\cos \theta}{r} \left(\frac{\sin \theta}{r} - \kappa_s \right) + \frac{q_s}{B} \right], \quad (8.65)$$

$$\frac{dt_s}{ds} = \alpha_s A \left[\frac{\cos \theta}{r} (f_\varphi - f_s) + \kappa_s \frac{q_s}{A} - \frac{\tau_s}{A} \right], \quad (8.66)$$

$$\frac{dq_s}{dS} = \alpha_s A \left[\frac{q_n}{A} - \kappa_s f_s - \frac{\sin \theta}{r} f_\varphi - \frac{q_s}{A} \frac{\cos \theta}{r} \right], \quad (8.67)$$

where (8.65) is obtained from (8.49) using the constitutive relation (8.61) and (8.5) is used to express κ_φ in terms of r and θ . In (8.66) and (8.67), t_s and t_φ are expressed in terms of α_s and α_φ through the scaled constitutive relations (8.60–8.60), and Equation (8.66) is converted into a differential equation for α_s by eliminating α_φ through the relation $\alpha_\varphi = r/R$.

The six ordinary differential equations (8.62–8.67) together with the relationships (8.60–8.61) and $\alpha_\varphi = r/R$ form a closed system for the variables $(z, r, \theta, \kappa_s, \alpha_s, q_s)$ that can be solved for a given initial profile $R(S)$, elastic parameters A, B , prescribed normal and tangential stresses q_n and τ_n , and appropriate boundary conditions.

When bending moments are neglected, the shell no longer supports an out-of-plane shear force, which implies $q_s = 0$. Then, (8.67) reduces to

$$q_n = A (\kappa_s f_s + \kappa_\varphi f_\varphi) = \kappa_s t_s + \kappa_\varphi t_\varphi, \quad (8.68)$$

and we recover Laplace's law as seen before. The system of shell equations then simplifies to the general form of the membrane equation in large deformations, namely

$$\frac{dz}{dS} = -\alpha_s \sin \theta, \quad (8.69)$$

$$\frac{dr}{dS} = \alpha_s \cos \theta, \quad (8.70)$$

$$\frac{d\theta}{dS} = \alpha_s \kappa_s, \quad (8.71)$$

$$\frac{d\kappa_s}{dS} = \alpha_s \left[\frac{\cos \theta}{r} \left(\frac{\sin \theta}{r} - \kappa_s \right) \right], \quad (8.72)$$

$$\frac{dt_s}{ds} = \alpha_s A \left[\frac{\cos \theta}{r} (f_\varphi - f_s) - \frac{\tau_s}{A} \right]. \quad (8.73)$$

As before, using the constitutive relationship $t_s = A f_s(\alpha_s, r/R)$ results in a closed system of five equations for $(z, r, \theta, \kappa_s, \alpha_s)$ with initial profile $R(s)$, tangential shear τ_s , and boundary values.

8.2.2 Scalings

It is useful to introduce the following dimensionless number for the problem:

$$\xi = \frac{P_{\text{eff}} w}{3A}, \quad (8.74)$$

where w is a characteristic length, P_{eff} is a measure of the normal force per unit area acting on the walls and A characterizes the wall's elastic properties. The number ξ

gives a measure of the magnitude of the deformation: Shells under different normal loads and with different elastic properties will experience the same magnitude of deformation from their initial unstressed state when measured in terms of their length w . High values of ξ , representing either a soft material or a high pressure, result in large elastic deformations, whereas low values of ξ , corresponding to either a rigid material or low pressure, result in small elastic deformations. For a neo-Hookean material we can relate A to the Young's modulus $E = 3A/H$, where H is the thickness of the shell or membrane, so that

$$\xi = \frac{P_{\text{eff}} w}{HE}. \quad (8.75)$$

To set the scales, estimates of the elastic and bending moduli are required. An order of magnitude estimate can be obtained from the Laplace's law for a spherical membrane under pressure. For a pressure difference ΔP across the membrane wall of thickness H , the sphere radius R , and membrane stresses T , we have

$$\Delta P = 2 \frac{HT}{R}, \quad (8.76)$$

and, to a first approximation, these stresses scale as $T \sim E$, where E is the membrane's elastic modulus.

8.2.3 Application: The Rice Blast Fungus

8.2.3.1 Background

The fungus *Magnaporthe grisea*, commonly referred to as the rice blast fungus, is a pathogen that attacks the rice leaves. The fungus attaches to the rice leaf and forms a dome-shaped structure, the *appressorium*, in which enormous turgor pressures are generated and used to blast a penetration peg through the rice cell walls and infect the plant. A cartoon of the overall process is given in Figure 8.8. The process is as follows: A *conidium*, i.e. a small spore, lands on the rice leaf surface. Once attached, a germ tube grows out of the conidium, hooks into the surface of the rice leaf, and begins to form an appressorium. The germ tube is eventually shut off from the appressorium leaving the latter as a separate, independent unit. The mechanics of the free standing appressorium and how it manages to develop sufficient pressures to blast through the leaf is the subject of our analysis.

The appressorium, shown in Figure 8.9, adheres to the plant surface by means of a highly potent adhesive in a ring around its base. The inner region of contact between the appressorium and leaf surface lacks any obvious appressorial cell wall structure.

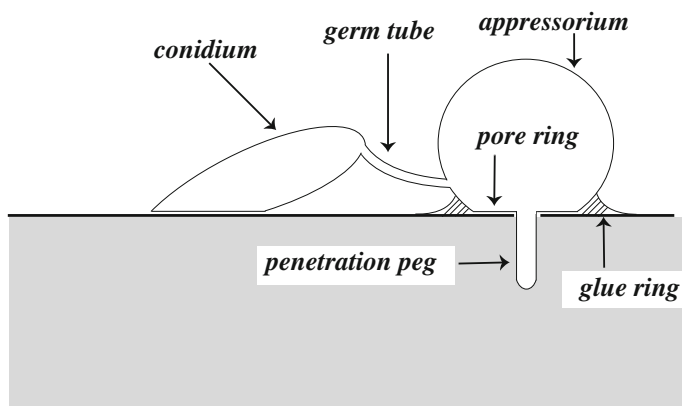


Figure 8.8 Pictorial representation of the development of the rice blast fungus.

From the available electron micrographs the overall appressorial wall thickness is of the order of $0.1\ \mu\text{m}$ as illustrated in Figure 8.9. Once firmly attached, a melanin layer about $100\ \text{nm}$ thick develops within the appressorium. This dark melanin layer allows only water molecules to permeate the wall, and on interaction with an internal glycerol concentration of approximately $3.2\ \text{M}$ [673], enormous internal pressures of

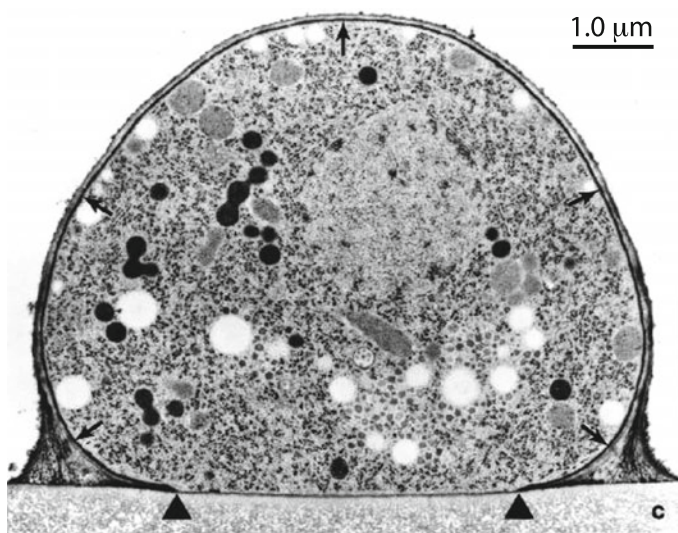


Figure 8.9 A typical wild-type appressorial structure prior to peg penetration [625]. The two arrowheads at the base of the appressorium indicate the range of the appressorial pore. The dark inner circle, indicated by the small arrows, is the melanin layer. In this image the appressorium is sitting on a cellophane substrate.

the order of 3–5 atmospheres (0.3–0.5 MPa) can develop in the appressorium [900].

After melanization, at least a threefold increase in turgor pressure occurs which may reach up to 80 atmospheres (8 MPa) [624]. Interestingly, despite the large increase in pressure, there does not appear to be any significant change in the size of the appressorium. After a period ranging from tens of hours to a few days, during which time turgor pressure builds up, a penetration peg is blasted through the surface of the rice leaf [718]. The forces involved are so great that, as demonstrated in laboratory experiments [623], the peg can penetrate thin sheets of mylar. Estimates for the forces involved can be found in [481]. Once invasion takes place, a network of hyphae develop, then break through the leaf surface depositing new conidia and the life cycle is perpetuated.

8.2.3.2 A Model

We model the appressorium as an axisymmetric elastic shell with basic geometry shown in Figure 8.10. The characteristic length scale $w \approx 3 \mu\text{m}$ is chosen to be that of the appressorial radius. We assume that the appressorium is glued in a small

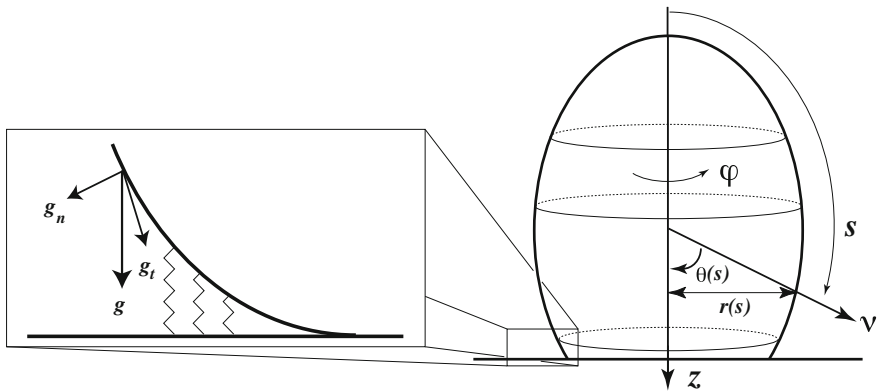


Figure 8.10 Basic geometry of the appressorium. The origin of the z -axis is set at the top of the appressorium. The arc length, s , to a given material point is measured from the top of the shell, $r(s)$ is the radial distance from the vertical axis to that point, and ν denotes the normal direction. The shell is taken to be axisymmetric where φ is the azimuthal angle. The glue is modeled as a downward, Hookean force connecting the shell to the leaf surface. The glueing force $\mathbf{g}$ is assumed proportional to the thickness of the glue at each point and is resolved into both normal, g_n , and tangential, g_s , components.

region close to the surface through a linear foundation between the shell and the leaf surface, and proportional to the glue layer thickness at each point. The glueing force is expressed as

$$\mathbf{g} = -\mu z \mathbf{e}_z, \quad (8.77)$$

where, μ is the foundation stiffness, z is the vertical thickness of the glue layer at each point, and $\mathbf{e}_z$ is the vertical unit vector. The glueing force is resolved into normal, g_n , and tangential, g_s , components. The net effect of g_n is to increase the shell pressure in the glueing region. This effect is taken into account by identifying g_n with τ_n , while g_s plays the role of τ_s in Equation (8.66). The extent of the glueing region is characterized by a parameter η representing this quantity in terms of a percentage of the total arc length from the base of the appressorium to its top. The beginning of the glue ring is taken to coincide with the initial point in the numerical boundary-value problem (in effect corresponding to the edge of the appressorial pore). Therefore, if L is the initial arc length of the profile and in the absence of other external stress, we can identify

$$(\tau_s, \tau_n) = \begin{cases} (g_s, g_n) & \text{for } 0 \leq \sigma \leq \eta L, \\ 0 & \text{otherwise.} \end{cases} \quad (8.78)$$

To estimate the parameters, we note that a typical radius of a microscopic spherical shell is about $3 \mu\text{m}$, and the recorded pressure is $P \approx 1 - 8 \text{ MPa}$ with a wall thickness of $h \approx 0.1 \mu\text{m}$. The Young's modulus E is of the order of magnitude

$$E \approx 10 - 100 \text{ MPa},$$

which is consistent with that of many other biological materials shown in the elastic moduli atlases of Ashby *et al.* [41]. We also note that this estimate is based on a linear constitutive relationship, so if the radius stays approximately constant under an increase in turgor pressure, the corresponding estimate of the elastic modulus increases proportionately. Thus, if the turgor pressure increases fivefold and the radius is, to a first approximation, unchanged, then the elastic modulus of the wall could be considered to have increased fivefold. This change of apparent stiffness can be explained by assuming that the wall material has a nonlinear stress-stiffening response. For instance, this behavior is compatible with the Fung model with a large parameter γ .

Elastic shell theory [761] also tells us that, within the framework of linear elasticity theory, the bending modulus for a thin sheet is given by the relation

$$B = \frac{EH^3}{12(1 - \nu^2)}, \quad (8.79)$$

where ν is the Poisson's ratio. Although not typically known for many cellular walls, we can assume $\nu = 1/2$, i.e., an incompressible material. For the same example, this leads to the estimate

$$B \approx 10 - 100 \times 10^{-13} \text{ Nm.}$$

Clearly, bending effects will only be significant if the cell wall exhibits regions of very high curvature. These types of estimates for E and B have been used by Boudaoud [114] to analyze morphological scaling laws for a large class of microorganisms. They have been used to distinguish families that are either tension dominated, where E is the significant parameter, or bending dominated, where B is the significant parameter.

8.2.3.3 Analysis

A detailed analysis of the effect of the different parameters of the system was performed in [1241] where it was shown that for regular pressure levels after melanization, but well before the occurrence of peg penetration, a simple neo-Hookean model captures correctly the shape of the appressorium, as shown in Figure 8.11.

Of particular interest is the persistence of the shape after melanization and large pressure increase. Within a neo-Hookean model, a large increase in pressure implies a large change in shape which is not observed experimentally. This observation suggests that a Mooney–Rivlin material is not suitable to model the increased rigidity under high stresses. However, if we use a stress-stiffening model such as the Fung

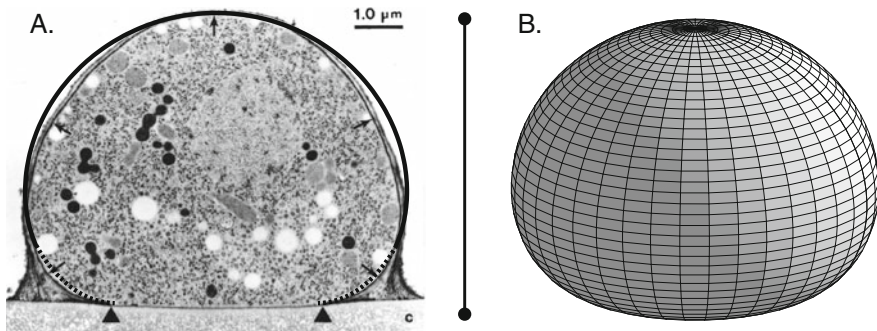


Figure 8.11 Computed appressorial shape for a neo-Hookean model (heavy line). The dashed line represents the glued portion of the appressorium. Parameters: $\xi = 1$, $\mu = 3$, $\eta = 0.2$, $B = 0.1$. The plot in B. is the 3-dimensional version of the numerical solution for the same profile shown in A.

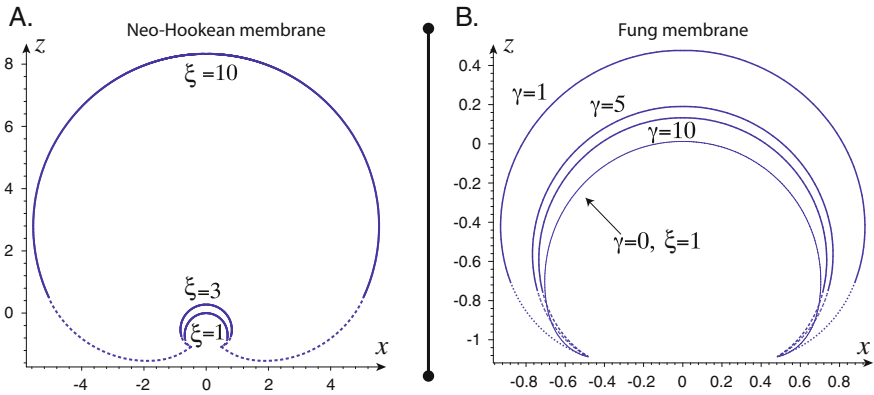


Figure 8.12 Comparison of pressure increase. A. A neo-Hookean model shows a large increase in radius when the pressure is raised from $\xi = 1$ to $\xi = 10$. B. For a Fung model, the same increase of pressure $\xi = 10$ for all curves except the inner one leads to little change in the appressorial shape when the Fung exponent γ is large enough. Parameters: $\xi = 1$, $\mu = 3$, $\eta = 0.25$, $B = 0.1$, all length units scaled to the original width before pressurization.

model (8.59), this effect is well captured as shown in Figure 8.12. This process clearly establishes the importance of both nonlinearity and large deformations theory to model significant changes in stress even at the scale of microscopic organisms.

Chapter 9

Growing Membranes



In the previous chapter we gave a theory of axisymmetric elastic shells and membranes. Biological membranes have the additional ability to change their internal configuration to grow and remodel. Since we are considering biological membranes, we are mostly interested in systems in which the membrane is under pressure. At the mechanical level when an elastic shell in its *reference configuration* is pressurized it will expand until a new stress equilibrium is achieved in its *current configuration*. During the course of this deformation the initially uniformly distributed material points will become redistributed, typically separated under expansion, as a manifestation of the new strained configuration. Furthermore, the shell expansion leads to a reduction in the shell wall thickness—although this may not be uniform around the shell. Once equilibrium has been achieved no further expansion will occur unless there is a further increase in pressure, or the stresses in the shell are somehow relieved. Through a number of mechanisms, such as addition of material, unfurling of membranes, contractile phenomena, remodeling of fibers and so on, a biological shell may further evolve. Due to this internal reconfiguration, if loads are removed, the shell will retract to a shape that is different from the reference configuration. The evolution of this new *virtual reference configuration* characterizes the growth and remodeling of the biological shell.

9.1 Morphoelastic Membranes

At the mathematical level, the process of growth is achieved by considering an evolving reference configuration parameterized by a slow time t . At any given time, the current configuration is obtained by loading the reference configuration with the pressure P and computing the resulting shape for the given boundary conditions. The problem is then to describe the evolution of this reference configuration.

Following the discussion in the one-dimensional context of Sections 4.4 and 6.2, the basic idea of shell *morphoelasticity* is that the geometric stretches defined between the initial configuration and the current configurations are decomposed into growth stretches and elastic stretches. We denote again with a subscript “0” all variables relevant to the initial configuration, that is, the reference configuration at time $t = 0$.

We define the initial profile $\mathbf{C}_0$ by

$$\mathbf{R}_0 = R_0(S_0)\mathbf{e}_r + Z_0(S_0)\mathbf{e}_z, \quad S_0 \in [0, L_0], \quad (9.1)$$

where S_0 is, as before, the arc length of the contour with total length L_0 . The *geometric stretches* between the initial and current configurations are defined as

$$\lambda_s = \frac{\partial s}{\partial S_0}, \quad \lambda_\varphi = \frac{r}{R_0}. \quad (9.2)$$

We further define an evolving virtual reference configuration by the pair $(S(S_0, t), R(S_0, t))$ with initial values $S(S_0, 0) = S_0$ and $R(S_0, 0) = R_0$, or equivalently, by the *growth stretches*

$$\gamma_s = \frac{\partial S}{\partial S_0}, \quad \gamma_\varphi = \frac{R}{R_0}. \quad (9.3)$$

The *current configuration* at time t is defined by $(s(S, t), r(S, t))$ and is obtained by solving the mechanical problem of the shell under load, that is, by computing the *elastic stretches* from the reference configuration at time t to the current configuration

$$\alpha_s = \frac{\partial s}{\partial S}, \quad \alpha_\varphi = \frac{r}{R}. \quad (9.4)$$

Therefore, the geometric stretches can be decomposed according to the morphoelastic decomposition as follows:

$$\lambda_s = \alpha_s \gamma_s \iff \frac{\partial s}{\partial S_0} = \frac{\partial s}{\partial S} \frac{\partial S}{\partial S_0}, \quad (9.5)$$

$$\lambda_\varphi = \alpha_\varphi \gamma_\varphi \iff \frac{r}{R_0} = \frac{r}{R} \frac{R}{R_0}. \quad (9.6)$$

This decomposition is a particular case of the general principle, described in Chapter 12, whereby the deformation tensor is decomposed into the product of two tensors. The *growth tensor* maps the initial configuration to an unstressed configuration and the *elastic deformation tensor* maps the evolving reference configuration to the current configuration.

The introduction of growth stretches requires new constitutive relationships. Since they describe the evolution of the material in time, these relationships are usually referred to as *evolution laws* and take the convenient form of differential equations in the slow time t as they relate the reference and current configurations at time t to a new reference configuration at a later time. If we assume that the remodeling process depends possibly on the stress and the material position, these evolution laws take the general form

$$\frac{\partial \gamma_s}{\partial t} = \eta \gamma_s \mathcal{G}_s(\gamma_s, t_s, t_\varphi, S), \quad (9.7)$$

$$\frac{\partial \gamma_\varphi}{\partial t} = \eta \gamma_\varphi \mathcal{G}_\varphi(\gamma_\varphi, t_s, t_\varphi, S), \quad (9.8)$$

where η^{-1} is a characteristic relaxation time.

In the simple case where we assume that, at any given time, the reference configuration relaxes toward the current configuration, the evolution law takes the simpler form

$$\frac{\partial \gamma_s}{\partial t} = \eta(\lambda_s - \gamma_s), \quad \frac{\partial \gamma_\varphi}{\partial t} = \eta(\lambda_\varphi - \gamma_\varphi). \quad (9.9)$$

Taking advantage of the fact that the time scale for the growth process is much larger than the elastic or viscoelastic relaxation time scales, minutes or hours compared to milliseconds in most cases, we assume that the shell is in a quasi-static equilibrium at all times. A new elastic equilibrium is obtained by considering the evolution of the new reference configuration. In the long-time limit, this amounts to re-parameterizing the distribution of material points around the shell back to a uniform distribution thereby making the current stressed configuration a new reference configuration. We may also think of this process as equivalent to having rebuilt the wall back to its original thickness while relieving all stresses.

Computationally, the growth process is discretized, that is, we start with an initial shape as shown in Figure 9.1 defined by the function $R_0(S_0, t)$, $0 \leq S_0 \leq L_0$, and compute the new shape $r(S, t)$ by solving the mechanical equations subject to the boundary condition $r(L_0) = R_0$, $r(0) = 0$. The new shape $r(S, t)$ represents the new mechanical equilibrium of the membrane. The new reference shape $R(S, t + dt)$ and parameterization $S(S_0, t)$ is computed based on the current configuration. The shape $R(S, t + dt)$ is then used to compute a new mechanical equilibrium $r(S, t + dt)$ and so on.

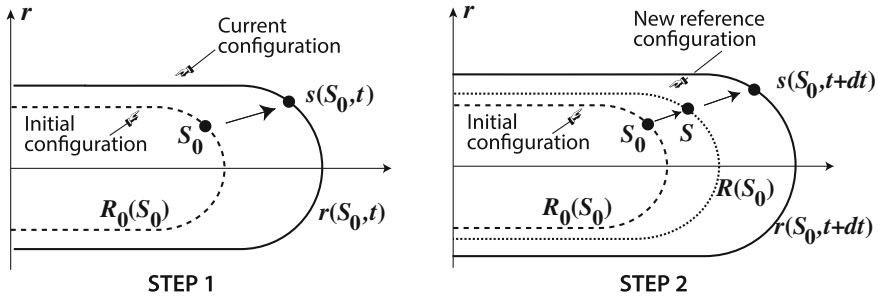


Figure 9.1 A sketch of membrane growth in the context of tip growth. In Step 1, the membrane is inflated to an equilibrium shape. In Step 2, a new reference configuration is computed based on the profile of Step 1. Since the reference configuration has evolved, a new current configuration is obtained and the evolution of the membrane proceeds.

9.2 Application: Microbial Tip Growth

9.2.1 Background

At the microbial level, tip growth or *apical growth* is the dominant process for mass addition. It is observed in different systems, such as bacterial filaments, fungi, root hairs, pollen tubes. Despite appearing in vastly different organisms, it shares some common notable features. For example, the actual shapes of the tip vary for different cells, and for the same cell under different conditions. Also, there are periods in which tip growth appears to be self-similar. In that case, the tip is just a translation of the tip shape at the previous instant [480]. Another interesting feature is that growth is mostly “normal,” that is, labeled points on the tip appear to move in a direction normal to the tip surface. This possibility was discussed in the late nineteenth century by Reinhardt [1073] and has been confirmed in experimental studies of fungal filaments [63] and root hair [313, 1143], as shown in Figure 9.2. Despite these common features in the overall growth dynamics there are major differences in the biological mechanisms that drive the growth for different cell types [428, 430]. Therefore, before modeling tip growth, we briefly review key characteristics of various microorganisms.

9.2.2 Bacterial Filaments: Actinomycetes

Actinomycetes have been a topic of considerable interest to microbiologists as a model organism for filamentous bacterial growth since their discovery by Ferdinand Cohn in 1875 [220, 775] (see Figure 9.3). They are broadly defined as a family of gram-positive prokaryotic organisms with DNA high in cytosine and guanine content. Their cellular structure is composed of linear nuclear material in a cytoplasmic

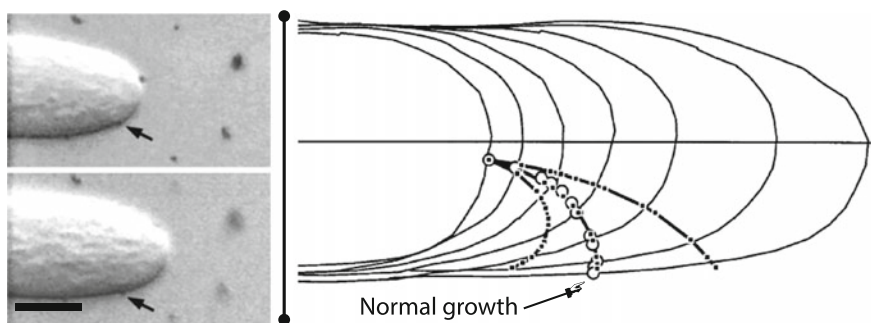
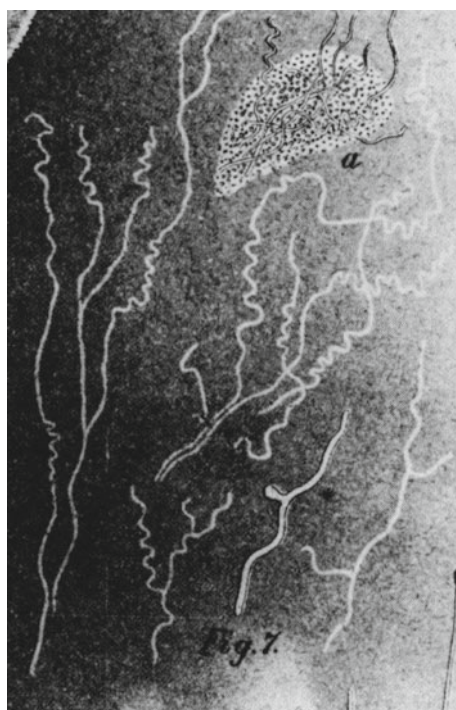


Figure 9.2 Observation of normal growth. The analysis of trajectories of material points in the fungus *Rhizoctonia solani* shows that markers (indicated by arrows on and circles) follow a trajectory normal to the surface (Bar is, $5\ \mu\text{m}$. Adapted from [63]). The other lines correspond to possible trajectories when a non-normal component of the velocity is included.

Figure 9.3 First description of actinomycetes by Cohn in 1875 (adapted from [1]).



medium. Their cell wall structure is dominated by a characteristic network of stiff chitin molecules embedded in a polymer complex [183, 1314]. The streptomycetes are of particular interest since they are a natural source of antibiotics.

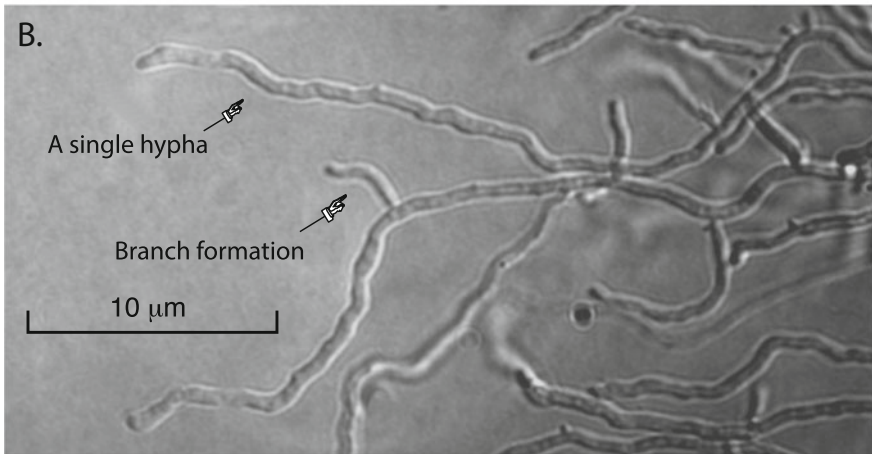
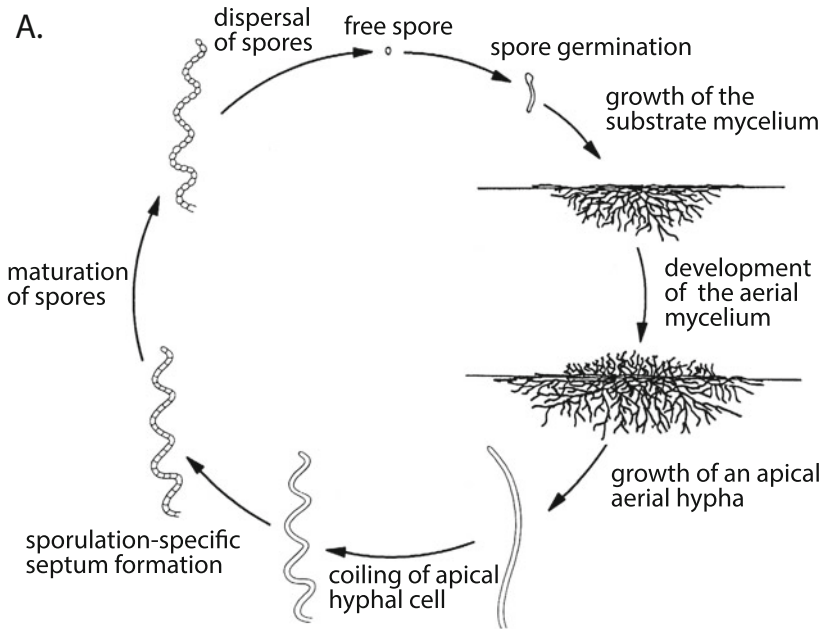


Figure 9.4 A. Life cycle of *Streptomyces*. B. Mycelial growth of *S. coelicolor* on solid agar medium (microscopy performed by Michael Tabor and the author).

In a typical growth cycle, the streptomycete spores bud into long filamentary hyphae which grow in and on a nutrient source. The growing hypha eventually undergo branching leading to the formation of a dense mycelium as illustrated in Figure 9.4.

In this so-called *vegetative phase*, apical growth is energetically more efficient than growth along the entire filament since the latter would result in more friction

with the nutrient medium. A typical filament of *Streptomyces coelicolor* in this phase is less than 1 μm in diameter and can grow to lengths of 50–100 μm . The vegetative phase creates an intricate network of filaments called *mycelium*. This phase is usually followed by an *aerial phase* of growth in which the hyphae grow out of the mycelium, sometimes deforming into helical structures, and ultimately breaking up into spores—which then begin the growth cycle again [1]. We note that in the aerial phase hyphal growth is no longer apical, but it is distributed along the length of the filament.

The apical growth of streptomycetes in the vegetative phase has been demonstrated in a variety of studies tracking the presence of tritiated GlcNAc, a precursor of peptidoglycan. For example, Gray et al. [497] used this technique in their study of *Streptomyces coelicolor* A3(2) to demonstrate that the bulk of the labeled material was incorporated close to the hyphal apex.

The interplay between turgor pressure and cell wall rigidity has also been demonstrated by the action of lysing agents which degrade the cell wall. In their studies of *Streptomyces coelicolor*, Gray et al. [497] showed that *b*-lactam antibiotics caused apical swelling of the hyphae leading, in some cases, to lysis. These and other experimental studies of hyphal extension in *Streptomyces coelicolor* show that the main factors determining growth in the vegetative phase are (i) turgor pressure, (ii) addition of newly synthesized wall-building material in the apical extension zone, and (iii) the rigidification of the distal cell wall. Thus the mechanism of growth, consistent with these observations, is a continuous and complex process in which wall-building materials are transported to, and incorporated into the tip, which is stretched by the turgor pressure, and as the tip is continually stretched and rebuilt, the more remote portions of the hyphal wall rigidify [1046].

9.2.3 Fungi

Filamentous fungi are typically at least an order of magnitude bigger than actinomycetes and have a much more complex internal cellular structure. Their highly complex and multilayered cell wall typically consists of a network of chitin with cross-linking *b*-glucan chains [1314]. Despite all of these differences, there are still striking similarities with the overall growth dynamics of other filamentous cells—especially those of apical hyphal growth. For example, studies of *Neurospora crassa* showed that the incorporation of tritiated wall precursors decreased rapidly from the hyphal tip [457]. For most fungi, turgor pressure also appears to be a factor in the growth process, but there is some experimental evidence indicating that oomycetes continue to grow even when they do not maintain turgor. Therefore, the precise role of turgor has been the topic of some discussion [541, 542, 899]. However for all fungi, it seems clear that the cytoskeleton plays a central role both in the growth process and in transporting wall-building materials to the tip, although a complete understanding of the different roles played by actin filaments and microtubules in the tip growth process is still evolving. Current thinking suggests that the inhibition of



Figure 9.5 Oscillatory growth in *Candida albicans* (picture courtesy of Alexandra Brand [123]).

actin can stop hyphal elongation and results in the formation of bulbous tips, whereas the inhibition of microtubules may result in distortion of the hyphal morphology [62].

It has also been proposed that a *vesicle supply center*, or *Spitzenkörper*, organizes and/or directs the traffic of vesicles containing the wall-building materials to the apical region [517]. Although the Spitzenkörper is not always visible under optical microscopy, studies using electron microscopy indicate a dense region near the tip consistent with the Spitzenkörper concept. Furthermore, laser tweezers can be used to manipulate the Spitzenkörper trajectory and directly influence changes in the hyphal growth direction [122, 1342].

A striking result is the observed normal cell wall expansion in filamentous fungi. By tracking carbon particle markers on the tip of *Rhizoctonia solani*, Bartnicki-Garcia et al. [63] were able to show that the markers moved in a direction perpendicular to the surface of the hyphal apex, thereby confirming the old prediction of Reinhardt concerning normal growth. Their results also support the view that turgor pressure is a major driving force in the hyphal growth process.

Another interesting aspect of growth is that depending on the substrate, the hyphae may present different morphologies. For instance, on hard surfaces, the hyphae of the dimorphic fungus, *Candida albicans*, follow, typically, a linear trajectory. However, on semisolid surfaces, the hyphae of *Candida albicans* grow in an oscillatory manner [123], as shown in Figure 9.5.

However, for all these complexities and subtleties, the overall picture parallels that of hyphal growth in filamentous bacteria, namely, apical growth is driven by a complex process involving transport of wall-building materials and a tip-straining mechanism [429].

9.2.4 Root Hairs

Root hairs have been one of the most enduring topics of study in microbiology with scientific publications dating back almost two hundred and fifty years as discussed in Section 1.1.1. As with filamentary fungi, it was established long ago that cell wall expansion is concentrated at the tip [171]. More refined microscopic studies have also shown that the expansion is both inhomogeneous, that is, the rate of expansion is maximal around the tip, and anisotropic: The meridional expansion is greater than the hoop expansion. The latter observation suggests a varying stiffness of the cell

wall, perhaps due to a corresponding variation in microfibril cross-linking. Further experimental studies of growth in *Medicago truncatula* root hair [1143] also support the notion of normal motion of material points on the growing tip.

9.2.5 Modeling of Tip Growth

The mathematical modeling of hyphal growth involves three equally important levels of description: The biomechanical level aims to describe the growth and morphology based on mechanical principles. The biophysical level aims to translate the structural details of the cell wall into macroscopic material properties and must be incorporated in the mechanical models. Finally, the biomolecular level aims to understand the molecular basis for the detailed structure and expression of the cell.

The first attempts to model tip growth were mostly based on geometric arguments. In these models the increase in wall area of an advancing tip is balanced with the rate of incorporation of wall building material [64, 1082]. Other models consider the consequences of having a given tip shape, such as a hemisphere or an ellipse [1121, 1249].

A geometric model following the idea that the local velocity vector attached at a point on the surface is a function of the curvature was investigated in [467] (see Figure 9.6). While this approach can sometimes yield formulas for idealized tip shapes, it cannot capture the fundamental interplay between the mechanical stresses and the material responses of the cell wall.

By contrast, mechanical models can capture the tip growth process through a proper description of the physical stresses and strains experienced by the growing hypha. Different mechanical modeling approaches have also been proposed. Early models [715] that draw on concepts from shell theory and the Laplace law for membranes suggest connections between experimentally observed tip shapes and their

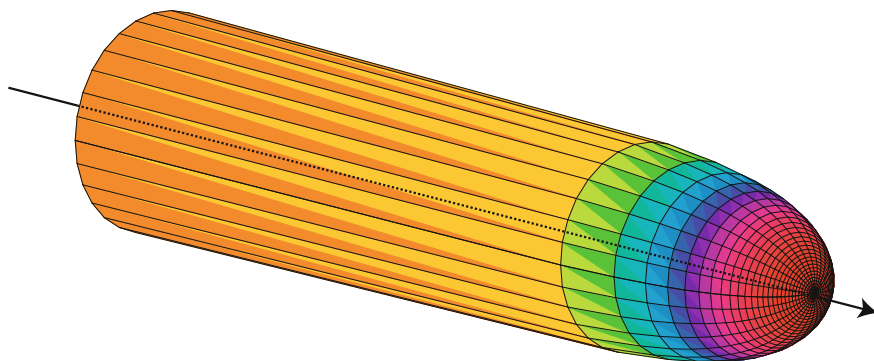


Figure 9.6 Tip profile in a geometric model. The shape is obtained by assuming that areal growth is proportional to the Gauss curvature [467].

material properties. Other models are based on the use of linear plasticity theory to model irreversible extensions of the cell wall [314]. This approach follows the idea behind the Lockhart model of plant cell growth described in Section 4.5. We now turn to the modeling of tip growth as a morphoelastic process by following the general method presented in this chapter.

9.2.6 A Model for Hyphal Growth

We model the tip of growing hyphae as a morphoelastic membrane or shell. Here, we consider an idealized situation where we do not explicitly model the material transport. Therefore, our general framework is suitable for the modeling of many systems exhibiting tip growth. First, we consider the case of turgor-driven growth for actinomycetes and second the case of fungal hyphae when taking into account the role of surface traction.

We start with an elastic membrane at rest. Due to a local weakening of the membrane, a *soft-spot*, the membrane will deform and reach a new steady state. Assuming that the reference configuration remodels according to the shape of the current configuration, the turgor pressure will further expand the membrane and this process is repeated as shown in Figure 9.7.

We are particularly interested in answering whether this process of localized weakening, turgor inflation, and reference configuration remodeling leads to a tip solution? If so, what is the profile shape? Is it self-similar? Can we further understand

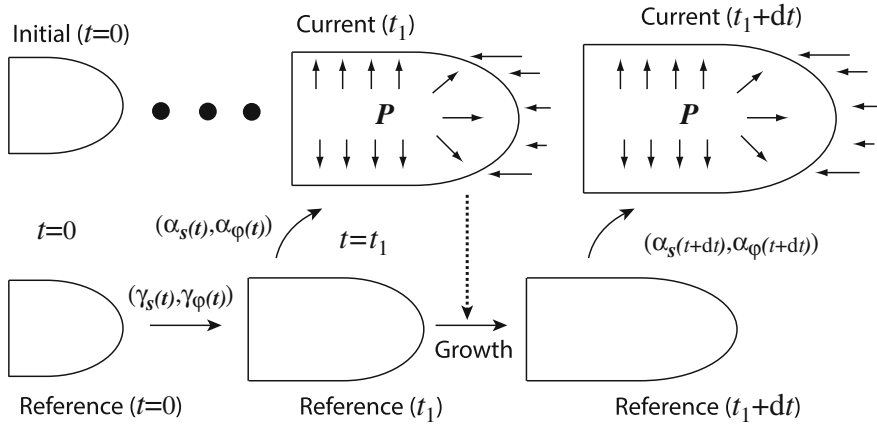


Figure 9.7 An initial reference configuration is defined at $t = 0$. The growth strains $(\gamma_s, \gamma_\varphi)$ brings the initial reference configuration to the reference configuration at time t_1 . The current (observable) configuration is computed by applying loads and is characterized by the elastic strains $(\alpha_s, \alpha_\varphi)$. The new reference configuration at time $t_1 + dt$ is obtained by solving (9.7)–(9.8) with data from the current configuration (dashed line). The growth process is then iterated.

beading? What is the effect of external friction due to the medium? Is normal growth a consequence of mechanics and growth?

9.2.6.1 The Soft-Spot Hypothesis: Variable Moduli

As discussed in Section 8.1.4.1, the existence of tip shapes for an elastic membrane requires a softening of the tip. The softening of cell walls close to the tip can easily be taken into account using a material-dependent elastic function $A = A(S)$. The general form of $p = P/A$ that we choose is

$$p = \frac{P}{2} \left[1 - \tanh \left(\frac{S - S_1}{a_1} \right) \right] + p_\infty, \quad (9.10)$$

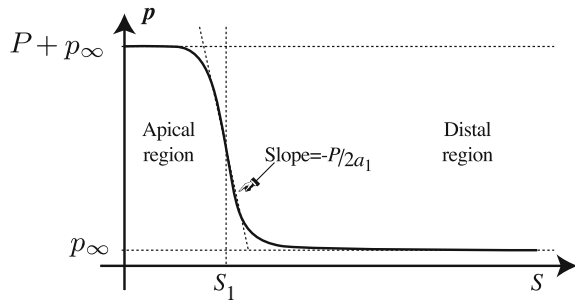
where P is the turgor pressure and the parameters S_1 and a_1 describe the length of the apical extension zone as shown in Figure 9.8. Since $p \rightarrow p_\infty$ as $S \rightarrow \infty$, the parameter p_∞ describes the effective pressure in distal regions.

It is important to note that in our model the critical parameters of pressure and modulus only appear in the ratio P/A . Thus a decreased modulus or increased pressure is, at the mechanical level, indistinguishable. We will return to this point in our discussion of lysis. The idea of a geometry-dependent elastic modulus is biophysically plausible as classic results in polymer physics [1247] tell us that the modulus increases with the degree of polymeric cross-linking, and in the current context this is consistent with the process of wall rigidification.

9.2.7 Tip Shapes for Filamentous Bacteria

We first consider the case of bacterial hyphae and use information and data from the model organism *Streptomyces coelicolor* A3(2). The effective pressure profile in Figure 9.8 can be fitted from published data on the rate of incorporation of tritiated markers along the hyphae of *Streptomyces coelicolor* A3(2) [497] and provides a

Figure 9.8 A typical plot of the renormalized pressure $p = P/A(S)$. Close to the tip ($S = 0$), the walls are soft and the elastic coefficient minimal. In the distal regions, the walls are set and, comparatively, the elastic coefficient A is very large, so that the effective pressure is small (equal to p_∞).



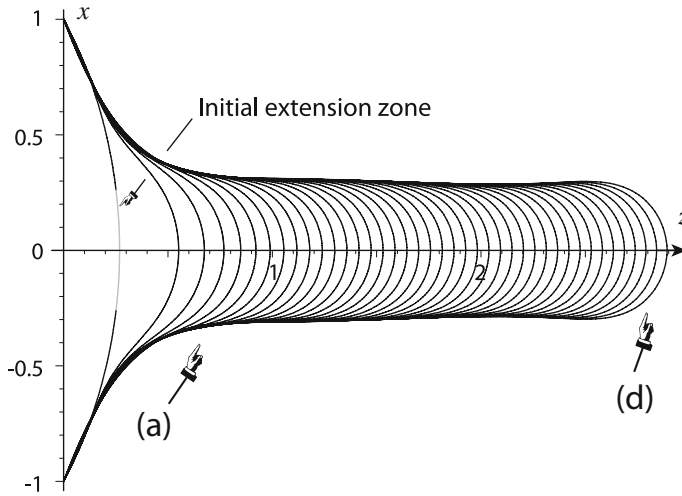


Figure 9.9 Sequence of growth obtained from an initial spherical shape of radius 2. ($S_1 = \pi/12$, $P = 1$, $a_1 = 1/8$, $p_\infty = 10^{-6}$). The corresponding three-dimensional representations for the profiles (a) and (d) are shown in Figure 9.10.

characteristic length scale for the soft-spot as done in [479]. Here we use the linear constitutive laws given in Section 8.1.3.1.

The computation of a growth profile is performed as a discrete sequence of boundary-value problems; time evolution is performed, as described above, by re-parameterization of the initial profile. A typical computation is shown in Figure 9.9 where it is seen that a tip rapidly emerged through this process. Remarkably, this process appears very robust as an asymptotic shape is obtained from different initial profiles and appears to depend only on the elastic parameters and pressure profile.

Before we try to determine the asymptotic shape, we investigate, computationally, the self-similarity of the process. When viewed in the reference frame of the tip, the tip shape, once established, is effectively *self-similar*, that is, at each step the new shape is a duplicate of the previous one properly translated, as shown in Figure 9.11. The asymptotic linear increase of arc length and area, shown in the same figure, is also consistent with a self-similar solution. The self-similar process is obtained after a combination of elastic expansion followed by a growth process. Therefore, the final tip shape, $r(S)$, is of the same functional form as the initial reference shape $R_0(S)$. The self-similar ansatz in this process, as illustrated in Figure 9.12, is simply to set

$$r(S) = R_0(s(S)). \quad (9.11)$$

After expansion, the value of the radial variable r for a given material point S is required to be the value of R_0 evaluated at the new position of S , expressed in terms of arc length, along the shell. The angular deformation variable, λ_φ , now takes the form

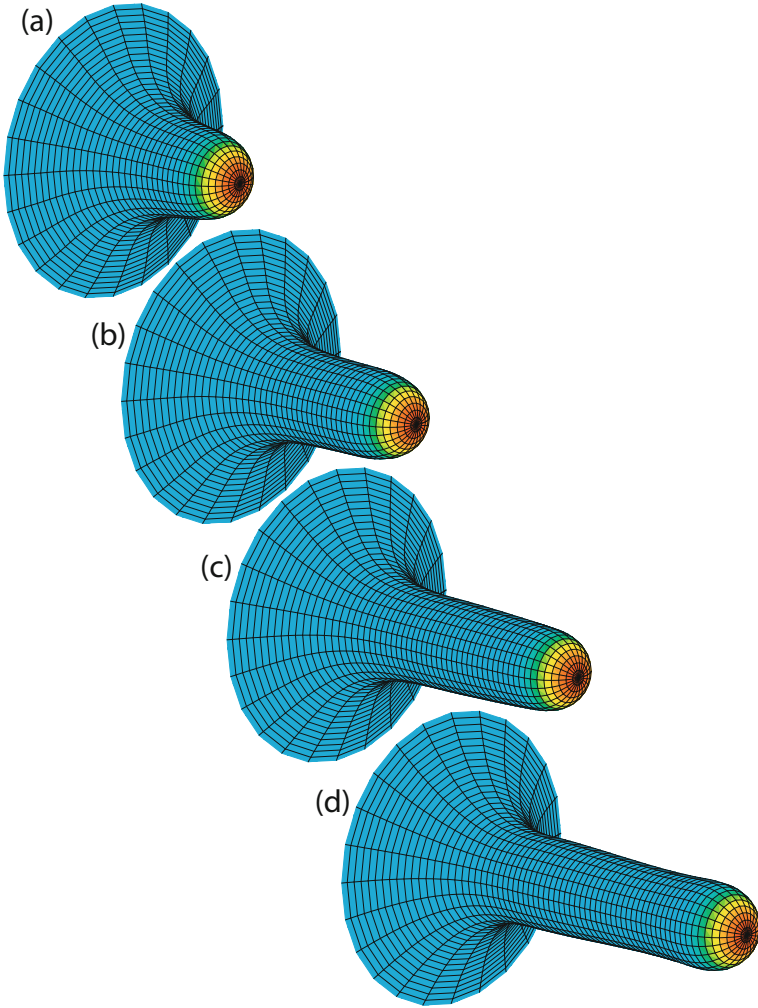


Figure 9.10 Three-dimensional graphics representation for iterates 50, 100, 150, and 200 of Figure 9.9.

$$\lambda_\varphi = R_0(s(S))/r_0(S). \quad (9.12)$$

This form is well suited for hyphal growth since far from the tip we expect to see, effectively, no material stretching and hence

$$\lambda_\varphi = \lim_{S \rightarrow \infty} r_0(s(S))/r_0(S) \approx r_0(S)/r_0(S) = 1. \quad (9.13)$$

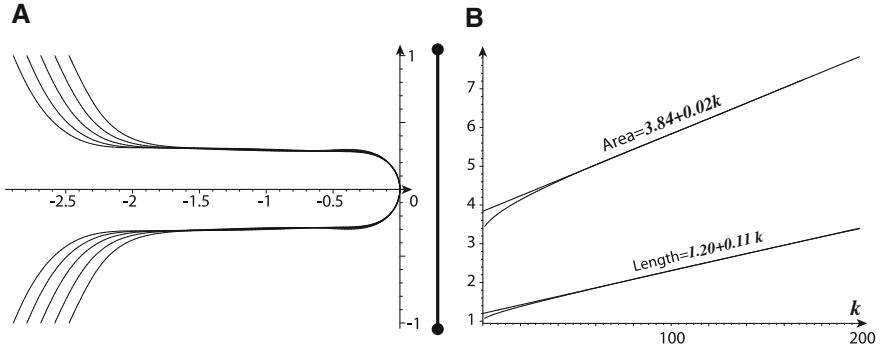


Figure 9.11 Self-similarity. A. For the same growth sequence as in previous figure, but viewed in the reference frame of the tip, the increase of total length and area during growth as a function of the number of growth iterates k are shown. B. After an initial phase, the increases of length and area are linear with time, as observed in experiments.

Note, however, that the functional relationship (9.11) is nonlocal since the arc length $s(S)$ is determined by integration of the metric along the curve up to the given point S .

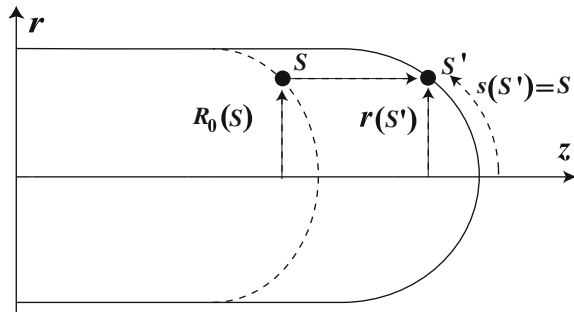
This self-similar ansatz maybe explored analytically by expanding all dependent variables asymptotically close to $S = 0$:

$$r = \sum_{i=1}^N r_i S^i + \mathcal{O}(S^{N+1}), \quad \theta = \sum_{i=1}^N \theta_i S^i + \mathcal{O}(S^{N+1}), \quad (9.14)$$

$$s = \sum_{i=1}^N s_i S^i + \mathcal{O}(S^{N+1}), \quad R_0 = \sum_{i=2}^N \rho_i S^i + \mathcal{O}(S^{N+1}). \quad (9.15)$$

Substitution of these expansions into the system (8.36–8.37) yields a set of algebraic relationships for the expansion coefficients with the constraint expanded to order N , that is, we have

Figure 9.12 Self-similar growth ansatz. We assume that after pressurization and growth response, the new profile is similar to the initial profile up to a translation.



$$\sum_i^N \rho_i \left(\sum_j^N s_j S^j \right)^i = \sum_i^N r_i S^i.$$

Here, for computational simplicity, we use a simpler renormalized pressure field and choose a limiting form of (9.10), namely

$$p = \begin{cases} p_{\max} & 0 \leq S \leq S_1, \\ 0, & S > S_1, \end{cases} \quad (9.16)$$

thereby making the membrane completely rigid outside the apical expansion zone $0 \leq S \leq S_1$. The outer profile is then a cylinder of radius $r(S_1)$ and we can solve for the inner solution. The equations for the coefficients of the asymptotic series are closed by requiring that the inner and outer solutions match, that is, $\theta(S_1) = \pi/2$.

A typical computation of the asymptotic form of the self-similar solution together with the corresponding numerical solution is shown in Figure 9.13. For the self-similar solution, there are only two length scales: The size of the hot-spot S_1 , and the ratio $A/p_{\max}$. We introduce a dimensionless number that characterizes the relative effect of the turgor pressure with respect to the elastic stiffness of the soft tip as

$$\xi = \frac{p_{\max} S_1}{A}. \quad (9.17)$$

It is now easy to compute numerically the width w and curvature κ of the self-similar profile as a function of ξ . Examples of such universal profiles are shown in Figure 9.14.

Figure 9.13 Comparison of growing membrane profile with self-similar solution. The inner profile (dashed line) corresponds to the self-similar solution with the same parameter values. The outermost profile is obtained numerically ($S_1 = \pi/6$, $P = A = 1$, $a_1 = 1/64$, $p_{\infty} = 10^{-2}$).

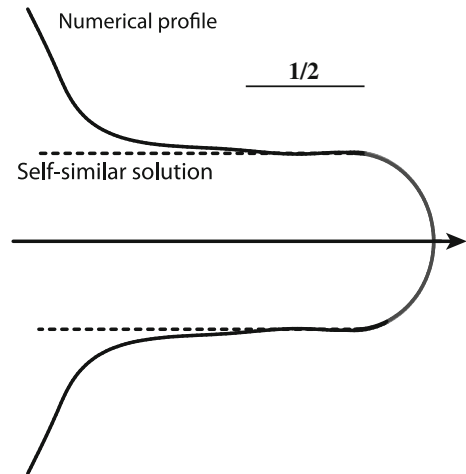
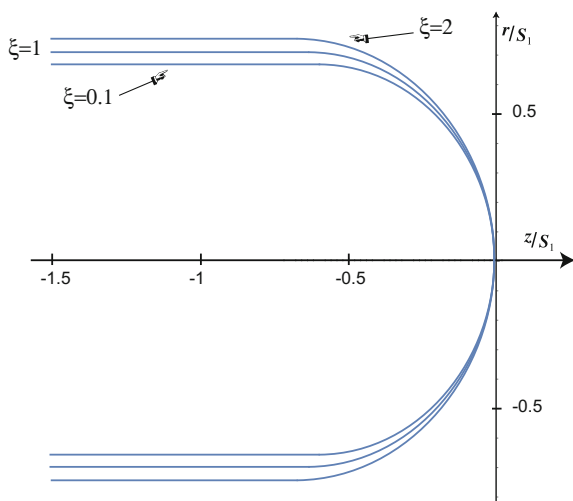


Figure 9.14 Self-similar profile for different values of the dimensionless number ξ .

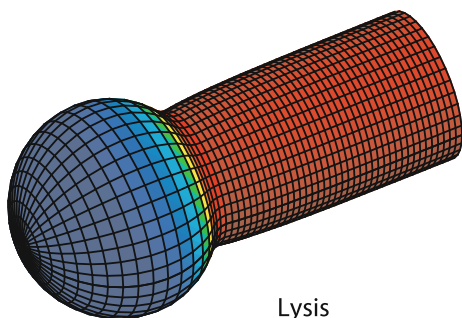


9.2.8 Lysis and Beading

It is now possible to consider two simple situations where modifications of the elastic properties of cell walls can lead to a change in morphology. First, when the hyphae are treated with β -lactam antibiotics, the rigidification of the wall is partly prevented and results in *apical swelling*. This effect is described as an “...*increase internal hydrostatic pressure acting on a cell wall of reduced rigidity*” [1046]; in our setting we see that both effects are represented by an increase of the effective pressure parameter p , as shown in Figure 9.15.

Instead, if the hyphae are treated with lysozyme, the hyphae can exhibit sudden *beading*, that is, generalized nonlocalized hyphal swelling. Again, this situation can be easily modeled by a variation of the parameter p along the hyphae. A typical example of such a profile is shown in Figure 9.16. Here the first dips in p correspond

Figure 9.15 Lysis is obtained by an increase of the pressure at the tip (or equivalently, a softening of the tip).



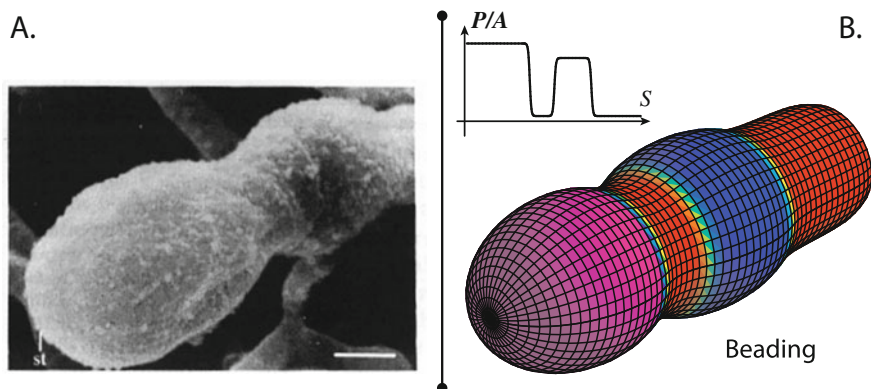


Figure 9.16 A. A swollen hyphal *Streptomyces Coelicolor* tip. The tip is approximately 2–5 μm in diameter and its surface appears roughened due to the lytic action of lysozyme (Bar is 1 μm . Picture courtesy of J. I. Prosser). B. An effective pressure profile capable of reproducing lysozyme induced beading (top). Beading obtained by allowing variations of p along the hyphae (bottom).

to a large increase in the elastic modulus. Since the beading is believed to be associated with septation, one would expect a significant increase in structural rigidity in the neighborhood of the septa that would survive the introduction of lysozyme.

9.2.9 Shear Stress and the Normal Growth Hypothesis

Next, we consider the effect of the environment on the shape of hyphae. The mechanical action of the external medium on the growing tip is to induce shear stress, repre-

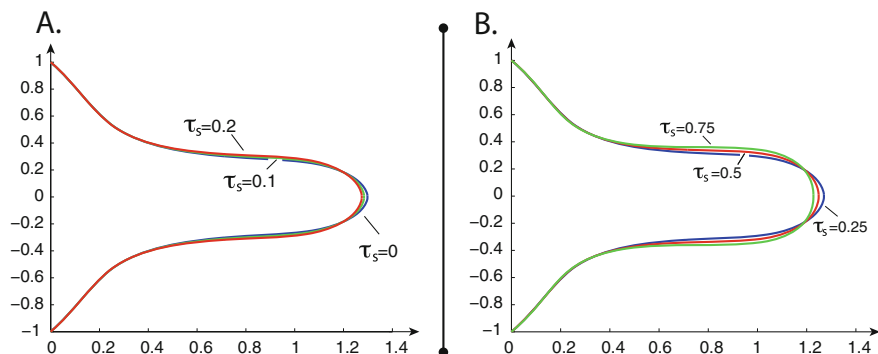
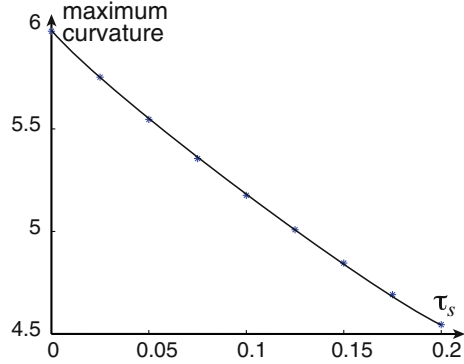


Figure 9.17 Comparison of the final shape of the tip for increasing values of external surface stress τ_s . As the external stress increases the curvature at the tip decreases and the tip flattens.

Figure 9.18 Evolution of the maximum of the curvature as τ_s increases.



sented by τ_s in (8.73). Here, we use a large deformation theory with a neo-Hookean strain-energy density function and an initially spherical shell with a soft-spot.

The effect of the external media on the surface friction is obtained by increasing the value of τ_s . In Figure 9.17, we compare tip shapes after 70 iterations with a series of values of τ_s with the same material parameters and initial conditions. The results clearly show a progressive “flattening” of the tip shape as τ_s is increased as indicated by looking at the maximum curvature as a function of τ , as shown in Figure 9.18.

We can now test the normal growth hypothesis by tracking the paths of material points on the surface of the tip and comparing them with what would be the equivalent normal paths starting with $\tau_s = 0$. As we see in Figure 9.19, the particle trajectories do not follow normal paths for $\tau_s = 0$. Therefore, in the absence of shear stresses, we do not expect growth to be normal.

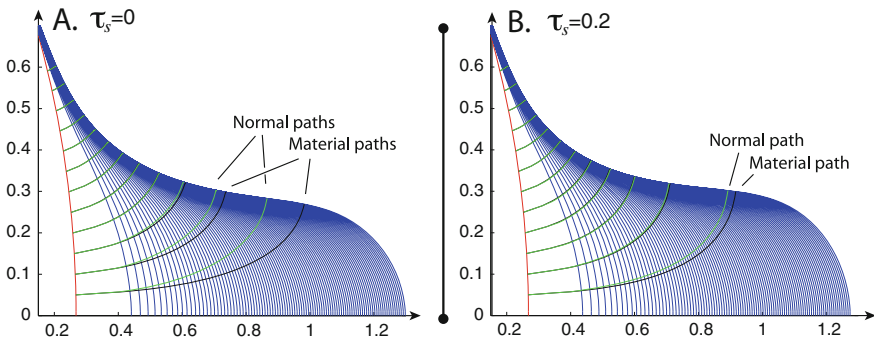


Figure 9.19 Testing the normal growth hypothesis. We compare the path of a material point on the tip with the path starting from the same material point, but following a trajectory normal to the curve for increasing values of τ_s . As can be seen the material trajectories tend to align with the normal trajectories.

As τ_s increases, the particle trajectories become evermore “normal.” Therefore, we conclude that a possible explanation for the normal growth hypothesis is simply the result of the shear stress exerted by the media on the surface. On an energetic level, this is a reasonable assumption as normal growth reduces the motion of material points in the media by following close to normal trajectory, that is, without having to work against external forces there is no energetic reason for the tip expansion to follow a normal path. However, once such forces are included, such paths are the most work-efficient ones to follow. This result suggests that normal growth is a consequence of the mechanics rather than being coded positionally at the level of the membrane.

Chapter 10

Morphoelastic Plates



So far, we have considered relatively simple two-dimensional structures, namely axisymmetric shells and membranes. It is important to develop a full theory of growing and remodeling for plates and shells. Indeed, many thin three-dimensional elastic bodies can be reduced to either elastic plates or shells: Shells are two-dimensional elastic bodies whose reference shape is not necessarily flat, while plates are a particular case of an initially flat shell. More generally, *morphoelastic shells* are elastic shells that can remodel and grow in time. These idealized objects are suitable models for many physical, engineering, and biological systems.

Work on classical elastic shells finds its root in the experimental work of Chladni, Germain, and Kirchhoff on vibrating plates [203, 437, 698], followed by the work of Love [805] who first obtained a consistent general theory for small strains of linear elastic shells. The governing equations of elastic shells in terms of stress and couple-stress tensors were first derived by the Cosserat brothers [235] followed by a coordinate-free theory by Synge and Chien [1204]. Many different alternative derivations and formulations of the governing equations for elastic shells were later proposed by [501, 719, 932, 966].

10.1 Elastic Plates

A number of attempts to generalize the theory of plates to include the effects of growth have been proposed [93, 323, 705, 851, 852]. Here, we briefly present the results of Ben Amar and co-workers [275, 277, 923] who presented a generalization of the classical Föppl-von Kármán equations for growth. To do so, we will require the basic geometric descriptions of a surface in terms of its curvatures.

10.1.1 Mean and Gaussian Curvatures

We consider here an orientable parameterized surface Σ defined by the position vectors

$$\mathbf{x} = \mathbf{x}(\xi^1, \xi^2) \in \mathbb{R}^3, \quad (\xi^1, \xi^2) \in \mathcal{D} \subseteq \mathbb{R}^2. \quad (10.1)$$

We assume that $\mathbf{x}$ is at least of class C^2 and such that the tangent vectors

$$\mathbf{r}_i = \frac{\partial \mathbf{x}}{\partial \xi^i}, \quad i = 1, 2, \quad (10.2)$$

are linearly independent for all $(\xi^1, \xi^2) \in \mathcal{D}$. Since Σ is orientable, we can define a normal vector

$$\mathbf{n} = \frac{\mathbf{r}_1 \times \mathbf{r}_2}{|\mathbf{r}_1 \times \mathbf{r}_2|}, \quad (10.3)$$

where $|\mathbf{a}| = \sqrt{\mathbf{a} \cdot \mathbf{a}}$ is the usual Euclidean norm.

By definition $\{\mathbf{r}_1, \mathbf{r}_2, \mathbf{n}\}$ forms a basis, but this basis is not necessarily orthonormal. The area of Σ is given by

$$A = \int_{\Sigma} dS = \iint_{\mathcal{D}} \sqrt{\det(\mathbf{M})} d\xi^1 d\xi^2, \quad (10.4)$$

where $M_{ij} = \mathbf{r}_i \cdot \mathbf{r}_j$ are the components of the *metric tensor* with matrix representation $[\mathbf{M}]_{ij} = M_{ij}$ (a full description of tensors will be given in Section 11.11).

Similarly, we can compute the length of a path ρ on Σ by defining a curve $\mathbf{r} = \mathbf{r}(t)$, $t \in \mathcal{I} \subset \mathbb{R}$,

$$L = \int_{\rho} ds = \int_{\mathcal{I}} \sqrt{M_{ij} \dot{\xi}^i \dot{\xi}^j} dt. \quad (10.5)$$

Associated with the metric we define the *first fundamental form*

$$ds^2 = M_{ij} d\xi^i d\xi^j. \quad (10.6)$$

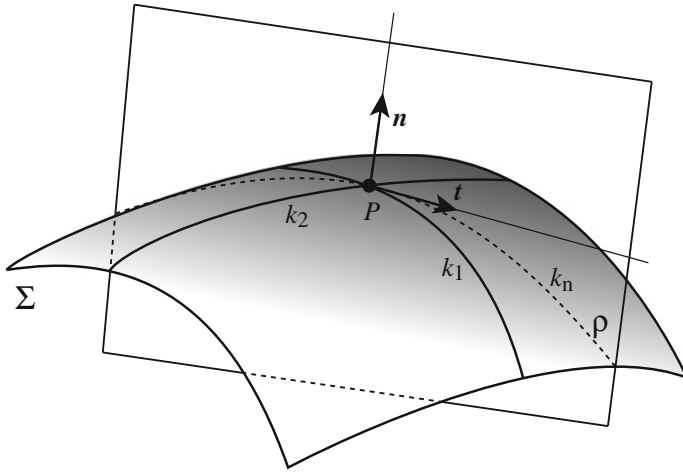


Figure 10.1 On a surface Σ , we define a curve ρ through a point P . Here, k_n is the curvature of the curve obtained by slicing the surface Σ at P by a plane spanned by the normal and tangent vectors. The principal curvatures $k_{1,2}$ are obtained as the extrema of k_n at P over all tangent vectors, that is by rotating the slicing plane.

We are interested in defining curvatures on the surface Σ . We consider a curve ρ on Σ passing through a point P and parameterized by its arc length s and define $\mathbf{t}$ as the tangent vector of ρ at P as shown in Figure 10.1. As defined by Equation (5.4), the curvature of the curve C at a point P is obtained as $|\mathbf{t}'|$, where the prime denotes differentiation with respect to s . It is therefore natural to define the curvature vector

$$\mathbf{k} = \frac{d\mathbf{t}}{ds}, \quad (10.7)$$

and decompose it into two components, the *normal curvature vector* $\mathbf{k}_n$ and the *geodesic curvature vector* $\mathbf{k}_g$

$$\mathbf{k} = \mathbf{k}_n + \mathbf{k}_g, \quad (10.8)$$

where $\mathbf{k}_n = -k_n \mathbf{n}$ is along the normal vector, which is

$$k_n = -\mathbf{n} \cdot \frac{d\mathbf{t}}{ds}, \quad k_g = |\mathbf{k}_g| = \left| \mathbf{t} \cdot \left(\frac{d\mathbf{t}}{ds} \times \mathbf{n} \right) \right|. \quad (10.9)$$

The *normal curvature* k_n is a property of the surface itself and gives the curvature in a planar slice spanned by the normal and tangent vectors, as shown in Figure 10.1. The *geodesic curvature* gives the curvature along the surface and is identically zero for a geodesic curve.

In terms of the coordinates, the normal curvature is given by

$$k_n = K_{ij}(\xi^i)'(\xi^j)', \quad (10.10)$$

where

$$K_{ij} = K_{ji} = -\mathbf{n} \cdot \frac{\partial \mathbf{r}_j}{\partial \xi^i}, \quad (10.11)$$

which naturally leads to the definition of $[\mathbf{K}] = [K_{ij}]$, the matrix of the *extrinsic curvature tensor*. This tensor is naturally associated with the *second fundamental form* $K_{ij}d\xi^i d\xi^j$.

From the extrinsic curvature tensor, we define the *principal curvatures* as the extremal values of the normal curvature as we vary the tangent vector at a fixed point P . The principal curvatures k_1 and k_2 are given by the eigenvalues of the *principal curvature matrix*

$$\mathbf{L} = \mathbf{M}^{-1} \mathbf{K}. \quad (10.12)$$

The principal curvatures can be used to define the *mean curvature* K_M and *Gaussian curvature* K_G as follows

$$K_M = \frac{1}{2} \text{tr}(\mathbf{L}) = \frac{k_1 + k_2}{2}, \quad (10.13)$$

$$K_G = \det(\mathbf{L}) = k_1 k_2. \quad (10.14)$$

The Gaussian curvature is intrinsic to the surface, in the sense that it only depends on the metric and not on the normal vector. This result is contained in Gauss' Theorema Egregium (remarkable theorem) [169, 496]. Note that K_G is independent of the parameterization but that K_M can change sign depending on the choice of the normal vector. It is used to classify surfaces as either *elliptic* ($K_G > 0$), *hyperbolic* ($K_G < 0$), or *parabolic* ($K_G = 0$). A *minimal surface* is such that $K_M = 0$ identically at all points. These surfaces play a particularly important role in a number of significant problems in mathematics and physics [1001].

10.1.2 Growing Elastic Plates

Next we consider an elastic plate as shown in Figure 10.2. In its reference configuration, the body has thickness H in the transverse direction and lateral sizes measured by a typical length scale L . The transverse (vertical) direction is aligned with the Z -axis and, accordingly, the middle surface in lateral directions is along the X and Y axes. We assume that the thickness is much smaller than the lateral size $H/L \ll 1$ and that the deformation is sufficiently small so that it can be fully characterized by the vertical displacement of the middle surface $\zeta(X, Y)$. We further assume that the curvatures of the plate remain small and that there is no shear through the thickness

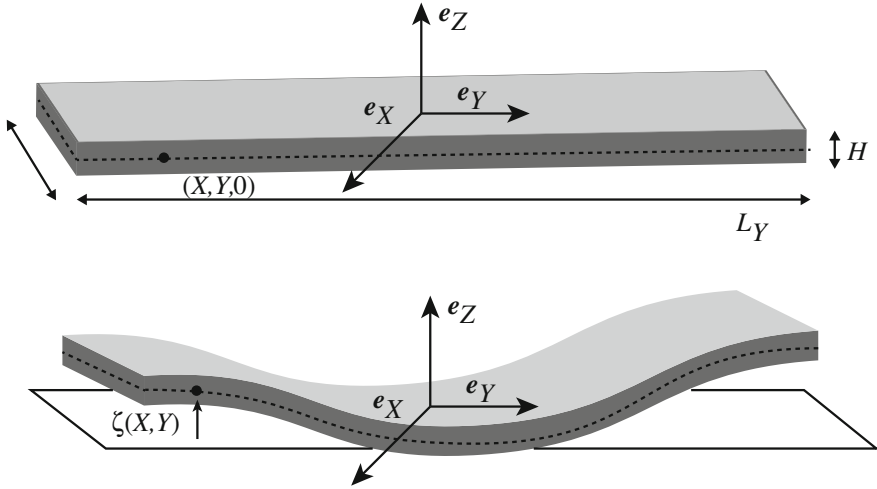


Figure 10.2 Deformation of a Föppl-von Kármán plate. Top: initial reference configuration. Bottom: deformed configuration. The deformation is fully characterized by the vertical displacement of the middle surface $\zeta(X, Y)$.

of the shell so that the normal vector remains close to the Z -direction. For the stress, we assume that the applied loads are sufficiently small and that the Z -components of the Cauchy stress tensor $\mathbf{T}$ vanish identically (see Section 11.2.2 for the general definition of stresses). It is convenient to introduce the Airy potential $\chi(X, Y)$ to express the remaining stresses on the middle surface through a single scalar quantity:

$$T_{XX} = \frac{\partial^2 \chi}{\partial Y^2}, \quad T_{YY} = \frac{\partial^2 \chi}{\partial X^2}, \quad T_{XY} = -\frac{\partial^2 \chi}{\partial X \partial Y}. \quad (10.15)$$

Using these assumptions, a systematic expansion of the three-dimensional equations for an elastic continuum in terms of the small parameter H/L leads to a set of two equations for the the displacement $\zeta(X, Y)$ and the Airy potential $\chi(X, Y)$:

$$D (\Delta^2 \zeta - \Delta \widehat{K}_M) - 2H[\chi, \zeta] = P, \quad (10.16)$$

$$\Delta^2 \chi + E ([\zeta, \zeta] - \widehat{K}_G) = 0, \quad (10.17)$$

where E is the Young's modulus, $D = EH^3/9$ is the bending rigidity of the plate, and P is the pressure acting on the plate along the normal to the surface. The bracket appearing in these equations is defined as

$$[f, g] = \frac{1}{2} \frac{\partial^2 f}{\partial X^2} \frac{\partial^2 g}{\partial Y^2} + \frac{1}{2} \frac{\partial^2 g}{\partial X^2} \frac{\partial^2 f}{\partial Y^2} - \frac{\partial^2 f}{\partial X \partial Y} \frac{\partial^2 g}{\partial X \partial Y}. \quad (10.18)$$

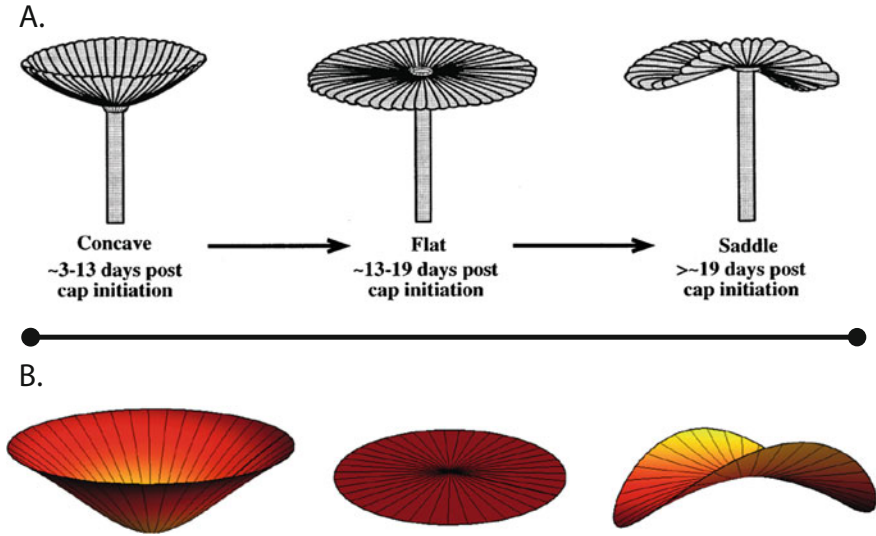


Figure 10.3 A. Shape changes in the algae *Acetabularia acetabulum* during morphogenesis (adapted from [1137]). B. Corresponding equilibrium shapes of a growing disc with different growth rates along its radius and angular directions [275].

In the absence of growth, i.e., $\hat{K}_M = \hat{K}_G = 0$, these equations were initially derived formally by Föppl and von Kármán [372, 1286]. Since then, various methods have been proposed to derive them rigorously [74, 209, 210, 394, 788, 934].

The effect of growth is contained in the two geometric parameters, $\hat{K}_M$, and $\hat{K}_G$ that can be interpreted as the mean and Gaussian curvatures of a new reference middle surface that the plate acquires through growth [323, 324, 705, 1140]. These two curvatures can be directly obtained from the growth strains. Therefore, growth can be interpreted as a source of intrinsic curvatures in a plate theory.

The effects of growth through Gaussian curvature can be understood by looking at the anisotropic growth of a disk as shown in Figures 10.3 and 10.4. If the disk grows isotropically, it remains flat with vanishing Gaussian curvature. However, if it grows slower inside than close to the edge, or grows faster in the hoop than in the radial direction, the disk will buckle to a cup shape with positive Gaussian curvature. Conversely, if the edge grows faster the disk will develop negative Gaussian curvature and release partly its residual stress by adopting a shape with wavy edges as shown in Figure 10.4 [1032, 1033].

The particular relationship between differential growth and Gaussian curvature in plates can be used to explain how plant leaves develop waviness or control flatness [830, 937, 1097, 1141, 1142]. Another example of a buckling instability in strips used to explain the wrinkling of leaves is shown in Figure 10.5.

The Föppl-von Kármán is the simplest model of an elastic plate. Relaxing some of the model assumptions leads to increasingly more complex models [209, 210]. For

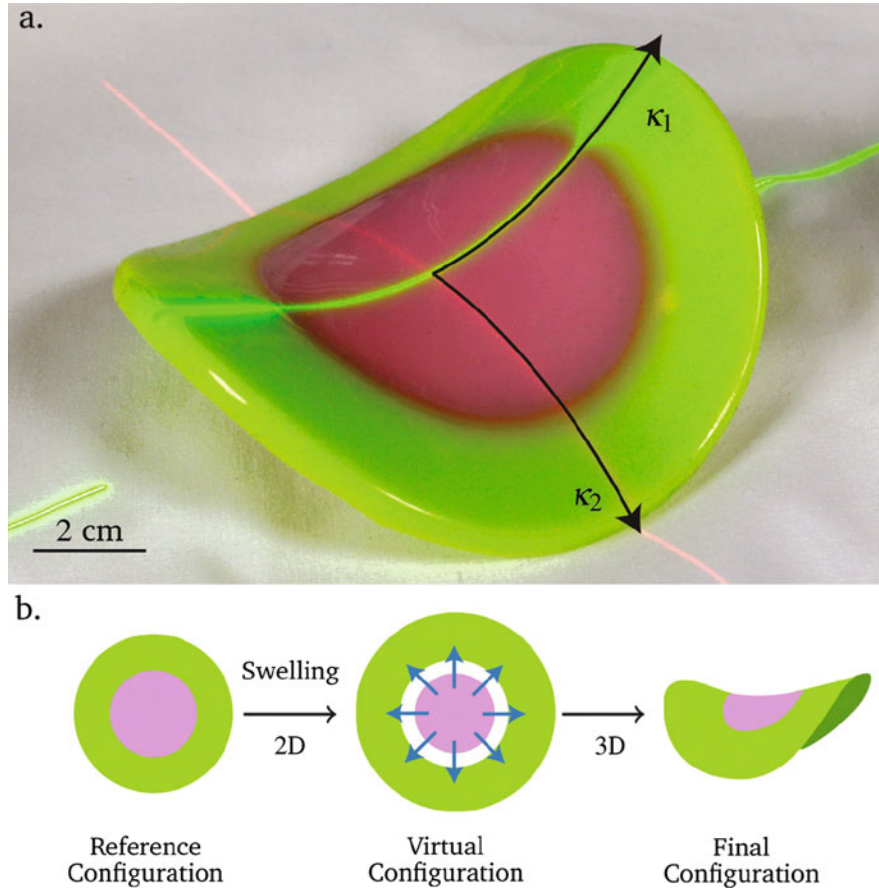


Figure 10.4 A negatively curved surface can be obtained by differential growth. The edge of the disk grow faster than the central part of the disk [1032].

instance, in the theory of Cosserat and Kirchhoff plates, the possible deformations of a three-dimensional body are constrained to deformations compatible with the two-dimensional geometry [33]. This approach can be used to explore the full nonlinear behavior of the material and does not restrict the analysis to thin bodies. It can also be generalized to the case of a growing body [851, 852] by directly using the three-dimensional theory of volumetric growth discussed in the next chapters.

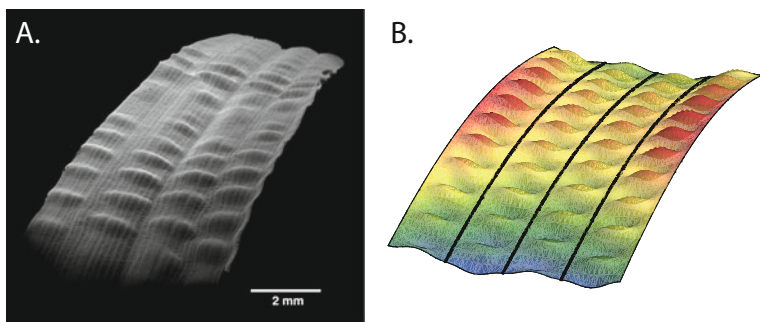


Figure 10.5 A. Picture of a grass blade (picture courtesy of Jacques Dumais). B. Instability of parallel clamped growing strips. Growth induces compression in the strips leading to rippling (from [277]).

In the case where the reference configuration is a shell rather than a plate, a general theory based on differential geometry can be used to derive the fundamental equations of growing shells [1110]. This general theory is particularly interesting as it shows explicitly the coupling between the intrinsic geometry of surfaces and the intrinsic geometry of growth as discussed in Section 12.5.

Part IV

Volumetric Growth: A Three-Dimensional Theory

*The sixth age shifts
Into the lean and slipper'd pantaloon,
With spectacles on nose and pouch on side,
His youthful hose, well sav'd, a world too wide
For his shrunk shank, and his big manly voice,
Turning again toward childish treble, pipes
And whistles in his sound. . .*

Chapter 11

Nonlinear Elasticity



Before introducing the effect of growth into a general mechanical theory, it is important to review the elements of continuum mechanics that describe the response of a material under loads, and in particular, the theory of elasticity. The traditional approach to elasticity is to consider the regime of small deformations, where a material is slightly perturbed from an unstressed configuration. In that regime, the governing equations and constitutive relationships are linear. This *theory of linear elasticity* has been successfully developed over the last two centuries to address many fundamental problems of physics and engineering [761].

Starting in the 1940s, it was found that the theory of linear elasticity was inadequate to model the response of elastomers such as rubbers in large deformations [1084, 1253]. Similarly, many tissues and organs also operate in large deformations. For instance, large arteries are typically stretched between 20% and 60% from their unloaded configurations [597, 635] and their response to loads is drastically different from the response of elastomers.

A striking example of the difference between rubbers and soft tissues is observed in experiments first performed in the nineteenth century and shown in Figure 11.1 [822, 1000]. In these experiments, a cylindrical elastic membrane made out of rubber or soft tissue is pressurized. At a critical pressure, the radius of the rubber cylinder

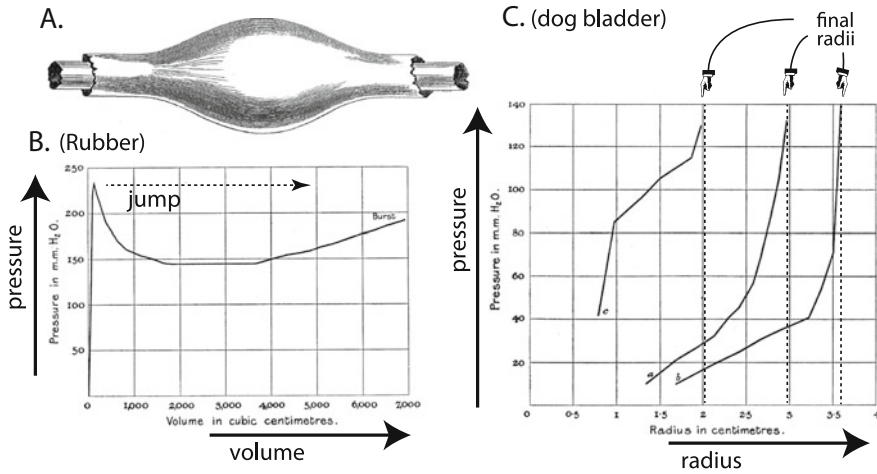


Figure 11.1 The importance of nonlinearities and large deformations is demonstrated in a pressure experiment as originally investigated by Mallock in 1890 [822]. A. The experiment consists in increasing the pressure inside a tube or a sphere while recording the radius of the bulge. B. In the case of rubber, the experiment of Osborne and Sutherland [1000] shows a sudden limit-point instability at a critical pressure. Past that pressure, the radius suddenly increases. C. In a similar experiment performed on a dog bladder, the behavior of the system is qualitatively different and the instability disappears. In this case, it will be increasingly harder to increase the size of the bulge by increasing the pressure.

will suddenly jump to a new equilibrium, whereas for soft tissues, the radius will evolve continuously to an asymptotic radius. Therefore, a continuum theory for the mechanical response of biological tissues requires the general *theory of nonlinear elasticity*, which, by contrast to the theory of linear elasticity, assumes neither small deformations, a particular choice of constitutive law, nor a particular symmetry of the material. As we will demonstrate in subsequent chapters, the nonlinear theory of elasticity is also the natural framework to develop a theory of growth and remodeling.

In this chapter, we briefly review the general theory of nonlinear elasticity, starting with the description of kinematics and moving to the Cauchy equations governing the response of a continuum. In the theory of elasticity, these equations are complemented by constitutive laws relating stresses to strains. The theory is presented at an elementary level and details can be found in the textbooks of Ogden [975], Gurtin, Fried, and Anand [525, 526], Truesdell and Noll [1251], or Antman [33].

11.1 Kinematics

Our first task consists in defining properly the deformation of a body in a three-dimensional space. To do so, we first define a body as occupying a region of a three-dimensional space. After a deformation, the body also occupies a region in space and the motion of each point of the body, from its initial to its current positions, can be defined by a mapping. The relative motion of nearby points can be extracted from

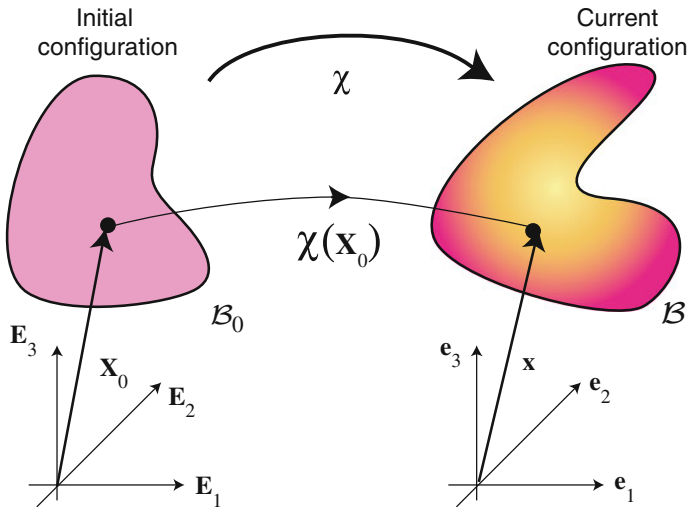


Figure 11.2 Basic kinematic of nonlinear elasticity. Two configurations are defined. The deformation is a 1–1 map between points in the reference configuration $\mathcal{B}_0$ and points in the current configuration $\mathcal{B}$.

this mapping through its derivatives in space and time. It allows us to define key quantities such as strains and stretches. Therefore, we first introduce basic notion of kinematics in three dimensions.

A *body* B is a set of material points whose elements can be put into a 1–1 correspondence (bijection) with points in a region $\mathcal{B} \subset \mathbb{E}^3$. As the body moves or deforms, this set can change with time $t \in \mathbb{R}$. In nonlinear elasticity, one considers multiple configurations for the description of a body and denotes by $\mathcal{B}_t$ (or $\mathcal{B}$, when there is no possibility of confusion) the *configuration* of B at time t .

We use $\mathcal{B}_0$ as the *initial configuration*, typically an unloaded configuration, and $\mathcal{B}$ for the *current configuration* where loads are applied. The initial configuration, $\mathcal{B}_0$, is parameterized by material points relative to the position vector $\mathbf{X}_0$ with origin $\mathbf{O}$ and the current configuration, $\mathcal{B}$, by the position vector $\mathbf{x}$ with origin $\mathbf{o}$.

The basic assumption for the deformation of a continuum is that the body retains its integrity and that material points do not overlap during a deformation. Therefore, both $\mathcal{B}_0$ and $\mathcal{B}$ are bijections of B , and there exists an invertible mapping, pictured in Figure 11.2, called *deformation* or *motion* $\chi : \mathcal{B}_0 \rightarrow \mathcal{B}_t$ such that

$$\mathbf{x} = \chi(\mathbf{X}, t), \quad \forall \mathbf{X} \in \mathcal{B}_0 \quad \text{and} \quad \mathbf{X} = \chi^{-1}(\mathbf{x}, t), \quad \forall \mathbf{x} \in \mathcal{B}_t. \quad (11.1)$$

In the absence of phase boundaries, singularities, or jumps, we assume that this mapping is twice continuously differentiable in space and smooth in time.

It is convenient to use two orthonormal rectangular Cartesian bases $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ and $\{\mathbf{E}_1, \mathbf{E}_2, \mathbf{E}_3\}$ to represent vectors in the initial and current configuration

$$\mathbf{x} = x_i \mathbf{e}_i, \quad \mathbf{X} = X_i \mathbf{E}_i, \quad (11.2)$$

where summation over repeated indices is always assumed unless explicitly specified.

The convention in continuum mechanics is to refer to coordinates in the current configuration, or quantities expressed with these coordinates, as *Eulerian* or *spatial*.

Coordinates in the initial configuration, or quantities expressed with these coordinates, are referred to as *Lagrangian*, *referential*, or *material*.

11.1.1 Scalars, Vectors, and Tensors

To describe the deformations of a body B , we attach, at each material point, physical quantities known as *fields*, which make continuum mechanics a theory of fields. These quantities can be scalar fields, such as density, temperature; vector fields, such as velocity, acceleration, force; or tensor fields, such as deformation gradients or stress and strain tensors. These different fields can all be understood as tensor fields of different orders. By definition, a scalar field is a tensor field of order 0 and a vector field is a first-order tensor field. Higher order tensor fields require the definition of the tensor product.

The *scalar product* between two vectors $\mathbf{a} = a_i \mathbf{e}_i$ and $\mathbf{b} = b_i \mathbf{e}_i$, in the same vector space, follows the usual definition:

$$\mathbf{u} \cdot \mathbf{v} = u_i v_i, \quad (11.3)$$

and is used to define the *Euclidean norm*

$$|\mathbf{v}| = \sqrt{\mathbf{v} \cdot \mathbf{v}}. \quad (11.4)$$

We can also use the scalar product to define the tensor product. Consider two vectors $\mathbf{u} = u_i \mathbf{e}_i$ and $\mathbf{v} = v_i \mathbf{E}_i$, not necessarily defined in the same vector space. Then, the *tensor product*, $\mathbf{u} \otimes \mathbf{v}$, of these two vectors is a second-order tensor such that, for an arbitrary vector $\mathbf{a} = a_i \mathbf{E}_i$,

$$(\mathbf{u} \otimes \mathbf{v})\mathbf{a} = (\mathbf{v} \cdot \mathbf{a})\mathbf{u}. \quad (11.5)$$

This definition implies that the vectors $\mathbf{v}$ and $\mathbf{a}$ must belong to the same vector space, but in general, $\mathbf{u}$ can belong to a different space. We see from this definition that a second-order tensor maps vectors from one vector space to vectors in another vector space.

Explicitly, the tensor product is

$$\mathbf{u} \otimes \mathbf{v} = u_i \mathbf{e}_i \otimes v_j \mathbf{E}_j = u_i v_j \mathbf{e}_i \otimes \mathbf{E}_j. \quad (11.6)$$

When there is no possibility of confusion, we can write the *components* of the second-order tensor $\mathbf{u} \otimes \mathbf{v}$ in the Cartesian bases $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ and $\{\mathbf{E}_1, \mathbf{E}_2, \mathbf{E}_3\}$ as $(\mathbf{u} \otimes \mathbf{v})_{ij} = u_i v_j$, $i, j = 1, 2, 3$.

Equipped with the tensor product, we can define a general *second-order tensor* in the Cartesian bases $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ and $\{\mathbf{E}_1, \mathbf{E}_2, \mathbf{E}_3\}$ as

$$\mathbf{T} = T_{ij}\mathbf{e}_i \otimes \mathbf{E}_j \iff T_{ij} = \mathbf{e}_i \cdot \mathbf{T}\mathbf{E}_j, \quad (11.7)$$

which implies that for a vector $\mathbf{a} = a_j\mathbf{E}_j$,

$$(\mathbf{T}\mathbf{a})_j = T_{ij}a_j. \quad (11.8)$$

We define the *matrix of components* of a tensor in Cartesian coordinates by $[\mathbf{T}]$ such that $[\mathbf{T}]_{ij} = T_{ij}$. We can then extend most definitions and identities of traditional linear algebra to tensors.

A particularly important class of second-order tensor is the tensors whose component matrices are square matrices. For these second-order tensors, the *determinant* and *trace* of a second-order tensor are defined, respectively, as

$$\det \mathbf{T} = \det([\mathbf{T}]), \quad \text{tr } \mathbf{T} = \text{tr } ([\mathbf{T}]) = T_{ii}. \quad (11.9)$$

In particular, in three dimensions, we have

$$\det \mathbf{T} = \det([\mathbf{T}]) = \epsilon^{ijk}T_{1i}T_{2j}T_{3k}, \quad (11.10)$$

where ϵ^{ijk} denotes the usual *Levi-Civita permutation symbols* or *permutation symbols*, that is, $\epsilon^{ijk} = 1$ if (i, j, k) is even permutation of $(1, 2, 3)$, -1 if it is an odd permutation, and 0 if index is repeated.

Similarly, the matrix of the transpose of a tensor is the transpose of the matrix, that is,

$$[\mathbf{T}^T] = [\mathbf{T}]^T \quad (11.11)$$

and a tensor is *symmetric*, $\mathbf{T}^T = \mathbf{T}$, if and only if $T_{ij} = T_{ji}$.

The product of two tensors $\mathbf{S}$ and $\mathbf{T}$ is only defined when the image of a vector by $\mathbf{T}$ is in the domain of $\mathbf{S}$. Then, for an arbitrary vector $\mathbf{a}$, we have

$$(\mathbf{S}\mathbf{T})\mathbf{a} = \mathbf{S}(\mathbf{T}\mathbf{a}). \quad (11.12)$$

In such cases, the matrix of the product is the product of the two matrices:

$$[\mathbf{S}\mathbf{T}] = [\mathbf{S}][\mathbf{T}]. \quad (11.13)$$

A tensor $\mathbf{S}$ is an *orthogonal tensor* if

$$\mathbf{S}\mathbf{S}^T = \mathbf{S}^T\mathbf{S} = \mathbf{1}, \quad (11.14)$$

where $\mathbf{1}$ is the identity tensor defined as $(\mathbf{1})\mathbf{a} = \mathbf{a} \forall \mathbf{a}$. As expected, it follows that the components of an orthogonal tensor form an orthogonal matrix. The group of

all orthogonal tensors in three dimensions is denoted $O(3)$. A *proper orthogonal tensor* is an orthogonal tensor with the additional property $\det \mathbf{S} = 1$. The group of all proper orthogonal tensors in three dimensions is denoted $SO(3)$. Orthogonal and proper orthogonal tensors are particularly useful to characterize rotations and proper rotations in a three-dimensional space.

We can also contract two tensors together to obtain a scalar by introducing the double contraction

$$\mathbf{S} : \mathbf{T} = \text{tr}(\mathbf{ST}) = S_{ij}T_{ji}. \quad (11.15)$$

If the determinant of a tensor $\mathbf{T}$ does not vanish, the matrix of *inverse* of $\mathbf{T}$ is the inverse of the matrix:

$$[\mathbf{T}^{-1}] = [\mathbf{T}]^{-1}. \quad (11.16)$$

Explicitly, for a tensor $\mathbf{T} = T_{ij}\mathbf{e}_i \otimes \mathbf{e}_j$, we have

$$\mathbf{T}^{-1} = ([\mathbf{T}]^{-1})_{ij}\mathbf{E}_i \otimes \mathbf{e}_j, \quad (11.17)$$

so that

$$\mathbf{T}\mathbf{T}^{-1} = \mathbf{1} = \delta_{ij}\mathbf{e}_i \otimes \mathbf{e}_j, \quad (11.18)$$

$$\mathbf{T}^{-1}\mathbf{T} = \mathbf{1} = \delta_{ij}\mathbf{E}_i \otimes \mathbf{E}_j, \quad (11.19)$$

where δ_{ij} is the usual Kronecker delta's symbol ($\delta_{ii} = 1$ and $\delta_{ij} = 0$ for $i \neq j$).

The tensor product can also be used to define higher order tensors. For instance, a third-order tensor, $\mathbf{Q}$, and a fourth-order tensor $\mathcal{Q}$, in the basis $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ are defined as

$$\mathbf{Q} = Q_{ijk}\mathbf{e}_i \otimes \mathbf{e}_j \otimes \mathbf{e}_k, \quad (11.20)$$

$$\mathcal{Q} = Q_{ijkl}\mathbf{e}_i \otimes \mathbf{e}_j \otimes \mathbf{e}_k \otimes \mathbf{e}_l. \quad (11.21)$$

However, in this case, the equivalence with linear algebra is lost and identities for higher order tensors must be obtained by following the rules defining the tensor products and playing the game of indices. Note that higher order tensors can also be defined with respect to multiple vector spaces.

11.1.2 Spatial Derivatives of Tensors

Next, we define spatial derivatives of scalar, vector, and tensor fields. We have two sets of spatial variables, the Lagrangian variables $\mathbf{X}$ and the Eulerian variables $\mathbf{x}$. We can therefore define different types of spatial derivatives depending on the description of a given quantity.

We first consider the case where ϕ , $\mathbf{u}$, and $\mathbf{T}$ are scalar, vector, and tensor fields, respectively, over $\mathbf{x}$, that is,

$$\phi = \phi(\mathbf{x}, t), \quad \mathbf{u} = u_i(\mathbf{x}, t)\mathbf{e}_i, \quad \mathbf{T} = T_{ij}(\mathbf{x}, t)\mathbf{e}_i \otimes \mathbf{e}_j. \quad (11.22)$$

We define the Eulerian *gradient* of scalar and vector functions as

$$\text{grad } \phi = \frac{\partial \phi}{\partial \mathbf{x}} = \frac{\partial \phi}{\partial x_i} \mathbf{e}_i, \quad (11.23)$$

$$\text{grad } \mathbf{u} = \frac{\partial \mathbf{u}}{\partial \mathbf{x}} = \frac{\partial \mathbf{u}}{\partial x_j} \otimes \mathbf{e}_j = \frac{\partial(u_i \mathbf{e}_i)}{\partial x_j} \otimes \mathbf{e}_j = \frac{\partial u_i}{\partial x_j} \mathbf{e}_i \otimes \mathbf{e}_j. \quad (11.24)$$

The gradient is an operation that increases the order of the tensor and is defined, in general, as the operation

$$\text{grad}(\cdot) = \frac{\partial(\cdot)}{\partial x_j} \otimes \mathbf{e}_j. \quad (11.25)$$

It follows from this definition that

$$\text{grad}(\phi \mathbf{u}) = \mathbf{u} \otimes \text{grad } \phi + \phi \text{ grad } \mathbf{u}. \quad (11.26)$$

Similarly, we define the gradient of a second-order tensor as

$$\text{grad } \mathbf{T} = \frac{\partial}{\partial x_k} (T_{ij} \mathbf{e}_i \otimes \mathbf{e}_j) \otimes \mathbf{e}_k = \frac{\partial T_{ij}}{\partial x_k} \mathbf{e}_i \otimes \mathbf{e}_j \otimes \mathbf{e}_k. \quad (11.27)$$

The *divergence* decreases the order of a tensor by contracting indices. For a vector, we have simply

$$\text{div } \mathbf{u} = \frac{\partial u_i}{\partial x_i}. \quad (11.28)$$

For a second-order tensor, the contraction can take place on the first or second index depending on the convention. Here, we choose to define the divergence as a contraction on the first index, that is,

$$\text{div } \mathbf{T} = \frac{\partial T_{ij}}{\partial x_k} \mathbf{e}_j (\mathbf{e}_i \cdot \mathbf{e}_k) = \frac{\partial T_{ij}}{\partial x_i} \mathbf{e}_j. \quad (11.29)$$

With this particular definition of the divergence operator, the *divergence theorem*, applied on a domain $\Omega \subset \mathbb{R}^3$, reads

$$\int_{\partial \Omega} \mathbf{T} \mathbf{n} \, da = \int_{\Omega} \text{div}(\mathbf{T}^T) \, dv. \quad (11.30)$$

Next, we consider spatial derivatives with respect to Lagrangian coordinates, that is, Φ , $\mathbf{U}$, and $\mathbf{T}$ are now fields over $\mathbf{X}$:

$$\Phi = \Phi(\mathbf{X}, t), \quad \mathbf{U} = u_i(\mathbf{X}, t)\mathbf{E}_i, \quad \mathbf{T} = T_{ij}(\mathbf{X}, t)\mathbf{E}_i \otimes \mathbf{E}_j. \quad (11.31)$$

The Lagrangian gradient is then the operation

$$\text{Grad}(\cdot) = \frac{\partial(\cdot)}{\partial X_j} \otimes \mathbf{E}_j. \quad (11.32)$$

Note that we use the lower case “grad” and “div” to describe spatial derivatives with respect to Eulerian coordinates and the upper case “Grad” and “Div” for spatial derivatives with respect to Lagrangian coordinates. Explicitly, we have

$$\text{Grad } \Phi = \frac{\partial \Phi}{\partial \mathbf{X}} = \frac{\partial \Phi}{\partial X_i} \mathbf{E}_i, \quad (11.33)$$

$$\text{Grad } \mathbf{U} = \frac{\partial \mathbf{U}}{\partial \mathbf{X}} = \frac{\partial \mathbf{U}}{\partial X_j} \otimes \mathbf{E}_j = \frac{\partial(U_i \mathbf{E}_i)}{\partial X_j} \otimes \mathbf{E}_j = \frac{\partial U_i}{\partial X_j} \mathbf{E}_i \otimes \mathbf{E}_j, \quad (11.34)$$

$$\text{Grad } \mathbf{T} = \frac{\partial}{\partial X_k} (T_{ij} \mathbf{e}_i \otimes \mathbf{E}_j) \otimes \mathbf{E}_k = \frac{\partial T_{ij}}{\partial X_k} \mathbf{e}_i \otimes \mathbf{E}_j \otimes \mathbf{E}_k. \quad (11.35)$$

The divergence is then

$$\text{Div } \mathbf{U} = \frac{\partial U_i}{\partial X_i}, \quad (11.36)$$

$$\text{Div } \mathbf{T} = \frac{\partial T_{ij}}{\partial X_k} \mathbf{e}_j (\mathbf{E}_i \cdot \mathbf{E}_k) = \frac{\partial T_{ij}}{\partial X_i} \mathbf{e}_j. \quad (11.37)$$

Note that these definitions can be appropriately modified for the case where $\mathbf{T} = T_{ij} \mathbf{E}_i \otimes \mathbf{E}_j$ by changing $\mathbf{e}_j \rightarrow \mathbf{E}_j$ in the definition of Grad and Div.

11.1.3 Derivatives in Curvilinear Coordinates

It is often convenient to describe a body and a deformation with respect to curvilinear coordinates. For instance, it is natural to use cylindrical coordinates to describe simple deformations of a cylinder. We use the curvilinear coordinates $\{q_1, q_2, q_3\}$ in the current configuration and $\{Q_1, Q_2, Q_3\}$ in the reference configuration. These coordinates are related to the Cartesian coordinates in each configuration through the position vectors $\mathbf{x} = \mathbf{x}(q_1, q_2, q_3)$ and $\mathbf{X} = \mathbf{X}(Q_1, Q_2, Q_3)$. Here, we use greek subscripts to denote quantities defined in non-Cartesian coordinates. For instance, we associate to each coordinate set, a set of basis vectors

$$\mathbf{e}_\alpha = h_\alpha^{-1} \frac{\partial \mathbf{x}}{\partial q_\alpha}, \quad \mathbf{E}_\alpha = H_\alpha^{-1} \frac{\partial \mathbf{X}}{\partial Q_\alpha}, \quad \alpha = 1, 2, 3, \quad (11.38)$$

where h_α and H_α are *scale factors*, used to normalize the basis vectors:

$$h_\alpha = \left| \frac{\partial \mathbf{x}}{\partial q_\alpha} \right|, \quad H_\alpha = \left| \frac{\partial \mathbf{X}}{\partial Q_\alpha} \right|, \quad \alpha = 1, 2, 3. \quad (11.39)$$

For brevity, we restrict our attention to a set of orthonormal coordinate, so that

$$\mathbf{e}_\alpha \cdot \mathbf{e}_\beta = \delta_{\alpha\beta}, \quad \mathbf{E}_\alpha \cdot \mathbf{E}_\beta = \delta_{\alpha\beta}, \quad \alpha, \beta = 1, 2, 3. \quad (11.40)$$

We define the gradient, $\text{grad } \mathbf{T} = \nabla \otimes \mathbf{T}$, of a tensor $\mathbf{T}$ at a point $\mathbf{x} \in \mathcal{B}$ as the tensor that maps a vector $\mathbf{v}$ in the tangent space of $\mathcal{B}$ at $\mathbf{x}$ onto the infinitesimal variation of $\mathbf{T}$ along a path going through $\mathbf{x}$ with tangent $\mathbf{v}$. For any given $\mathbf{v}$, we define a path Γ , parameterized by its arc length s , going through $\mathbf{x}$ and tangent to $\mathbf{v}$. The operation of the gradient on a vector $\mathbf{v}$ is

$$\begin{aligned} (\nabla \otimes \mathbf{T})\mathbf{v} &= \frac{d\mathbf{T}(\Gamma(s))}{ds} = \lim_{ds \rightarrow 0} \frac{\mathbf{T}(\Gamma(s + ds)) - \mathbf{T}(\Gamma(s))}{ds} \\ &= \frac{\partial \mathbf{T}(\mathbf{x})}{\partial x^\alpha} \frac{dx^\alpha}{ds} = \frac{\partial \mathbf{T}(\mathbf{x})}{\partial x^\alpha} \delta_{\alpha\beta} \frac{dx^\beta}{ds} \\ &= \frac{\partial \mathbf{T}}{\partial q_\alpha} (h_\alpha^{-1} \mathbf{e}_\alpha \cdot h_\beta \mathbf{e}_\beta) \frac{dq_\beta}{ds} \\ &= \left(\frac{\partial \mathbf{T}}{\partial q_\alpha} \otimes h_\alpha^{-1} \mathbf{e}_\alpha \right) (\mathbf{v}), \end{aligned} \quad (11.41)$$

where we have used the fact that the tangent to Γ at $\mathbf{x}$ is $h_\beta \mathbf{e}_\beta (dq_\beta/ds)$. Since this operation applies to arbitrary vectors $\mathbf{v}$, the *gradient of a tensor in orthogonal curvilinear coordinates* is

$$\text{grad } \mathbf{T} = h_\alpha^{-1} \frac{\partial \mathbf{T}}{\partial q_\alpha} \otimes \mathbf{e}_\alpha, \quad \text{Grad } \mathbf{T} = H_\alpha^{-1} \frac{\partial \mathbf{T}}{\partial Q_\alpha} \otimes \mathbf{E}_\alpha. \quad (11.42)$$

Similarly, we define the *divergence of a tensor field* $\mathbf{T}$ as $\text{div } \mathbf{T} = \nabla \cdot \mathbf{T}$, that is,

$$\text{div } \mathbf{T} = h_\alpha^{-1} \mathbf{e}_\alpha \cdot \frac{\partial \mathbf{T}}{\partial q_\alpha}, \quad \text{Div } \mathbf{T} = H_\alpha^{-1} \mathbf{E}_\alpha \cdot \frac{\partial \mathbf{T}}{\partial Q_\alpha}. \quad (11.43)$$

Note that we take the scalar product on the left which corresponds to the contraction on the first index of $\mathbf{T}$. Choosing Cartesian coordinates $\{q_1, q_2, q_3\} = \{x_1, x_2, x_3\}$ leads to $h_\alpha = 1 \forall \alpha$, and the definitions (11.42) and (11.43) reduce to those of the previous section.

As an example, consider the choice of polar coordinates $\{q_1, q_2\} = \{r, \theta\}$ in the Euclidean plane. The position vector is $\mathbf{x} = r \cos \theta \mathbf{e}_1 + r \sin \theta \mathbf{e}_2$, so that

$$\begin{aligned} \mathbf{e}_r &= \frac{\partial \mathbf{x}}{\partial r}, & h_r &= 1, \\ \mathbf{e}_\theta &= \frac{1}{r} \frac{\partial \mathbf{x}}{\partial \theta}, & h_\theta &= r. \end{aligned} \quad (11.44)$$

Hence, according to (11.42), the gradient of a scalar ϕ is

$$\text{grad } \phi = (\partial_r \phi) \mathbf{e}_r + \frac{1}{r} (\partial_\theta \phi) \mathbf{e}_\theta, \quad (11.45)$$

and we recover the usual formula of vector calculus. Similarly, if we write a second-order tensor $\mathbf{T}$ in polar representation:

$$\mathbf{T} = T_{rr} \mathbf{e}_r \otimes \mathbf{e}_r + T_{r\theta} \mathbf{e}_r \otimes \mathbf{e}_\theta + T_{\theta r} \mathbf{e}_\theta \otimes \mathbf{e}_r + T_{\theta\theta} \mathbf{e}_\theta \otimes \mathbf{e}_\theta, \quad (11.46)$$

then its divergence is the first-order tensor

$$\begin{aligned} \text{div } \mathbf{T} &= \left(\frac{1}{r} \frac{\partial}{\partial r} (r T_{rr}) + \frac{1}{r} \frac{\partial T_{\theta r}}{\partial \theta} - \frac{T_{\theta\theta}}{r} \right) \mathbf{e}_r \\ &\quad + \left(\frac{1}{r} \frac{\partial}{\partial r} (r T_{r\theta}) + \frac{1}{r} \frac{\partial T_{\theta\theta}}{\partial \theta} + \frac{T_{\theta r}}{r} \right) \mathbf{e}_\theta. \end{aligned} \quad (11.47)$$

And, the gradient of $\mathbf{T}$ is the third-order tensor

$$\begin{aligned} \text{grad } \mathbf{T} &= \frac{\partial \mathbf{T}}{\partial r} \otimes \mathbf{e}_r + \frac{1}{r} \frac{\partial \mathbf{T}}{\partial \theta} \otimes \mathbf{e}_\theta \\ &= (\partial_r T_{rr}) \mathbf{e}_r \otimes \mathbf{e}_r \otimes \mathbf{e}_r + (\partial_r T_{r\theta}) \mathbf{e}_r \otimes \mathbf{e}_\theta \otimes \mathbf{e}_r \\ &\quad + (\partial_r T_{\theta r}) \mathbf{e}_\theta \otimes \mathbf{e}_r \otimes \mathbf{e}_r + (\partial_r T_{\theta\theta}) \mathbf{e}_\theta \otimes \mathbf{e}_\theta \otimes \mathbf{e}_r \\ &\quad + \left(\frac{1}{r} (\partial_\theta T_{rr}) - T_{r\theta} - T_{\theta r} \right) \mathbf{e}_r \otimes \mathbf{e}_r \otimes \mathbf{e}_\theta \\ &\quad + \left(\frac{1}{r} (\partial_\theta T_{\theta r}) + T_{rr} - T_{\theta\theta} \right) \mathbf{e}_\theta \otimes \mathbf{e}_r \otimes \mathbf{e}_\theta \\ &\quad + \left(\frac{1}{r} (\partial_\theta T_{r\theta}) + T_{rr} - T_{\theta\theta} \right) \mathbf{e}_r \otimes \mathbf{e}_\theta \otimes \mathbf{e}_\theta \\ &\quad + \left(\frac{1}{r} (\partial_\theta T_{\theta\theta}) + T_{r\theta} + T_{\theta r} \right) \mathbf{e}_\theta \otimes \mathbf{e}_\theta \otimes \mathbf{e}_\theta. \end{aligned}$$

11.1.4 Derivatives of Scalar Functions of Tensors

We will also consider scalar functions of tensors and their derivatives with respect to a tensor. Let $\mathbf{A}$, $\mathbf{B}$, $\mathbf{C}$ be second-order tensors with Cartesian components in the basis $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ given by A_{ij} , B_{ij} , C_{ij} . Let $F = F(\mathbf{A})$ be a scalar function of $\mathbf{A}$. The derivative of the scalar function F with respect to the tensor $\mathbf{A}$ is a tensor with Cartesian components

$$\left(\frac{\partial F(\mathbf{A})}{\partial \mathbf{A}} \right)_{ij} = \frac{\partial F(\mathbf{A})}{\partial A_{ji}}, \quad (11.48)$$

that is,

$$\frac{\partial F(\mathbf{A})}{\partial \mathbf{A}} = \frac{\partial F}{\partial A_{ji}} \mathbf{e}_i \otimes \mathbf{e}_j. \quad (11.49)$$

Now, let $\mathbf{A} = \mathbf{B}\mathbf{C}$ and consider the derivative of F with respect to $\mathbf{B}$. In components, we have

$$\begin{aligned} \left(\frac{\partial F(\mathbf{A})}{\partial \mathbf{B}} \right)_{ij} &= \frac{\partial F(B_{kl}C_{lm})}{\partial B_{ji}} \\ &= \frac{\partial A_{km}}{\partial B_{ji}} \frac{\partial F(\mathbf{A})}{\partial A_{km}} = \frac{\partial B_{kl}C_{lm}}{\partial B_{ji}} \frac{\partial F(\mathbf{A})}{\partial A_{km}} \\ &= \delta_{jk}\delta_{il}C_{lm} \frac{\partial F(\mathbf{A})}{\partial A_{km}} = C_{im} \frac{\partial F(\mathbf{A})}{\partial A_{jm}} \\ &= C_{im} \left(\frac{\partial F(\mathbf{A})}{\partial \mathbf{A}} \right)_{mj}. \end{aligned} \quad (11.50)$$

So that, in general, we can write

$$\frac{\partial F(\mathbf{A})}{\partial \mathbf{B}} = \mathbf{C} \frac{\partial F(\mathbf{A})}{\partial \mathbf{A}}. \quad (11.51)$$

Other useful identities are *Jacobi's relations* for the first and second derivatives of a nonvanishing determinant,

$$\begin{aligned} \frac{\partial}{\partial \mathbf{A}} (\det(\mathbf{A})) &= \det(\mathbf{A}) \mathbf{A}^{-1}, \\ \text{tr} \left[\left(\frac{\partial}{\partial \mathbf{A}} \frac{\partial}{\partial \mathbf{A}} \det \mathbf{A} \right) \mathbf{B} \right] &= \det(\mathbf{A}) [\text{tr}(\mathbf{A}^{-1} \mathbf{B}) \mathbf{A}^{-1} - \mathbf{A}^{-1} \mathbf{B} \mathbf{A}^{-1}], \end{aligned} \quad (11.52)$$

$$(11.53)$$

where the contraction $\text{tr}(\mathcal{L}\mathbf{A})$ of a second-order tensor $\mathbf{A}$ with a fourth-order tensor $\mathcal{L}$ is defined by $(\text{tr}(\mathcal{L}\mathbf{A}))_{ij} = \mathcal{L}_{ijkl}A_{lk}$. In the last equality, the derivative of the inverse of a tensor by itself defines a fourth-order tensor such that

$$\text{tr} \left[\left(\frac{\partial}{\partial \mathbf{A}} \mathbf{A}^{-1} \right) \mathbf{B} \right] = -\mathbf{A}^{-1} \mathbf{B} \mathbf{A}^{-1}. \quad (11.54)$$

If $\mathbf{A} = \mathbf{A}(t)$, the derivative of a scalar function of $\mathbf{A}$ with respect to a parameter t can be obtained by the chain rule, that is,

$$\frac{d}{dt} F(\mathbf{A}) = \text{tr} \left(\frac{\partial F(\mathbf{A})}{\partial \mathbf{A}} \frac{d\mathbf{A}}{dt} \right). \quad (11.55)$$

As an example, the first Jacobi relation (11.52) can be used to compute the derivative of the determinant of a tensor with respect to a parameter

$$\frac{d}{dt}(\det(\mathbf{A})) = \text{tr} \left(\frac{\partial}{\partial \mathbf{A}}(\det(\mathbf{A})) \frac{d\mathbf{A}}{dt} \right) = \det(\mathbf{A}) \text{tr} \left(\mathbf{A}^{-1} \frac{d\mathbf{A}}{dt} \right). \quad (11.56)$$

11.1.5 The Deformation Gradient

The central geometric object of nonlinear elasticity that describes, locally, relative deformations is the *deformation gradient*. It is obtained as the spatial derivative of the mapping χ . Given a vector $\mathbf{x} = x_i(\mathbf{X})\mathbf{e}_i$, the deformation gradient tensor is $\mathbf{F} = \text{Grad } \chi$. In Cartesian coordinates, it reads

$$\mathbf{F} = \frac{\partial}{\partial X_j}(x_i \mathbf{e}_i) \otimes \mathbf{E}_j = \frac{\partial x_i}{\partial X_j} \mathbf{e}_i \otimes \mathbf{E}_j \equiv F_{ij} \mathbf{e}_i \otimes \mathbf{E}_j. \quad (11.57)$$

Note that the bases in which the gradient is taken are mixed. Geometrically, $\mathbf{F}$ is a linear map that transforms a vector $\mathbf{v}$ in the tangent space $T_p \mathcal{B}_0$ at a material point $p \in \mathcal{B}_0$ to a vector $\mathbf{Fv}$ in the tangent space $T_p \mathcal{B}$ at the same material point but in the current configuration, as shown in Figure 11.3.

We can also express the deformation gradient in curvilinear coordinates. Let $\{q_1, q_2, q_3\}$ and $\{Q_1, Q_2, Q_3\}$ be the coordinates in the reference and current configuration, respectively. The deformation χ in the bases $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ and $\{\mathbf{E}_1, \mathbf{E}_2, \mathbf{E}_3\}$ is

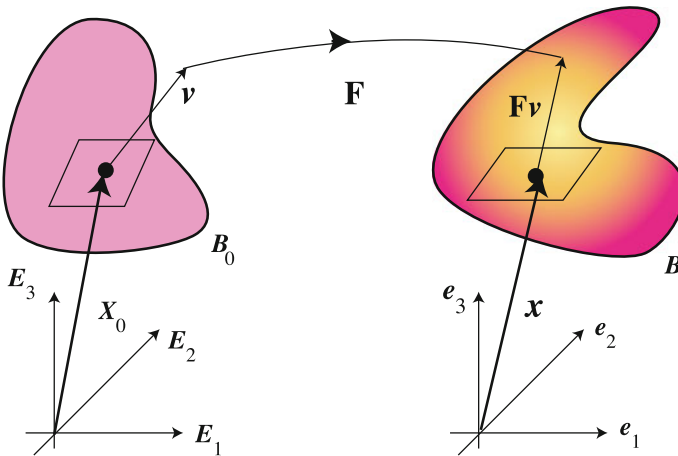


Figure 11.3 The deformation gradient maps vectors on the tangent space at a material point in the initial configuration to vectors in the tangent space in the current configuration at the same material point.

given by $q_\alpha = q_\alpha(Q_1, Q_2, Q_3)$, $\alpha = 1, 2, 3$. Then, following the definition of the gradient (11.42), we have

$$\begin{aligned} \text{Grad } \mathbf{x} &= H_\beta^{-1} \frac{\partial \mathbf{x}}{\partial Q_\beta} \otimes \mathbf{E}_\beta \\ &= H_\beta^{-1} \frac{\partial \mathbf{x}}{\partial q_\alpha} \frac{\partial q_\alpha}{\partial Q_\beta} \otimes \mathbf{E}_\beta \end{aligned} \quad (11.58)$$

$$= \frac{h_\alpha}{H_\beta} \frac{\partial q_\alpha}{\partial Q_\beta} \mathbf{e}_\alpha \otimes \mathbf{E}_\beta, \quad (11.59)$$

where we used $\frac{\partial \mathbf{x}}{\partial q_\beta} = h_\beta \mathbf{e}_\beta$ and the scale factors h_α, H_β given by (11.39). Then, we conclude that the matrix of coefficients of the deformation gradient $\mathbf{F} = F_{\alpha\beta} \mathbf{e}_\alpha \otimes \mathbf{E}_\beta$ is

$$[\mathbf{F}]_{\alpha\beta} = F_{\alpha\beta} = \frac{h_\alpha}{H_\beta} \frac{\partial q_\alpha}{\partial Q_\beta} \quad (\text{no summation on indices}). \quad (11.60)$$

As an example, we consider the deformation of a ring in a plane to another ring shown in Figure 11.4. In the two sets of polar coordinates $\{q_1, q_2\} = \{r, \theta\}$ and $\{Q_1, Q_2\} = \{R, \Theta\}$, this deformation is given by

$$r = f(R), \quad \theta = \Theta. \quad (11.61)$$

For these coordinates, we have $h_r = H_R = 1$ and $h_\theta = r, H_\Theta = R$, and the deformation gradient is

$$[\mathbf{F}] = \begin{bmatrix} \frac{h_r}{H_R} \frac{\partial r}{\partial R} & \frac{h_r}{H_\Theta} \frac{\partial r}{\partial \Theta} \\ \frac{h_\theta}{H_R} \frac{\partial \theta}{\partial R} & \frac{h_\theta}{H_\Theta} \frac{\partial \theta}{\partial \Theta} \end{bmatrix} = \begin{bmatrix} f'(R) & 0 \\ 0 & \frac{f(R)}{R} \end{bmatrix}, \quad (11.62)$$

that is,

$$\mathbf{F} = f'(R) \mathbf{e}_r \otimes \mathbf{E}_R + \frac{r}{R} \mathbf{e}_\theta \otimes \mathbf{E}_\Theta. \quad (11.63)$$

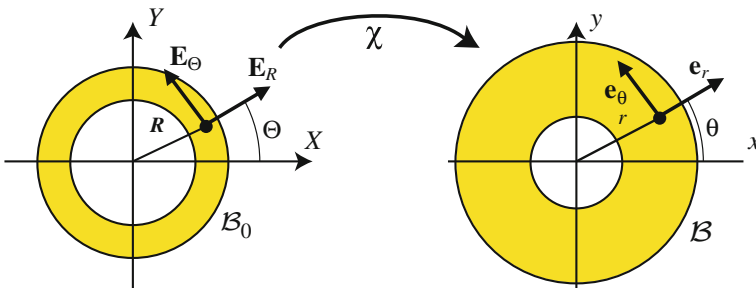


Figure 11.4 Deformation of a ring into another ring in the plane.

11.1.6 Volume, Surface, and Line Elements

The deformation of a body may change the relative size of material elements. First, consider a set of material points in the reference configuration $\Omega_0 \subseteq \mathcal{B}_0$. This set evolves in time and is deformed to a new volume $\Omega \subseteq \mathcal{B}$ in the current configuration. The new volume is related to the reference volume by

$$\int_{\Omega} dv = \int_{\Omega_0} J dV_0, \quad (11.64)$$

where

$$J(\mathbf{X}, t) = \det \mathbf{F}(\mathbf{X}, t), \quad (11.65)$$

is the Jacobian of the transformation that represents the local change of volume. That is, the image of an infinitesimal volume element dv at a material point p is

$$dv = J dV, \quad (11.66)$$

as shown in Figure 11.5.

Since volume elements are positive and cannot vanish in a deformation, we require that $J > 0$ in all deformations, which ensures the invertibility of the deformation gradient, that is, there exists a second-order tensor $\mathbf{F}^{-1}$ mapping vectors from $\mathcal{B}$ to $\mathcal{B}_0$, such that $\mathbf{F}^{-1}\mathbf{F} = \mathbf{1}$. Explicitly, this tensor is

$$\mathbf{F}^{-1} = \text{grad } \mathbf{X}(\mathbf{x}, t). \quad (11.67)$$

A transformation that conserves locally every volume element, that is $J = 1$, is said to be *isochoric*.

Similarly, we define an area element by considering a material area element normal to a given vector $\mathbf{N}$. Then, it is standard to show [975] that the surface integral transforms as

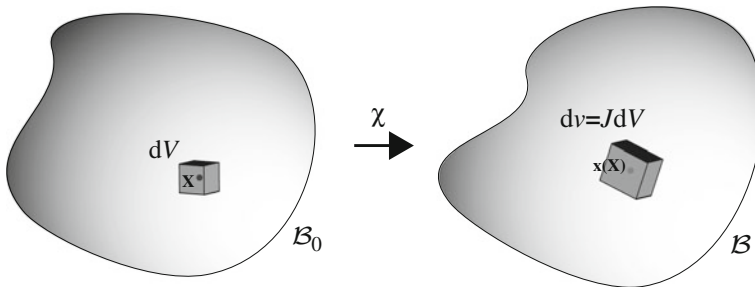


Figure 11.5 Transformation of volumes: In a deformation, an infinitesimal volume element dV at a material point evolves by a factor J to a new volume $dv = J dV$.

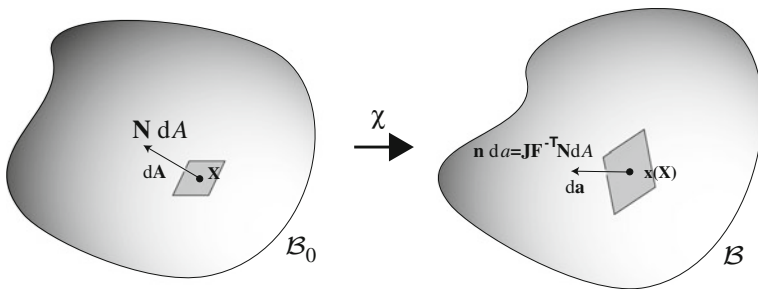


Figure 11.6 Transformation of areas: In a deformation, an infinitesimal area is transformed according to Nanson's rule.

$$\int_{\partial\Omega} \mathbf{n} da = \int_{\partial\Omega_0} J \mathbf{F}^{-T} \mathbf{N} dA, \quad (11.68)$$

where $\mathbf{n}(\mathbf{x}, t)$ and $\mathbf{N}(\mathbf{X}, t)$ are outward unit normals, dA and da are the area elements at a given point as shown in Figure 11.6, that is, an infinitesimal element of area defined in the reference configuration by a normal $\mathbf{N}$ and surface area dA is transformed into another element of area in the current configuration defined by a vector $\mathbf{n}$ with area da and related to the reference one by *Nanson's formula*:

$$\mathbf{n} da = J \mathbf{F}^{-T} \mathbf{N} dA. \quad (11.69)$$

Finally, consider a local infinitesimal vector $d\mathbf{X}$ tangent to a material line in $\mathcal{B}_0$ at a material point p . Then its image is $d\mathbf{x} = \mathbf{F}d\mathbf{X}$ as shown in Figure 11.7. If $\mathbf{M}$ is the unit vector along $d\mathbf{X}$, then

$$d\mathbf{X} = \mathbf{M} dS \quad \text{and} \quad d\mathbf{x} = \mathbf{m} ds, \quad (11.70)$$

where $dS = |d\mathbf{X}|$ and $ds = |d\mathbf{x}|$.

This last identity implies that $\mathbf{m} ds = \mathbf{F}\mathbf{M} dS$. Now take the norm of each side:

$$|ds|^2 = (\mathbf{F}\mathbf{M} \cdot \mathbf{F}\mathbf{M})|dS|^2 = (\mathbf{F}^T \mathbf{F}\mathbf{M}) \cdot \mathbf{M} |dS|^2. \quad (11.71)$$

Equivalently, we can write

$$\frac{ds}{dS} = \sqrt{(\mathbf{F}^T \mathbf{F}\mathbf{M}) \cdot \mathbf{M}}, \quad (11.72)$$

where ds/dS is the change of length of a material line in the direction $\mathbf{M}$. This last relationship is used to define the *stretch*, $\lambda = \lambda(\mathbf{M})$ of a material line in the direction $\mathbf{M}$ as

$$\lambda(\mathbf{M}) = \sqrt{(\mathbf{F}^T \mathbf{F}\mathbf{M}) \cdot \mathbf{M}}. \quad (11.73)$$

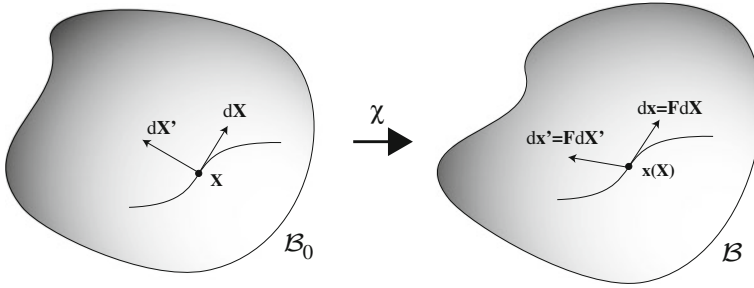


Figure 11.7 Transformation of material lines: In a deformation, an infinitesimal line element is mapped by the deformation gradient to a new line element.

Since we are interested in characterizing elastic materials, we need to characterize deformations that change the relative length of line elements. Therefore, stretches provide a natural measure of *strain* in a material. A material is said to be *unstrained* in the direction $\mathbf{M}$ if and only if $\lambda(\mathbf{M}) = 1$.

In (11.71), we see the appearance of an important tensor in the description of strain for a three-dimensional body, namely the *right Cauchy–Green tensor*

$$\mathbf{C} = \mathbf{F}^T \mathbf{F}. \quad (11.74)$$

A material is *unstrained* at a given point if it is unstrained in all directions, that is, $\lambda(\mathbf{M}) = 1 \ \forall \mathbf{M}$. In terms of the right Cauchy–Green tensor, this implies $\mathbf{C} = \mathbf{1}$.

Geometrically, the tensor $\mathbf{C}$ can be interpreted as a metric on $\mathcal{B}$ as it provides a way to measure distances and angles on the new body (see Section 12.5.1).

11.1.7 Polar Decomposition Theorem

The action of the deformation gradient $\mathbf{F}$ on a vector $\mathbf{M}$ can be decomposed into a rotation about a direction $\mathbf{m}$, followed by a stretch of size $\lambda(\mathbf{M})$. This decomposition into a stretch and a rotation can be applied directly to the deformation gradient through the polar decomposition theorem stating: *For a second-order tensor $\mathbf{F}$ such that $\det \mathbf{F} > 0$, there exist unique positive-definite symmetric tensors $\mathbf{U}$, $\mathbf{V}$ and a unique proper orthogonal tensor $\mathbf{R}$ such that*

$$\mathbf{F} = \mathbf{R}\mathbf{U} = \mathbf{V}\mathbf{R}.$$

The positive symmetric tensors $\mathbf{U}$ and $\mathbf{V}$ are called the *left* and *right stretch tensors*, respectively. Their squares can easily be obtained from $\mathbf{F}$ as follows:

$$\begin{aligned} \mathbf{F}^T \mathbf{F} &= \mathbf{U}^2 \equiv \mathbf{C}, & \text{the right Cauchy–Green tensor,} \\ \mathbf{F} \mathbf{F}^T &= \mathbf{V}^2 \equiv \mathbf{B}, & \text{the left Cauchy–Green tensor.} \end{aligned}$$

Since $\mathbf{V} = \mathbf{R}\mathbf{U}\mathbf{R}^\top$, $\mathbf{U}$ and $\mathbf{V}$ have the same eigenvalues $\{\lambda_1, \lambda_2, \lambda_3\}$. The *principal stretches* can be obtained conveniently as the square roots of the eigenvalues of either $\mathbf{C}$ or $\mathbf{B}$. Note that since $\mathbf{U}$ and $\mathbf{V}$ are positive symmetric, the principal stretches are positive and real and the corresponding eigenvectors $\{\mathbf{u}_1, \mathbf{u}_2, \mathbf{u}_3\}$ and $\{\mathbf{v}_1, \mathbf{v}_2, \mathbf{v}_3\}$ of $\mathbf{U}$ and $\mathbf{V}$ form two bases. Therefore, the stretch tensors can be written as

$$\mathbf{U} = \sum_{i=1}^3 \lambda_i \mathbf{u}_i \otimes \mathbf{u}_i, \quad (11.75)$$

$$\mathbf{V} = \sum_{i=1}^3 \lambda_i \mathbf{v}_i \otimes \mathbf{v}_i. \quad (11.76)$$

Since $J = \det \mathbf{F} = \det(\mathbf{R}\mathbf{U}) = (\det \mathbf{R})(\det \mathbf{U}) = \det \mathbf{U} = \det \mathbf{V}$, we have $J = \lambda_1 \lambda_2 \lambda_3$ and we can rewrite $\mathbf{F}$ as

$$\mathbf{F} = \sum_{i=1}^3 \lambda_i \mathbf{v}_i \otimes \mathbf{u}_i. \quad (11.77)$$

11.1.8 Velocity, Acceleration, and Velocity Gradient

The motion associated with a deformation $\mathbf{x} = \chi(\mathbf{X}, t)$, $\mathbf{X} \in \mathcal{B}_0$, is associated with change in time t . Since $\mathbf{X}$ is the position of a material point, the *velocity* and *acceleration* of this material point are, respectively,

$$\mathbf{v}(\mathbf{x}, t) = \frac{\partial}{\partial t} \chi(\mathbf{X}, t) \equiv \dot{\chi}(\mathbf{X}, t), \quad (11.78)$$

$$\mathbf{a}(\mathbf{x}, t) = \frac{\partial^2}{\partial t^2} \chi(\mathbf{X}, t) \equiv \ddot{\chi}(\mathbf{X}, t). \quad (11.79)$$

In general, we define the *material time derivative* d/dt as a total time derivative with respect to a fixed material coordinate $\mathbf{X}$. For a scalar field $\phi = \phi(\mathbf{x}, t)$, the material derivative is

$$\frac{d}{dt} \phi \equiv \left. \frac{d\phi}{dt} \right|_{\mathbf{X}} \equiv \dot{\phi} \equiv \frac{\partial \phi}{\partial t} + (\text{grad } \phi) \cdot \mathbf{v}, \quad (11.80)$$

and we define the derivative of a vector field $\mathbf{u} = \mathbf{u}(\mathbf{x}, t)$ similarly as

$$\frac{d}{dt} \mathbf{u} \equiv \frac{\partial \mathbf{u}}{\partial t} + (\text{grad } \mathbf{u}) \mathbf{v}. \quad (11.81)$$

Another important kinematic quantity is the *velocity gradient tensor*, defined as

$$\mathbf{L} = \text{grad } \mathbf{v}, \quad L_{ij} = \frac{\partial v_i}{\partial x_j}, \quad \mathbf{L} = L_{ij} \mathbf{e}_i \otimes \mathbf{e}_j. \quad (11.82)$$

Since, in general the chain rule gives $\text{Grad } \mathbf{u} = (\text{grad } \mathbf{u})\mathbf{F}$, we have

$$\text{Grad } \mathbf{v} = (\text{grad } \mathbf{v})\mathbf{F} = \mathbf{L}\mathbf{F}, \quad (11.83)$$

but also,

$$\text{Grad } \mathbf{v} = \text{Grad } \dot{\mathbf{x}} = \frac{\partial}{\partial t} \text{Grad } \mathbf{x} = \frac{\partial \mathbf{F}}{\partial t} = \dot{\mathbf{F}}, \quad (11.84)$$

so that the evolution of the deformation gradient can be expressed in terms of the velocity gradient tensor as

$$\dot{\mathbf{F}} = \mathbf{L}\mathbf{F}. \quad (11.85)$$

Taking the determinant of each side of this last equality and applying Jacobi's formula (11.56) for the derivative of the determinant of a nonsingular matrix

$$\frac{\partial}{\partial t} \det \mathbf{F} = (\det \mathbf{F}) \text{tr}(\mathbf{F}^{-1} \dot{\mathbf{F}}) = (\det \mathbf{F}) \text{tr}(\mathbf{L}), \quad (11.86)$$

leads to an equation for the evolution of the determinant:

$$\dot{J} = J \text{tr}(\mathbf{L}) = J \text{div } \mathbf{v}. \quad (11.87)$$

In particular, since $J \neq 0$, we note the well-known relationship between conservation of volume during motion and the vanishing of the divergence of the velocity:

$$\text{div } \mathbf{v} = 0 \quad \Longleftrightarrow \quad \dot{J} = 0. \quad (11.88)$$

11.2 Balance Laws

We have obtained a complete description of the deformation of a body. Starting with a mapping χ , we defined the deformation gradient $\mathbf{F}$. This tensor contains all information on relative deformations of a body, such as local changes of volume, area, and stretch. It was used to define secondary quantities, such as the left and right Cauchy–Green tensor, $\mathbf{B}$ and $\mathbf{C}$, that contain information on the strain developed during a deformation. Now that we have a complete kinematic description of the body, we can define physical fields at each point and used fundamental laws of physics to find local equations between these fields.

The governing equations of continuum mechanics are obtained by considering the balance of physical quantities: mass, linear momentum, angular momentum, and energy. The traditional approach to derive local laws consists in stating a balance law on an arbitrary subset of the body and, under suitable conditions, obtaining local relationships between physical quantities expressed as differential equations. We illustrate this process first on the balance of mass.

11.2.1 Balance of Mass

To describe the properties and response of a material, we attach physical quantities at each point of the body B . First, we define a scalar field $\rho = \rho(\mathbf{x}, t)$ and the *volume density* (mass per unit current volume) at each point of the body in the current configuration. We assume that the mass of any subset of the body $\Omega \subseteq B$ is conserved in time, that is,

$$\frac{d}{dt} \int_{\Omega} \rho(\mathbf{x}, t) dv = 0. \quad (11.89)$$

The problem is that the position of a material subset Ω evolves with time, and the time derivative cannot be directly applied to the integrand. Therefore, we first map the integral to the reference configuration

$$\frac{d}{dt} \int_{\Omega_0} \rho(\mathbf{x}(\mathbf{X}, t), t) J dV = 0, \quad (11.90)$$

where we have used the transformation of a volume element (11.66).

Second, since the domain Ω_0 is fixed, we can write

$$\frac{d}{dt} \int_{\Omega_0} J \rho(\mathbf{x}, t) dV = \int_{\Omega_0} \frac{d}{dt} (J \rho) dV = 0. \quad (11.91)$$

Third, since we wish to obtain a balance law in the current configuration, we map the integral back, that is,

$$\int_{\Omega_0} \frac{d}{dt} (J \rho) dV = \int_{\Omega} \frac{d}{dt} (J \rho) J^{-1} dv = \int_{\Omega} (\dot{\rho} + \rho \operatorname{div} \mathbf{v}) dv = 0, \quad (11.92)$$

where we have used (11.87).

Fourth, assuming that the integrand is continuous, the vanishing of an integral on an arbitrary domain implies that it vanishes pointwise, which leads to the usual *continuity equation* for the evolution of density in the current configuration [525]

$$\dot{\rho} + \rho \operatorname{div} \mathbf{v} = 0. \quad (11.93)$$

The procedure consisting in mapping an integral relationship between configurations and localizing this relationship to obtain a local differential equation is a two-step process called the *Maxwell transport* and *localization procedure*, respectively.

In the first step, integrals in the current configuration are transformed into integrals in the initial configuration that are expressed on a fixed domain. In this configuration, the balance law can be written as a single integral over a domain. Once this expression has been obtained, the integral can be mapped back to the current configuration.

In the second step, a local differential equation is obtained from the integral by assuming that it holds on an arbitrary subset and that the integrand is continuous.

Note that the localization procedure can be also applied directly to the first integral appearing in (11.92), that is,

$$\frac{d}{dt} (J\rho) = 0. \quad (11.94)$$

If we define the *reference density* $\rho_0(\mathbf{X}, t) = J(\mathbf{X}, t) \rho(\mathbf{x}(\mathbf{X}, t), t)$, then the *mass conservation* in the reference configuration is simply

$$\frac{\partial}{\partial t} \rho_0 = 0. \quad (11.95)$$

11.2.1.1 Transport Formulas

We will be making systematic use of the Maxwell transport to obtain balance laws. It is therefore important to obtain general transport relationships for any scalar ϕ and vector field $\mathbf{u}$ associated with the moving body in the current configuration. Following the same steps as in (11.90–11.92), we obtain [977] the useful transport formulas:

$$\frac{d}{dt} \int_{\Omega} \phi \, dv = \int_{\Omega} (\dot{\phi} + (\operatorname{div} \mathbf{v})\phi) \, dv, \quad (11.96)$$

$$\frac{d}{dt} \int_{\Omega} \mathbf{u} \, dv = \int_{\Omega} (\dot{\mathbf{u}} + (\operatorname{div} \mathbf{v})\mathbf{u}) \, dv, \quad (11.97)$$

where $\Omega \subseteq \mathcal{B}$ is an arbitrary subset.

11.2.2 Balance of Linear Momentum

The balance of linear momentum expresses the fundamental relationship between the rate of change of linear momentum of a body as a result of the force applied to the body. When applied to a rigid body, it simply leads to the well-known Newton's second law. However, in the case of a deformable body, the body also experiences internal forces that need to be taken into account.

In the current configuration, the total linear momentum on any part of the body $\Omega \subseteq \mathcal{B}$ is simply

$$\int_{\Omega} \rho(\mathbf{x}, t) \mathbf{v}(\mathbf{x}, t) dv, \quad (11.98)$$

where $\rho(\mathbf{x}, t)$ is the density and $\mathbf{v}(\mathbf{x}, t)$ is the velocity of a point at $(\mathbf{x}, t)$.

The total force acting on a point $\mathbf{x} \in \Omega$ includes a *body force* density $\mathbf{b}$, representing the contributions of external forces and a *contact force* density $\mathbf{t}_n$, representing the force per unit area resulting in contact. Therefore, the total force acting on Ω is

$$\int_{\Omega} \rho(\mathbf{x}, t) \mathbf{b}(\mathbf{x}, t) dv + \int_{\partial\Omega} \mathbf{t}_n da. \quad (11.99)$$

Euler's first law of motion then states that the rate of change of the linear momentum on any part of the body $\Omega \subseteq \mathcal{B}$ is equal to the sum of the forces acting on Ω [1251]. Therefore, in our context, this law reads

$$\underbrace{\frac{d}{dt} \int_{\Omega} \rho(\mathbf{x}, t) \mathbf{v}(\mathbf{x}, t) dv}_{\text{rate of change of linear momentum}} = \underbrace{\int_{\Omega} \rho(\mathbf{x}, t) \mathbf{b}(\mathbf{x}, t) dv + \int_{\partial\Omega} \mathbf{t}_n da}_{\text{sum of body and contact forces}}. \quad (11.100)$$

We apply the transport formula (11.97) by mapping the rate of linear momentum to the reference configuration

$$\begin{aligned} \frac{d}{dt} \int_{\Omega} \rho \mathbf{v} dv &= \frac{d}{dt} \int_{\Omega_0} \rho \mathbf{v} J dV = \int_{\Omega_0} \frac{d}{dt} (\rho \mathbf{v} J) dV \\ &= \int_{\Omega_0} (\rho \dot{\mathbf{v}} + \underbrace{\rho \mathbf{v} \text{div } \mathbf{v}}_{=0, \text{ per continuity}}) J dV \\ &= \int_{\Omega} \rho \dot{\mathbf{v}} dv, \end{aligned} \quad (11.101)$$

where we have used the identity (11.87).

In order to apply the localization procedure, we need to express all the quantities as a single integral. However, the last integral in (11.100) is a surface integral. Therefore, it needs to be expressed to a volume integral. The standard way to transform a surface integral to a volume integral is to use the divergence theorem. However, the integrand does not have the required form for a direct application of the divergence theorem. This difficulty prompts us to reexpress the contact force density $\mathbf{t}_n$ in a tensorial form.

We first use the *Cauchy's stress principle* stating that the contact force density depends continuously on the unit normal $\mathbf{n}$. Then, Cauchy's tetrahedral argument [975] can be used to show that the contact force density depends linearly on the unit normal, so that

$$\mathbf{t}_n = \mathbf{T} \mathbf{n}, \quad (11.102)$$

where $\mathbf{T}$ is a second-order tensor independent of $\mathbf{n}$. This last identity has the correct form for the application of the divergence theorem (11.30):

$$\int_{\partial\Omega} \mathbf{t}_n \, da = \int_{\partial\Omega} \mathbf{T}\mathbf{n} \, da = \int_{\Omega} \operatorname{div}(\mathbf{T}^\top) \, dv. \quad (11.103)$$

The tensor $\mathbf{T}$ is the *Cauchy stress tensor*, a central quantity describing forces per unit area in a material. Using this last equality, Euler's law (11.100) simplifies to

$$\int_{\Omega} \rho \dot{\mathbf{v}} \, dv = \int_{\Omega} \rho \mathbf{b} \, dv + \int_{\Omega} \operatorname{div}(\mathbf{T}^\top) \, dv, \quad (11.104)$$

and the localization procedure leads to the first *Cauchy equation*:

$$\operatorname{div}(\mathbf{T}^\top) + \rho \mathbf{b} = \rho \dot{\mathbf{v}}. \quad (11.105)$$

11.2.3 Balance of Angular Momentum

In a continuum both forces and torques have to be balanced. The corresponding balance for torque is Euler's second law of motion stating that the rate of change of angular momentum of an arbitrary material subset $\Omega \subseteq \mathcal{B}$ with respect to a given point is equal to the sum of all torques acting on Ω with respect to the same point.

The total angular momentum of Ω is

$$\int_{\Omega} \rho \mathbf{x} \times \mathbf{v} \, dv, \quad (11.106)$$

where, without loss of generality, we choose to express the angular momentum with respect to the origin.

If we assume here that the material under consideration is *nonpolar*, that is, the body is not subject to extra body or contact torques and cannot support couple stresses, then the total torque due to body and traction forces acting on Ω , with respect to the origin, is

$$\int_{\Omega} \rho \mathbf{x} \times \mathbf{b} \, dv + \int_{\partial\Omega} \mathbf{x} \times \mathbf{t}_n \, da. \quad (11.107)$$

Then, Euler's second law can be written as

$$\underbrace{\frac{d}{dt} \int_{\Omega} \rho \mathbf{x} \times \mathbf{v} \, dv}_{\text{rate of change of angular momentum}} = \underbrace{\int_{\Omega} \rho \mathbf{x} \times \mathbf{b} \, dv + \int_{\partial\Omega} \mathbf{x} \times \mathbf{t}_n \, da}_{\text{torques due to body and traction forces}}. \quad (11.108)$$

The transport procedure and the continuity equation can be used to simplify this expression to

$$\int_{\Omega} \rho \mathbf{x} \times (\dot{\mathbf{v}} - \mathbf{b}) \, dv = \int_{\partial\Omega} \mathbf{x} \times \mathbf{Tn} \, da, \quad (11.109)$$

where we have expressed the contact force in terms of the Cauchy stress tensor, $\mathbf{t}_n = \mathbf{Tn}$. Cauchy's first equation (11.105) can be used to transform the right-hand side of this expression to obtain

$$\int_{\Omega} \mathbf{x} \times \operatorname{div}(\mathbf{T}^T) \, dv = \int_{\partial\Omega} \mathbf{x} \times \mathbf{Tn} \, da. \quad (11.110)$$

By application of the divergence theorem and the localization procedure, the last integral implies that the Cauchy stress tensor is symmetric, that is,

$$\mathbf{T}^T = \mathbf{T}. \quad (11.111)$$

We can now simplify (11.105) to obtain the standard form of Cauchy's equation, also known as *the equation of motion* for a continuum:

$$\operatorname{div} \mathbf{T} + \rho \mathbf{b} = \rho \dot{\mathbf{v}}. \quad (11.112)$$

11.2.4 Many Stress Tensors

The Cauchy stress tensor is the natural measure for contact forces measured in the current configuration per unit area in the current configuration. The contact forces acting on the boundary $\partial\Omega$ of a region Ω can be extracted from $\mathbf{T}$ by considering different directions with respect to the boundary. Let $\mathbf{n}$ be the normal vector to $\partial\Omega$ at a point p in the body. Then, the *normal stress*, that is, the force per area normal to $\partial\Omega$, applied at p is

$$\mathbf{n} \cdot \mathbf{t}_n = \mathbf{n} \cdot (\mathbf{Tn}). \quad (11.113)$$

Considering a vector $\mathbf{m}$ tangent to $\partial\Omega$ at p (that is, $\mathbf{m} \cdot \mathbf{n} = 0$), the product

$$\mathbf{m} \cdot \mathbf{t}_n = \mathbf{m} \cdot (\mathbf{Tn}). \quad (11.114)$$

is a *shear stress* acting on Ω at p along $\mathbf{m}$.

While the Cauchy stress is a natural measure for forces acting on a continuum it is not always a convenient quantity for computation since the area in the current configuration changes during the deformation. Therefore, it is often useful to measure contact forces with respect to areas measured initially in the reference configuration. To do so, we apply Nanson's formula $\mathbf{n} \, da = J \mathbf{F}^{-T} \mathbf{N} \, dA$ to the traction vector to obtain the contact force on a material area element:

$$\mathbf{t}_n \, da = \mathbf{T} \mathbf{n} \, da = (J \mathbf{T} \mathbf{F}^{-\top}) \mathbf{N} \, dA = \mathbf{S}^\top \mathbf{N} \, dA, \quad (11.115)$$

where

$$\mathbf{S} = J \mathbf{F}^{-1} \mathbf{T}, \quad (11.116)$$

is the *nominal stress tensor*. Its transpose, $\mathbf{S}^\top$, is the *first Piola-Kirchhoff stress tensor*. It is also called the *engineering stress tensor*, as it is a convenient quantity for experimental measurements.

Since $\mathbf{T}$ is symmetric, we have

$$\mathbf{S}^\top \mathbf{F}^\top = \mathbf{F} \mathbf{S}. \quad (11.117)$$

11.2.5 Balance of Energy for Elastic Materials

The equations for the stress and mass density derived so far are valid for a large class of continuum bodies independently of their specific material characteristics, including solids and fluids. To close the system of equations, constitutive relationships between stress, deformation gradient, rate of deformation, and density must be imposed to characterize the particular body under consideration. The balance of energy provides restriction on the form of these constitutive relationships. Here, we turn our attention to elastic materials.

The general principle for the balance energy states that for any part of a body $\Omega \subseteq \mathcal{B}$, the rate of change of the total mechanical energy $\mathcal{E}$ is balanced by the power of the forces $\mathcal{P}$. If we ignore heat dissipation, the total energy for an elastic material is the sum of the kinetic energy and an internal elastic energy, that is

$$\mathcal{E} = \underbrace{\frac{1}{2} \int_{\Omega} \rho \mathbf{v} \cdot \mathbf{v} \, dv}_{\text{kinetic energy}} + \underbrace{\int_{\Omega} J^{-1} W \, dv}_{\text{internal energy}}, \quad (11.118)$$

where W is the internal elastic energy density per unit reference volume.

The power of the forces acting on Ω is given by

$$\mathcal{P} = \int_{\Omega} \rho \mathbf{b} \cdot \mathbf{v} \, dv + \int_{\partial\Omega} \mathbf{t}_n \cdot \mathbf{v} \, da. \quad (11.119)$$

The balance of energy is then

$$\frac{d\mathcal{E}}{dt} = \mathcal{P}. \quad (11.120)$$

The transport and localization procedure applied to the energy principle together with the equations of continuity and motion lead to a local form of energy balance

[975] for the *stress power*

$$\frac{dW}{dt} = \text{tr}(\mathbf{S}\dot{\mathbf{F}}). \quad (11.121)$$

From a thermodynamic point of view, the combination of $\mathbf{S}$ and $\mathbf{F}$ in the stress power $\text{tr}(\mathbf{S}\dot{\mathbf{F}})$ identifies these two tensors as being *work conjugate*, that is, they form a conjugate pair of stress and deformation tensors.

11.3 Constitutive Equations for Hyperelastic Materials

We further assume that the material is *hyperelastic*. That is, the internal energy density W is a function of $\mathbf{F}$ alone. Explicitly, we posit that

$$W(\mathbf{X}, t) = W(\mathbf{F}(\mathbf{X}, t), \mathbf{X}), \quad (11.122)$$

in which case, W is referred to as the *strain-energy function* of the system. Using (11.55), the time derivative of W is

$$\frac{d}{dt} W(\mathbf{F}) = \text{tr} \left(\frac{\partial W}{\partial \mathbf{F}} \dot{\mathbf{F}} \right), \quad (11.123)$$

so that the energy balance (11.121) reads now

$$\text{tr} \left[\left(\frac{\partial W}{\partial \mathbf{F}} - \mathbf{S} \right) \dot{\mathbf{F}} \right] = 0. \quad (11.124)$$

Since this identity must be true for all motions, we conclude that

$$\mathbf{S} = \frac{\partial W}{\partial \mathbf{F}}, \quad (11.125)$$

where we used the derivative of a scalar W with respect to the second-order tensor $\mathbf{F}$ defined with respect to Cartesian bases in the reference and current configurations, by

$$\frac{\partial W}{\partial \mathbf{F}} = \frac{\partial W}{\partial F_{ji}} \mathbf{E}_i \otimes \mathbf{e}_j, \quad \left(\frac{\partial W}{\partial \mathbf{F}} \right)_{ij} = \frac{\partial W}{\partial F_{ji}}. \quad (11.126)$$

Written in terms of the Cauchy stress this identity provides a *constitutive relationship* relating the Cauchy stress to the deformation gradient:

$$\mathbf{T} = J^{-1} \mathbf{F} \frac{\partial W}{\partial \mathbf{F}}. \quad (11.127)$$

11.3.1 Internal Material Constraints

If we consider a material where the possible deformations are constrained during all motions, extra internal material constraints must be satisfied. We consider the case where these constraints take the form $C(\mathbf{F}) = 0$ where $C(\mathbf{F})$ is a smooth scalar function of the deformation gradient. For instance, in the case of an incompressible material, we assume that all deformations must preserve volume, which implies $\det(\mathbf{F}) = 1$. In this case, $C(\mathbf{F}) = \det(\mathbf{F}) - 1$.

A simple way to ensure that a constraint holds is to introduce a Lagrangian multiplier $p = p(\mathbf{X}, t)$ and modify accordingly the energy density $W \rightarrow W - pC$ so that Equation (11.124) reads now

$$\text{tr} \left[\left(\frac{\partial}{\partial \mathbf{F}} (W - pC) - \mathbf{S} \right) \dot{\mathbf{F}} \right] = 0, \quad (11.128)$$

which leads to

$$\mathbf{S} = \frac{\partial W}{\partial \mathbf{F}} - p \frac{\partial C}{\partial \mathbf{F}}. \quad (11.129)$$

In terms of the Cauchy stress, we have

$$\mathbf{T} = J^{-1} \mathbf{F} \mathbf{S} = J^{-1} \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{N}, \quad (11.130)$$

where

$$\mathbf{N} = J^{-1} \mathbf{F} \frac{\partial C}{\partial \mathbf{F}}, \quad (11.131)$$

is the *reaction stress* enforcing the constraint. In particular, for incompressible materials, we have

$$\frac{\partial C}{\partial \mathbf{F}} = (\det \mathbf{F}) \mathbf{F}^{-1} = J \mathbf{F}^{-1}, \quad (11.132)$$

that is, $\mathbf{N} = \mathbf{1}$. The constitutive relationship for an incompressible hyperelastic material is then

$$\mathbf{T} = \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{1}. \quad (11.133)$$

Recalling that a *hydrostatic pressure* is a stress that is a multiple of the identity, we can identify the reaction stress in (11.133) with a hydrostatic pressure. Physically, we see that a pressure p is required to enforce locally the conservation of volume.

For a given $W = W(\mathbf{F})$, the Cauchy stress for compressible or incompressible materials can be written in the general form

$$\mathbf{T} = J^{-1} \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{1}, \quad (11.134)$$

where $J = 1$ for an incompressible material and $p = p(\mathbf{x}, t)$ must be determined. If the material is unconstrained, then $p = 0$.

11.4 Summary of Equations

We can now collect the different equations from the previous chapters to obtain a closed set of equations

$$\dot{\rho} + \rho \operatorname{div} \mathbf{v} = 0, \quad \text{continuity equation} \quad (11.135)$$

$$\operatorname{div} \mathbf{T} + \rho \mathbf{b} = \rho \dot{\mathbf{v}}, \quad \text{equation of motion} \quad (11.136)$$

$$\mathbf{T}^\top = \mathbf{T}, \quad \text{symmetry of Cauchy stress tensor} \quad (11.137)$$

$$\mathbf{T} = J^{-1} \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{1}, \quad \text{constitutive law} \quad (11.138)$$

Since the elements of $\mathbf{F}$ are related to the motion χ by $\mathbf{F} = \operatorname{Grad} \chi$, and $\mathbf{v} = \partial_t \chi(\mathbf{X}(\mathbf{x}, t), t)$, there are ten unknowns in this system: the scalar field ρ , the vector field χ , and the six components of the symmetric tensor $\mathbf{T}$ for ten equations (excluding the third equation that reduces the number of unknowns in $\mathbf{T}$).

It is also sometimes convenient to write these equations with respect to the reference variables [975]:

$$\dot{\rho}_0 = 0, \quad \text{continuity equation} \quad (11.139)$$

$$\operatorname{Div} \mathbf{S} + \rho_0 \mathbf{B} = \rho_0 \dot{\mathbf{v}}, \quad \text{equation of motion} \quad (11.140)$$

$$\mathbf{S}^\top \mathbf{F}^\top = \mathbf{F} \mathbf{S}, \quad \text{symmetry of Cauchy stress tensor} \quad (11.141)$$

$$\mathbf{S} = \frac{\partial \mathbf{W}}{\partial \mathbf{F}} - p \mathbf{J} \mathbf{F}^{-1}, \quad \text{constitutive law} \quad (11.142)$$

where the divergence and gradient are now taken in the initial reference configuration, $\rho_0 = J(\mathbf{X}, t) \rho(\mathbf{x}(\mathbf{X}, t), t)$ is the reference density at a material point, $\mathbf{B} = \mathbf{b}(\mathbf{x}(\mathbf{X}, t), t)$ is the body force acting at the same point, and $\dot{\mathbf{v}} = \dot{\mathbf{v}}(\mathbf{x}(\mathbf{X}, t), t)$ is the acceleration of a material point.

11.5 Boundary Conditions

Equilibrium and static solutions are obtained by setting $\mathbf{v}(\mathbf{X}, t) = \mathbf{0}$ for all $\mathbf{X} \in \mathcal{B}_0$ and for all time t . The equilibrium solutions must satisfy the conditions imposed on the boundary. Depending on the setting, different types of boundary conditions can be applied and it is well appreciated that the solutions will depend crucially on these conditions. The two main types of boundary conditions are dead loading and rigid loading.

In *dead loading*, a traction is prescribed and maintained constant throughout the deformation, i.e., the prescribed traction is independent of the deformation. A typical example of dead loading is *hydrostatic loading* where a constant pressure $P > 0$ is applied at the boundary in the current configuration. In this case, $\mathbf{t}_n = -P\mathbf{n}$, so that $\mathbf{T} = -P\mathbf{1}$ on the boundary.

In *rigid loading*, fixed displacements are prescribed at the boundary.

In *mixed loading*, a surface traction $\mathbf{t}_b$ and deformation $\mathbf{x}_b$ are prescribed at the boundary:

$$\mathbf{T}\mathbf{n} = \mathbf{t}_b \quad \text{for } \mathbf{X} \in \partial\mathcal{B}_0^t \quad (11.143)$$

$$\mathbf{x}(\mathbf{X}) = \mathbf{x}_b \quad \text{for } \mathbf{X} \in \partial\mathcal{B}_0^d \quad (11.144)$$

where $\partial\mathcal{B}_0^t$ and $\partial\mathcal{B}_0^d$ are parts of the body boundary such that $\partial\mathcal{B}_0^t \cup \partial\mathcal{B}_0^d = \partial\mathcal{B}_0$ and $\partial\mathcal{B}_0^t \cap \partial\mathcal{B}_0^d = \emptyset$. Note that $\mathbf{t}_b$ can be a function of the deformation gradient as well as of the position.

11.6 Objectivity and Material Symmetry

The functional form of the elastic energy can be restricted by combining a fundamental principle, the principle of objectivity, together with symmetry properties of the material.

The *principle of objectivity* or *material-frame indifference* [1251] states that material properties are independent of superimposed rigid-body motions. For hyperelastic materials, the principle of objectivity implies

$$W(\mathbf{Q}\mathbf{F}) = W(\mathbf{F}), \quad \forall \mathbf{Q} \in SO(3), \quad (11.145)$$

where $SO(3)$ is the set of all proper orthogonal tensors. The principle of objectivity implies that W only depends on $\mathbf{F}$ through $\mathbf{C}$, so that we can write $W(\mathbf{F}) = \bar{W}(\mathbf{C})$. Here, to simplify the notation we will drop the overbar and simply write $W(\mathbf{F}) = W(\mathbf{C})$.

Next, we consider the implication of material symmetries. A material is said to be *symmetric with respect to a linear transformation* if the reference configuration is mapped by this transformation to another configuration which is mechanically indis-

tinguishable from it. The set of all such linear transformations constitutes a symmetry group $\mathbb{Q} \subseteq SO(3)$. The symmetry condition for a hyperelastic material is [975]

$$W(\mathbf{FQ}) = W(\mathbf{F}), \quad \forall \mathbf{Q} \in \mathbb{Q}. \quad (11.146)$$

11.7 Isotropic Materials

The maximal possible symmetry group is $SO(3)$, which defines an *isotropic material*. The case of isotropic materials is particularly important both for its simplicity and its wide applicability. Isotropy implies that the strain-energy function depends on $\mathbf{F}$ only through $\mathbf{V}$, where $\mathbf{V}$ is the symmetric second-order tensor appearing in the polar decomposition $\mathbf{F} = \mathbf{VR}$. Indeed, choosing $\mathbf{Q} = \mathbf{R}^T$ in (11.146) leads to

$$W(\mathbf{FQ}) = W(\mathbf{FR}^T) = W(\mathbf{VRR}^T) = W(\mathbf{V}). \quad (11.147)$$

Combining isotropy with objectivity, we have

$$W(\mathbf{QFQ}^T) = W(\mathbf{FQ}^T) = W(\mathbf{F}) = W(\mathbf{V}), \quad \forall \mathbf{Q}, \tilde{\mathbf{Q}} \in SO(3), \quad (11.148)$$

and choosing $\tilde{\mathbf{Q}} = \mathbf{QR}$ in $W(\mathbf{QFQ}^T)$ leads to the conclusion that the strain-energy function satisfies

$$W(\mathbf{V}) = W(\mathbf{QVQ}^T), \quad \forall \mathbf{Q} \in SO(3). \quad (11.149)$$

The property (11.149) defines W as an *isotropic function* of $\mathbf{V}$. By inspection, it can readily be observed that the determinant and trace are simple examples of isotropic functions of a second-order tensor. More generally, an isotropic function of $\mathbf{V}$ can only depend on $\mathbf{V}$ through its three principal invariants

$$\{\text{tr}(\mathbf{V}), \frac{1}{2} (\text{tr}(\mathbf{V})^2 - \text{tr}(\mathbf{V}^2)), \det(\mathbf{V})\}. \quad (11.150)$$

However, since $\mathbf{V}$ is a symmetric positive-definite tensor, it is often more convenient to express W through the principal invariants of the left Cauchy–Green tensor $\mathbf{B} = \mathbf{V}^2 = \mathbf{FF}^T$:

$$I_1 = \text{tr}(\mathbf{B}) = \lambda_1^2 + \lambda_2^2 + \lambda_3^2, \quad (11.151)$$

$$I_2 = \frac{1}{2} (I_1^2 - \text{tr}(\mathbf{B}^2)) = \lambda_2^2 \lambda_3^2 + \lambda_3^2 \lambda_1^2 + \lambda_1^2 \lambda_2^2, \quad (11.152)$$

$$I_3 = \det(\mathbf{B}) = \lambda_1^2 \lambda_2^2 \lambda_3^2. \quad (11.153)$$

Equivalently, it implies that W only depends on $\mathbf{F}$ through its principal stretches λ_1 , λ_2 , and λ_3 (the square roots of the principal values of $\mathbf{B}$). With a slight abuse of notation, we write either $W = W(I_1, I_2, I_3)$ or $W = W(\lambda_1, \lambda_2, \lambda_3)$.

For an isotropic compressible material, we have $J = 1$, which implies that $\lambda_3 = 1/(\lambda_1 \lambda_2)$. Therefore, W can be either expressed in terms of $\{\lambda_1, \lambda_2\}$ or $\{I_1, I_2\}$.

The explicit form of the Cauchy stress tensor for a compressible material in terms of the invariants and their derivatives is

$$\mathbf{T} = w_0 \mathbf{1} + w_1 \mathbf{B} + w_2 \mathbf{B}^2, \quad (11.154)$$

where the functions w_i depend on the invariants and are given explicitly by

$$w_0 = 2J \frac{\partial W}{\partial I_3} - p, \quad (11.155)$$

$$w_1 = 2J^{-1} \frac{\partial W}{\partial I_1} + 2J^{-1} \frac{\partial W}{\partial I_2} I_1, \quad (11.156)$$

$$w_2 = -2J^{-1} \frac{\partial W}{\partial I_2}. \quad (11.157)$$

As before we choose $p = 0$ for compressible materials and $J = I_3 = 1$ for incompressible materials. If the reference configuration is assumed to be stress-free, then we must have $\mathbf{T}(\mathbf{F} = \mathbf{1}) = \mathbf{0}$, that is the functions $w_i = w_i(I_1, I_2, I_3)$ satisfy

$$w_0(3, 3, 1) + w_1(3, 3, 1) + w_2(3, 3, 1) = 0. \quad (11.158)$$

A convenient alternative representation, the *Rivlin–Ericksen representation*, is obtained from (11.154) by using Cayley–Hamilton’s theorem [525] for $\mathbf{B}$. In terms of the invariants, the Cayley–Hamilton theorem in three dimensions reads

$$\mathbf{B}^3 - I_1 \mathbf{B}^2 + I_2 \mathbf{B} - I_3 \mathbf{1} = \mathbf{0}. \quad (11.159)$$

Substituting $\mathbf{B}^2 = I_1 \mathbf{B} - I_2 \mathbf{1} + I_3 \mathbf{B}^{-1}$ in (11.154) gives

$$\mathbf{T} = \beta_0 \mathbf{1} + \beta_1 \mathbf{B} + \beta_{-1} \mathbf{B}^{-1}, \quad (11.160)$$

where

$$\beta_0 = 2J \frac{\partial W}{\partial I_3} + 2J^{-1} I_2 \frac{\partial W}{\partial I_2} - p, \quad (11.161)$$

$$\beta_1 = 2J^{-1} \frac{\partial W}{\partial I_1}, \quad (11.162)$$

$$\beta_{-1} = -2J \frac{\partial W}{\partial I_2}. \quad (11.163)$$

11.7.1 *Adscititious Inequalities*

The principle of objectivity together with isotropy leads to a representation of the strain-energy function in terms of three invariants. This formulation still leads to many choices for a suitable functional form of W . If we want to establish general results independent of the particular choice of strain-energy function, we can impose certain desired behaviors [1291]. For instance, we may require that, in simple extension, an isotropic elastic body extends rather than shrinks. These conditions take the form of inequalities either on the coefficients of the constitutive relations, or on the principal stresses and strains. They are called *adscititious inequalities* as they come from outside the theory and are derived empirically from everyday experience or experiments [1253]. We mention here three standard inequalities often used in elasticity and suitable for most elastomers.

- **Baker–Ericksen inequalities.** The Baker–Ericksen inequalities follow from the requirement that the greater principal stress occurs in the direction of the greater principal stretch [51] which implies

$$\lambda_i \neq \lambda_j \Rightarrow (t_i - t_j)(\lambda_i - \lambda_j) > 0, \quad i, j = 1, 2, 3, \quad (11.164)$$

where $\{t_1, t_2, t_3\}$ and $\{\lambda_1, \lambda_2, \lambda_3\}$ are the principal stresses and principal stretches obtained by the spectral decomposition

$$\mathbf{V} = \sum_{i=1}^3 \lambda_i \mathbf{v}_i \otimes \mathbf{v}_i, \quad \mathbf{T} = \sum_{i=1}^3 t_i \mathbf{v}_i \otimes \mathbf{v}_i. \quad (11.165)$$

Condition (11.164) imposes the following restrictions on the coefficients in (11.160):

$$\lambda_i^2 \lambda_j^2 \beta_1 > \beta_{-1}, \quad \text{if } \lambda_i \neq \lambda_j, \quad (11.166)$$

$$\lambda_i^4 \beta_1 \geq \beta_{-1}, \quad \text{if } \lambda_i = \lambda_j. \quad (11.167)$$

For a hyperelastic body under uniaxial tension, the deformation is a simple extension in the direction of the (positive) tensile force. The ratio of the tensile strain to the strain in the perpendicular direction is greater than one if and only if the Baker–Ericksen inequalities hold [836].

- **The ordered-forces inequalities.** Similar to the Baker–Ericksen inequalities, the *ordered-forces inequalities* state that the greater stretch occurs in the direction of the greater force. While similar, the two sets of inequalities do not imply each other [1251, p. 157]. However, it can be shown that if two of the three principal stresses are nonnegative, then the Baker–Ericksen inequalities follow from the ordered-forces inequalities, and if two of the three principal stresses are non-positive, then the ordered-forces inequalities are implied by the Baker–Ericksen inequalities.

- **Empirical inequalities.** Based on experimental observations in elastomers, the following *empirical inequalities* on the coefficients of (11.160) have been postulated [901]:

$$\beta_0 \leq 0, \quad \beta_1 > 0, \quad \beta_{-1} \leq 0, \quad (11.168)$$

for the compressible case. For the incompressible case, only the last two inequalities are considered. These inequalities directly imply the Baker–Ericksen inequalities (11.166) but not conversely.

11.7.1.1 Example: Pure Shear of an Elastic Cube

The adscititious inequalities can be used to establish general qualitative trends. For instance, consider a homogeneous isotropic hyperelastic cube subject to a *pure shear stress* on its top face as shown in Figure 11.8. In Cartesian coordinates, this stress can be written as $\mathbf{T} = T(\mathbf{e}_1 \otimes \mathbf{e}_2 + \mathbf{e}_2 \otimes \mathbf{e}_1)$, where $T > 0$ is constant. Equivalently, in matrix form, it reads

$$[T] = \begin{bmatrix} 0 & T & 0 \\ T & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}. \quad (11.169)$$

Since T is constant, in the absence of body force, the equation of motion is identically satisfied. The corresponding deformation is homogeneous, that is, the deformation gradient is independent of the position. For a pure shear stress, it reads

$$x = aX + \sqrt{b^2 - a^2}Y, \quad y = bY, \quad z = cZ. \quad (11.170)$$

It consists of a triaxial stretch, a pure strain deformation, combined with a simple shear in the *direction* of the shear force *if and only if* the Baker–Ericksen inequalities hold. Therefore, the Baker–Ericksen inequalities guarantee that the shear strain is in the same direction as the shear force.

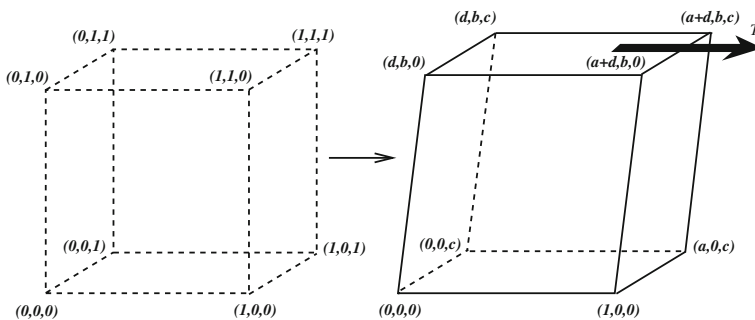


Figure 11.8 A cube deformed under pure shear stress T applied to the top face ($d = \sqrt{b^2 - a^2}$).

If the Baker–Ericksen inequalities are not satisfied, the material would shear in the direction opposite to the direction of the shear stress. This behavior would be unrealistic, even though there is no fundamental principle that would rule it out. It is only through our own experience of everyday materials that we infer its physical impossibility.

For the deformation (11.170), obtained under pure shear, we define the *Poynting effect* as $0 < b \neq 1$ [901]. Specifically, if a cube is deformed under pure shear, the *positive Poynting effect* occurs when $b > 1$ [99], i.e., the sheared faces spread apart, whereas the *negative Poynting effect* is obtained when $b < 1$, i.e., the sheared faces are drawn together. It can be shown that the validity of the empirical inequalities (with $\beta_{-1} < 0$) is a necessary and sufficient condition for the positive Poynting effect as found in rubber materials [888]. However, experimental observations suggest that semi-flexible polymer gels exhibit a *negative* Poynting effect [663], which implies $\beta_{-1} > 0$. Therefore, it appears that the last of the empirical inequalities may not hold for some biological materials and should be replaced by the *generalized empirical inequalities* [889] which simply state $\beta_0 \leq 0$ and $\beta_1 > 0$.

11.7.2 Choice of Strain-Energy Functions

The choice of strain-energy functions $W = W(\mathbf{F})$ for particular applications is a controversial and difficult problem. Methods based on a statistical analysis of the microstructure have been proposed [119, 368]. However, typically, phenomenological models are used to capture the essential features of a material such as its behavior under shear or its strain-hardening or strain-softening properties [617, 620, 1106], while respecting basic material properties such as convexity and objectivity [1324]. Note that the words *model* and *material* are used exchangeably to describe these particular strain-energy functions. For instance, a neo-Hookean material is a material described by the neo-Hookean model, that is, a hyperelastic material with the particular form of strain-energy density function given below. These models can be calibrated and fitted to uniaxial or biaxial experiments [603, 604, 751, 768, 1108, 1109, 1273, 1283]. Here, we limit our presentation to a few key popular models for incompressible materials that capture specific features and are widely used in applications. A summary is given in Table 11.1.

- **Neo-Hookean materials.** The simplest model, and the starting point of many theories, is the *neo-Hookean model* [370]:

$$W_{\text{nh}} = \frac{C_1}{2}(I_1 - 3). \quad (11.171)$$

This strain-energy function can be derived from statistical mechanics as a macroscopic limit of the energy density of an amorphous cross-linked network of polymeric molecules [367, 368, 1245, 1246]. Each molecule in this network is a freely

jointed chain with the same number of monomer units and their end-to-end distances follow a Gaussian distribution.

For small deformations, the macroscopic parameter C_1 can be identified with the shear modulus μ and is proportional to the product $k_B T$ of the Boltzmann constant with the absolute temperature. The Young's modulus is then related to C_1 by

$$E = 3\mu = 3C_1. \quad (11.172)$$

A simple generalization of neo-Hookean materials is obtained by assuming that the strain-energy function is only a function of the first invariant, $W(\mathbf{F}) = W(I_1)$. This class of models is known as *generalized neo-Hookean* materials [13, 1327], for which general results can easily be established [800].

- **Mooney–Rivlin materials.** The neo-Hookean model can be interpreted as the lowest approximation of a strain-energy function with respect to the strain tensor $\mathbf{E} = (\mathbf{F}^T \mathbf{F} - \mathbf{1})/2$, the so-called *second-order elasticity* approximation. This model is a good descriptor for many elastomers in tension or compression but it often fails to capture quantitatively behaviors associated with shear or torsion. The next order approximation for incompressible isotropic elasticity gives rise to *third-order elasticity* [267, 281, 486]. Expressed in terms of invariants, it takes the form of the Mooney–Rivlin strain-energy function

$$W_{mr} = \frac{C_1}{2}(I_1 - 3) + \frac{C_2}{2}(I_2 - 3). \quad (11.173)$$

The combination $C_1 + C_2 = \mu$ can be identified again as the shear modulus. Therefore, we can write

$$C_1 = \mu\left(\frac{1}{2} + \alpha\right), \quad C_2 = \mu\left(\frac{1}{2} - \alpha\right). \quad (11.174)$$

The Baker–Ericksen inequalities imply that $\alpha \in [-1/2, 1/2]$. This model can also be derived from statistical mechanics arguments by relaxing some of the assumptions that lead to the neo-Hookean model [392].

- **Ogden materials.** A general approach for material modeling, originally proposed by Ogden [974, 976, 978], consists in considering a general expansion with N terms of the form

$$W_{ogN} = \sum_{i=1}^N \frac{\mu_i}{\alpha_i} (\lambda_1^{\alpha_i} + \lambda_2^{\alpha_i} + \lambda_3^{\alpha_i} - 3). \quad (11.175)$$

Each parameter μ_i and α_i is a material constant to be determined. These constants are related to the shear modulus μ of small deformations by

$$\sum_{i=1}^N \mu_i \alpha_i = 2\mu. \quad (11.176)$$

In practice, the number of terms is limited to $N \leq 6$. The possibility of having a large number of parameters provides a systematic way to explore many different behaviors and can be used to fit experimental data of both elastomers and biological tissues [628, 887, 1305, 1307].

- **Fung–Demiray materials.** Many soft tissues and elastomers exhibit strong strain-hardening properties. That is, in simple extension, it becomes increasingly difficult to further extend the material. Examples of generalized neo-Hookean materials that have been used to capture this effect in soft tissues are the Fung and Gent models. The *Fung model* [404, 405, 766, 1202], in its simplest form, reads

$$W_{\text{fu}} = \frac{\mu}{2\beta} [\exp(\beta(I_1 - 3)) - 1], \quad (11.177)$$

where $\beta > 0$ controls the strain-hardening property. In the limit $\beta \rightarrow 0$ the Fung model reduces to the standard neo-Hookean model. This particular form of the Fung model was first proposed by Demiray in 1972 [270, 271].

- **Gent materials.** Another popular model is the *Gent model* that has finite-chain extensibility enforced by a singular limit of the strain-energy function [432, 618, 620]

Table 11.1 A list of phenomenological strain-energy functions for isotropic incompressible materials. Note that the materials have been written so that they share the same infinitesimal shear modulus μ . The limits $\beta \rightarrow 2$ in W_{og1} and, $\beta \rightarrow 0$ in W_{fu} and W_{ge} all lead to the neo-Hookean strain-energy function. Estimates for 1-term Ogden are from [109, 1145], Gent [432, 435, 617, 619], Fung [269, 601].

Name	Definition	Soft tissues	Elastomers
neo-Hookean	$W_{\text{nh}} = \frac{C_1}{2}(I_1 - 3)$		
Mooney–Rivlin	$W_{\text{mr}} = \frac{C_1}{2}(I_1 - 3) + \frac{C_2}{2}(I_2 - 3)$		
Ogden 1	$W_{\text{og1}} = \frac{2\mu}{\beta^2}(\lambda_1^\beta + \lambda_2^\beta + \lambda_3^\beta - 3)$	$\beta \geq 9$	$\beta \approx 3$
Fung	$W_{\text{fu}} = \frac{\mu}{2\beta}[\exp \beta(I_1 - 3) - 1]$	$3 < \beta < 20$	
Gent	$W_{\text{ge}} = -\frac{\mu}{2\beta} \log[1 - \beta(I_1 - 3)]$	$0.4 < \beta < 3$	$0.005 < \beta < 0.05$

$$W_{\text{ge}} = -\frac{\mu}{2\beta} \log[1 - \beta(I_1 - 3)]. \quad (11.178)$$

The neo-Hookean model is obtained in the limit $\beta \rightarrow 0$.

For a compressible material, there is an extra dependence on the invariant $I_3 = J^2$. Again, a choice must be made to take into account the energy associated with local changes of the volume. Typically, an additive choice is made for which the strain-energy function is separated into an incompressible part and a compressible part [614, 801] so that

$$W = W_{\text{inc}}(I_1, I_2) + W_{\text{comp}}(I_3) \quad (11.179)$$

and a model from Table 11.1 is adopted for $W_{\text{inc}}(I_1, I_2)$. Possible choices for $W_{\text{comp}}(I_3)$ include $\mu_c(I_3 - 1)$, $\mu_c(J - 1)^2$, $\mu_c \ln I_3$, $\mu_c \ln J$, where μ_c is a material parameter related to the bulk modulus.

11.8 Examples

11.8.1 A Simple Homogeneous Deformation

Homogeneous deformations are specified by a constant deformation gradient so that

$$\mathbf{x} = \mathbf{F}\mathbf{X} + \mathbf{c}, \quad (11.180)$$

where $\mathbf{F}$ and $\mathbf{c}$ are constant.

For a homogeneous isotropic compressible material, this choice implies that $\mathbf{T}$ is constant, and in the absence of a body load, the equilibrium equations are therefore trivially satisfied. The solution is then fully specified by the boundary conditions and the constitutive law [1105].

Consider for example, the diagonal deformation of a cuboid into another cuboid shown in Figure 11.9 and described by

$$x_i = \lambda_i X_i, \quad i = 1, 2, 3 \text{ (no summation over } i\text{)}. \quad (11.181)$$

The corresponding deformation gradient is $[\mathbf{F}] = \text{diag}(\lambda_1, \lambda_2, \lambda_3)$ and, consequently, the Cauchy stress tensor is also diagonal: $[\mathbf{T}] = \text{diag}(t_1, t_2, t_3)$. The deformation and stresses are then obtained from the constitutive law

$$t_i = \frac{\lambda_i}{J} \frac{\partial W}{\partial \lambda_i}, \quad i = 1, 2, 3 \text{ (no summation over } i\text{)}. \quad (11.182)$$

For instance, in a hydrostatic uniaxial extension, the stress is prescribed in one direction, that is, $t_3 = N$ and $t_1 = t_2 = 0$. By symmetry, we have $\lambda_1 = \lambda_2$ and

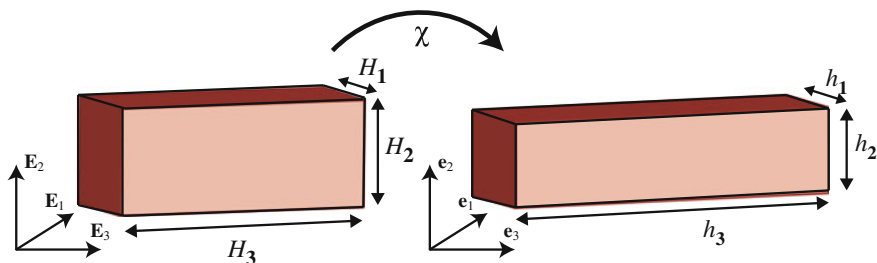


Figure 11.9 A simple diagonal homogeneous deformation transforming a cuboid into another cuboid. The deformation is characterized by the three constants $\lambda_i = h_i/H_i$, $i = 1, 2, 3$.

$$t_2 = \frac{1}{\lambda_2 \lambda_3} W_2 = 0, \quad t_3 = \frac{1}{\lambda_2^2} W_3 = N. \quad (11.183)$$

These equations constitute a system of two equations for two unknowns. If we further specialize these equations to a compressible neo-Hookean material with a strain-energy function of the form

$$W = \frac{\mu_1}{2}(I_1 - 3) - \frac{\mu_1}{2}(I_3 - 1) + \frac{\mu_2}{4}(I_3 - 1)^2. \quad (11.184)$$

This particular form is chosen so that all stresses vanish at $\lambda_1 = \lambda_2 = \lambda_3 = 1$. Equations (11.127) then read

$$0 = \mu_1 \left(\frac{1}{\lambda_3} - \lambda_2^2 \lambda_3 \right) + \mu_2 \lambda_2^2 \lambda_3 (\lambda_2^4 \lambda_3^2 - 1), \quad (11.185)$$

$$N = \mu_1 \left(\frac{\lambda_3}{\lambda_2^2} - \lambda_2^2 \lambda_3 \right) + \mu_2 \lambda_2^2 \lambda_3 (\lambda_2^4 \lambda_3^2 - 1). \quad (11.186)$$

The Young's modulus E is obtained for small deformations as the ratio of uniaxial stress to the uniaxial stretch, that is

$$\begin{aligned} E &= \left. \frac{\partial N(\lambda_2, \lambda_3)}{\partial \lambda_3} \right|_{\lambda_2=\lambda_3=1} + \left(\frac{\partial N(\lambda_2, \lambda_3)}{\partial \lambda_2} \frac{\partial \lambda_2}{\partial \lambda_3} \right) \Big|_{\lambda_2=\lambda_3=1} \\ &= 2\mu_1 \frac{2\mu_1 - 3\mu_2}{\mu_1 - 2\mu_2}. \end{aligned} \quad (11.187)$$

If we now consider the same deformation but for an incompressible material with a neo-Hookean strain-energy function $W = \mu(I_1 - 3)/2$, we have $\lambda_1 = \lambda_2$ again by symmetry, but $\lambda_3 \lambda_2^2 = 1$ by incompressibility. We replace the constitutive law (11.133) by

$$t_i = \lambda_i \frac{\partial W}{\partial \lambda_i} - p \quad i = 1, 2, 3 \text{ (no summation over } i). \quad (11.188)$$

The boundary conditions lead to

$$p = \frac{\mu}{\lambda_3}, \quad N(\lambda_3) = \frac{(\lambda_3^3 - 1)\mu}{\lambda_3}, \quad (11.189)$$

which defines a Young's modulus

$$E = \left. \frac{\partial N(\lambda_3)}{\partial \lambda_3} \right|_{\lambda_3=1} = 3\mu. \quad (11.190)$$

11.8.2 The Half-Plane in Compression

As a second example, we consider an incompressible hyperelastic half-space with a free surface, characterized by $W = W(\lambda_1, \lambda_2, \lambda_3)$, under pure homogeneous static deformation with principal stretch ratios $\lambda_1, \lambda_2, \lambda_3$ [103, 504]. We take $\mathbf{e}_2 = \mathbf{E}_2$ normal to the surface with the half-space located in $X_2 > 0$, so that λ_2 is the stretch ratio in the direction normal to the free surface. We consider homogeneous loadings so that the Cauchy stress tensor, in Cartesian coordinates, can be written $[\mathbf{T}] = \text{diag}(t_1, t_2, t_3)$ with deformation gradient $[\mathbf{F}] = \text{diag}(\lambda_1, \lambda_2, \lambda_3)$.

There are three typical types of loading which are of interest as shown in Figure 11.10:

- **Equibiaxial strain.** An *equibiaxial strain* is associated with deformations with equal strains in the plane, that is $\lambda_1 = \lambda_3$. In this case, the half-space is compressed with equal forces in the 1- and 3-directions, and expands freely in the 2-direction, so that

$$t_1 = \lambda_1 W_1 - \lambda_2 W_2, \quad t_2 = 0, \quad t_3 = t_1, \quad (11.191)$$

where $W_i = \partial_{\lambda_i} W$.

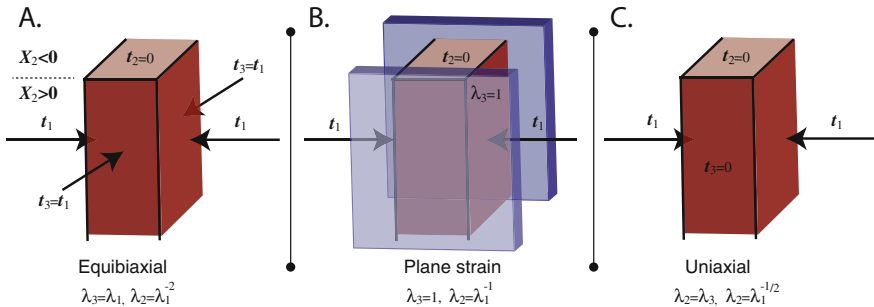


Figure 11.10 Three typical deformations of a half-space. A. Equibiaxial strain. B. Plane strain. C. Uniaxial strain.

- **Plane strain.** *Plane strain* corresponds to the condition $\lambda_3 = 1$. It corresponds to a half-space compressed in the 1-direction and prevented from expanding/contracting in the 3-direction. Thus, it expands in the 2-direction, normal to the free surface. This deformation is maintained by applying the tractions

$$t_1 = \lambda_1 W_1 - \lambda_2 W_2, \quad t_2 = 0, \quad t_3 = \lambda_3 W_3 - \lambda_2 W_2 \neq t_1. \quad (11.192)$$

- **Uniaxial strain.** A *uniaxial strain* is defined by $t_3 = 0$. That is, the half-space is free to expand in the 2- and 3-directions, and

$$t_1 = \lambda_1 W_1 - \lambda_2 W_2, \quad t_2 = 0, \quad t_3 = 0. \quad (11.193)$$

It follows from the incompressibility condition that $\lambda_1 \lambda_2 \lambda_3 = 1$ and therefore the three cases can be written in general as

$$\lambda_2 = \lambda_1^n \quad \text{with} \quad \begin{cases} n = -2 & \text{equibiaxial,} \\ n = -1 & \text{plane strain,} \\ n = -\frac{1}{2} & \text{uniaxial.} \end{cases} \quad (11.194)$$

Therefore, we can use λ_1 to fully characterize the deformation. For a given strain-energy function, the stresses developed as a function of λ_1 can be computed by direct evaluation of the relations (11.191–11.193).

Once the stresses are known, a natural problem is to look for possible bifurcations, that is, we wish to identify a critical value of λ_1 such that the half-space develops surface wrinkles as one would expect when compressing a large rubber block. We will consider this problem in Section 11.10.

11.8.3 The Inflation–Extension of a Tube

As an example of nonhomogeneous static deformations, we consider the problem of an incompressible hyperelastic cylindrical shell subject to combined extension and inflation [311, 621, 699] in the absence of body loads. We consider a simple thought experiment in which the tube is capped at both ends and subject to an axial extension ζ due to an internal pressure P and to a total axial load N on the top cap. The tube of initial inner radius A and outer radius $B > A$ and height H is then deformed into a tube with radii a, b and height h as shown in Figure 11.11. We consider a finite deformation in which the cylinder is allowed to inflate and extend while remaining cylindrical at all times regardless of possible stability issues [96, 197, 484, 552, 553].

For this problem, the deformation $\mathbf{x} = \chi(\mathbf{X}, t)$, in cylindrical coordinates $\{r, \theta, z\}$ and $\{R, \Theta, Z\}$ reads

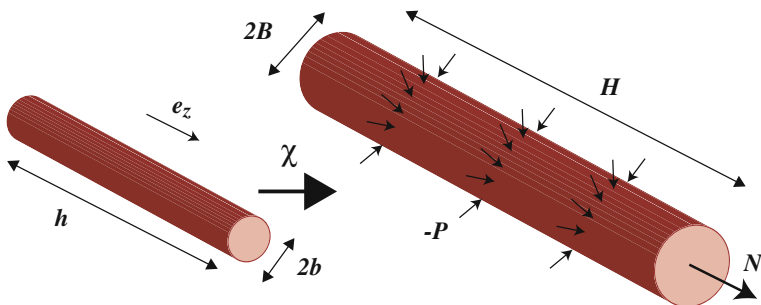


Figure 11.11 Inflation–extension of a tube. The tube is inflated with an internal pressure P (which is equivalent to an external pressure $-P$ as shown) and an axial load N resulting from an applied load and the pressure acting on the end caps.

$$r = r(R), \quad \theta = \Theta, \quad z = \zeta Z, \quad (11.195)$$

where ζ is the constant axial stretch of the cylinder such that $h = \zeta H$. The position vectors in the reference and current configurations are

$$\mathbf{X} = R\mathbf{E}_R + Z\mathbf{E}_Z, \quad \mathbf{x} = r(R)\mathbf{e}_r + \zeta Z\mathbf{e}_z, \quad (11.196)$$

where $\{\mathbf{E}_R, \mathbf{E}_\Theta, \mathbf{E}_Z\}$ and $\{\mathbf{e}_r, \mathbf{e}_\theta, \mathbf{e}_z\}$ are the two standard cylindrical bases. Following the identity (11.60), the deformation gradient $\mathbf{F} = \text{Grad}(\chi)$ with respect to these coordinates is given by

$$\mathbf{F} = r'\mathbf{e}_r \otimes \mathbf{E}_R + \frac{r}{R}\mathbf{e}_\theta \otimes \mathbf{E}_\Theta + \zeta\mathbf{e}_z \otimes \mathbf{E}_Z, \quad (11.197)$$

where the prime denotes differentiation with respect to R . Equivalently, we can write

$$[\mathbf{F}] = \text{diag}(r', \frac{r}{R}, \zeta) \equiv \text{diag}(\lambda_r, \lambda_\theta, \lambda_z), \quad (11.198)$$

which defines the three principle stretches $\{\lambda_r, \lambda_\theta, \lambda_z\}$.

The incompressibility condition $\det(\mathbf{F}) = 1 = \lambda_r \lambda_\theta \lambda_z$ gives

$$r'r = \frac{R}{\zeta}, \quad (11.199)$$

which, together with $r(A) = a$, leads to

$$r = \sqrt{a^2 + \frac{R^2 - A^2}{\zeta}}. \quad (11.200)$$

Then, $\lambda = \lambda_\theta$ is given by

$$\lambda = \frac{r}{R} = \frac{1}{R} \sqrt{a^2 + \frac{R^2 - A^2}{\zeta}}. \quad (11.201)$$

Therefore, the deformation is fully specified by two parameters: the axial stretch ζ and the radial stretch of the inner wall $\lambda_a = a/A$ so that

$$\lambda_b = \frac{b}{R} = \frac{1}{\zeta} \sqrt{1 + \frac{A^2}{B^2} (\zeta \lambda_a^2 - 1)}. \quad (11.202)$$

Since the deformation is diagonal in cylindrical coordinates and only depends on R , it follows from Equation (11.154) that the Cauchy stress tensor is also diagonal in these coordinates so that

$$[\mathbf{T}] = \text{diag}(t_r, t_\theta, t_z) \Leftrightarrow \mathbf{T} = t_r \mathbf{e}_r \otimes \mathbf{e}_r + t_\theta \mathbf{e}_\theta \otimes \mathbf{e}_\theta + t_z \mathbf{e}_z \otimes \mathbf{e}_z. \quad (11.203)$$

This particular form of the Cauchy stress tensor implies that the Cauchy equation $\text{div } \mathbf{T} = \mathbf{0}$ in cylindrical coordinates reduces to a single scalar equation

$$\frac{dt_r}{dr} + \frac{1}{r}(t_r - t_\theta) = 0. \quad (11.204)$$

This equation can be integrated once over r to obtain:

$$t_r(r) = t_r(a) + \int_a^r \frac{t_\theta - t_r}{r} dr, \quad r \in [a, b]. \quad (11.205)$$

We now examine the boundary conditions. First, due to inflation, the jump in pressure between the inner and outer sides of the cylinder is $P = t_r(b) - t_r(a)$. Without loss of generality, we choose

$$t_r(a) = -P, \quad t_r(b) = 0, \quad (11.206)$$

which in (11.205) implies

$$P = \int_a^b \frac{t_\theta - t_r}{r} dr. \quad (11.207)$$

Second, the boundary conditions on the two *caps* of the tube, defined as the two disks at $z = 0$ and $z = h$, can be written as

$$t_z(z = 0) = N_z, \quad t_z(z = h) = N_z. \quad (11.208)$$

However, since a constant axial stretch ζ cannot be used to fit a constant N_z , we replace this pointwise condition on the caps of the cylinder by an integral condition for the total axial load applied on the cap [1085, 1086]

$$2\pi \int_a^b N_z r dr = N \equiv F + \chi P \pi a^2, \quad (11.209)$$

thereby eliminating the explicit dependence on the variable r . The total axial load N is further decomposed into an external applied load F , which corresponds to pulling or compressing the tube, and the load created by the internal pressure acting over the cap. That load is simply the pressure multiplied by the projected area of the cap. The coefficient χ is 1 for a capped cylinder, and 0 for an infinite cylinder [207, 484].

For incompressible materials, this last expression is not the most practical one as the term t_z will contain an arbitrary pressure. An equivalent expression can be obtained by adding and subtracting T_r to obtain

$$2\pi \int_a^b T_z r dr = 2\pi \int_a^b (T_z - T_r + T_r) r dr. \quad (11.210)$$

The last term can be integrated by parts, and use of the balance law (11.204) gives

$$2\pi \int_a^b T_z r dr = \pi \int_a^b (2T_z - T_r - T_\theta) r dr + P \pi a^2, \quad (11.211)$$

which implies

$$\pi \int_a^b (2T_z - T_r - T_\theta) r dr = F + (\chi - 1) P \pi a^2, \quad (11.212)$$

and the last term vanishes for a capped cylinder.

To close the system, we use the constitutive law:

$$t_r = \lambda_r \frac{\partial W}{\partial \lambda_r} - p, \quad t_\theta = \lambda_\theta \frac{\partial W}{\partial \lambda_\theta} - p, \quad t_z = \lambda_z \frac{\partial W}{\partial \lambda_z} - p, \quad (11.213)$$

and substitute the functions of $(\lambda_r = 1/(\lambda\zeta), \lambda_\theta = \lambda, \lambda_z = \zeta)$ in (11.207–11.209) so that $t_\theta - t_r = Q(r, \lambda_a, \zeta)$.

The semi-inverse problem consists in finding the values of (λ_a, ζ) corresponding to the two external loads (F, P) through the analysis of the two equations (11.207–11.209). Note that once (λ_a, ζ) is known, the stress $t_r(r)$ can be computed as

$$t_r(r) = -P + \int_a^r Q(r, \lambda_a, \zeta) dr, \quad (11.214)$$

and the remaining stresses are obtained from (11.213).

11.8.3.1 A Toy Model for an Artery

As an example, we consider a toy model for an artery subject to pressure and tensile stretch. The artery is modeled as a capped tube ($\chi = 1$) made of a Fung material with values taken from Table 11.1. The system is subjected to a fixed axial force F and varying pressure P [1275]. We solve Equations (11.207)–(11.209) for (λ_a, ζ) and plot P as a function of ζ , so that if the pressure is controlled, one can determine the amount of axial stretch in the tube.

First, we consider the case of a neo-Hookean material. The curve $P(\zeta)$ shown in Figure 11.12 is non-monotonic and presents a maximal value of pressure after which unbounded extensional growth follows. This behavior is a drawback of the neo-Hookean model which is not well defined for arbitrarily large deformations and stresses.

Second, we consider the effect of the strain-stiffening parameter β . In Figure 11.13, we see that for small values of β , a non-monotonic behavior is observed in moderate deformations, followed by a rapidly increasing pressure for larger deformations. For larger values of the strain-stiffening parameter, the behavior is monotonic and increasingly large pressures are needed for further small incremental extensions.

We conclude that the behavior of the neo-Hookean model is qualitatively different from the behavior of the Fung model even for very small values of the strain-stiffening parameter β . In particular, typical axial stretches in arteries are around 1.3 to 1.6, in the region where the response of the structure clearly depends on the choice of the material model. This simple computation clearly demonstrates the importance of the choice of the material model for a given problem and the need to use nonlinear rather than linear elasticity to study these problems.

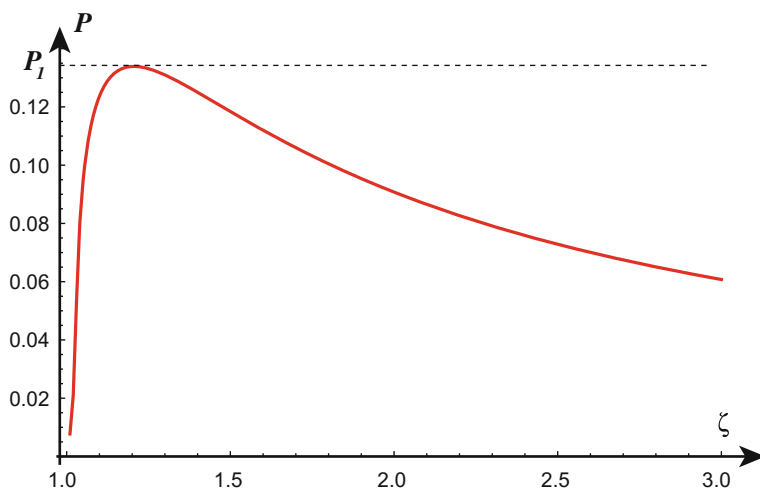


Figure 11.12 Behavior of a tube under pressure and axial force for a neo-Hookean material ($A = 1$, $B = 1.2$, $\mu = 1$, $F = 0.1$, $\chi = 1$). The neo-Hookean model is ill-defined past a critical pressure P_I .

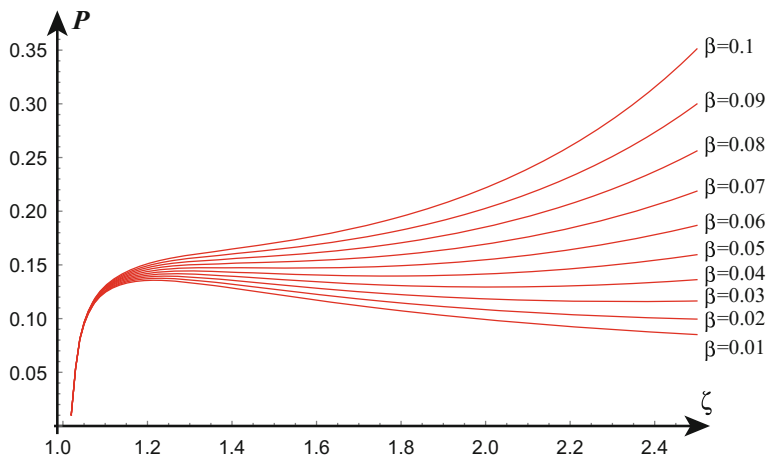


Figure 11.13 Behavior of a tube under pressure and axial force for a Fung material ($\beta > 0$). Parameters for all figures: $A = 1$, $B = 1.2$, $\mu = 1$, $F = 0.1$, $\chi = 1$.

The non-monotonic behavior shown in Figure 11.14, for intermediate values of β , is the well-known *limit-point instability* that already appeared in the experiment by Osborne and Sutherland (compare Figure 11.1 with Figure 11.14) for spherical and cylindrical shells under internal pressure [8, 17, 198, 433, 922, 974]. For certain materials, the pressure–stretch curve for spherical shells may present a maximum, followed by a minimum. In that case, once the maximum is reached, and the pressure is increased, the stretch will “jump” to a significantly higher value. In spherical shells, several authors have shown that this limit-point instability disappears as the strain-hardening parameter is increased [72, 109, 635, 975].

It is tempting to associate certain pathologies such as aneurysms appearing in arteries to a possible mechanical instability. However, the stabilizing effect due to strain-stiffening leads us to conclude that a simple explanation for the formation of aneurysms in terms of limit-point instability is not plausible [262, 746]. The same general trend is exhibited by more realistic models of arteries, involving multiple layers, fiber anisotropy, and residual stress discussed in Section 16.5. Nevertheless, various authors have looked at the interesting possibility that aneurysms could be triggered by a *local* mechanical instability resulting in a localized, but stable, bulged configuration that would then evolve slowly and remodel [398–400, 1021, 1022, 1092]. Aneurysms are such complex progressive diseases that it is unlikely that their formation could be explained simply as a mechanical phenomenon. Still, it is now appreciated that mechanics and mechanical feedback play an important role in the proper function of arteries and in the formation of aneurysms [425, 1083].

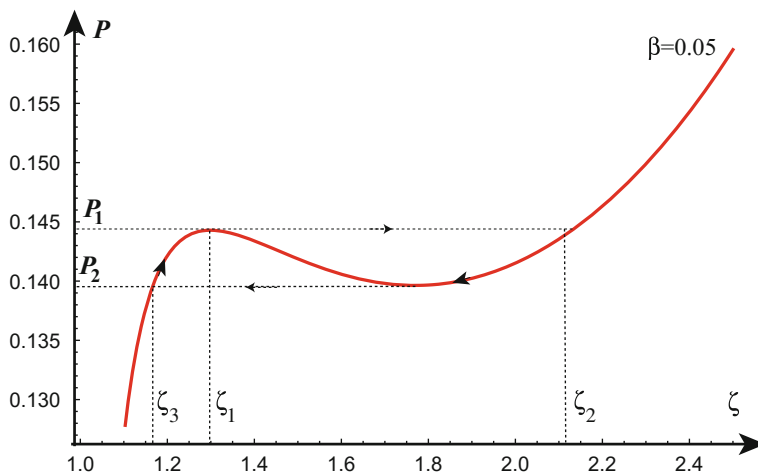


Figure 11.14 Limit-point instability of a tube under pressure and axial force for a Fung material ($\beta = 0.05$). The curve $P(\zeta)$ has a minimum and a maximum. If the internal pressure of the tube is raised to P_1 , a sudden extension occurs through a jump from ζ_1 to ζ_2 . When the pressure is then decreased to P_2 , a second jump occurs to ζ_3 (lower arrow).

11.9 Universal Deformations for Isotropic Materials

One of the advantages of the general formalism of nonlinear elasticity is the possibility of solving boundary-value problems for arbitrary strain-energy functions. However, it is not clear that a given class of deformations can exist for any strain-energy function in the absence of body loads. A *semi-inverse problem* consists in specifying a class of deformations (for instance the inflation of a sphere) with several unknown functions or constants that are determined through the equilibrium equations. The question is then to determine all transformations that can be effected through boundary traction in every homogeneous isotropic hyperelastic material, and in the absence of body forces, the so-called *universal deformations* for which the semi-inverse problem is well defined [71, 342, 343].

For compressible materials, Ericksen [343] proved that the homogeneous deformations given in Section 11.8.1 are the only possible universal deformations. That is, without further restricting the class of strain-energy functions or applying body loads, homogeneous deformations are the only ones that can be sustained for arbitrary strain-energy functions [1047].

For incompressible materials, a number of interesting universal deformations are known, but the general problem of determining all such possible deformations is still open [71, 373]. In addition to homogeneous deformations (classified as Family 0), there are five known families of universal deformations. Each family of solutions exists for all strain-energy functions and suitable boundary tractions. Since the deformation is known, the boundary tractions needed to maintain a given solution can be

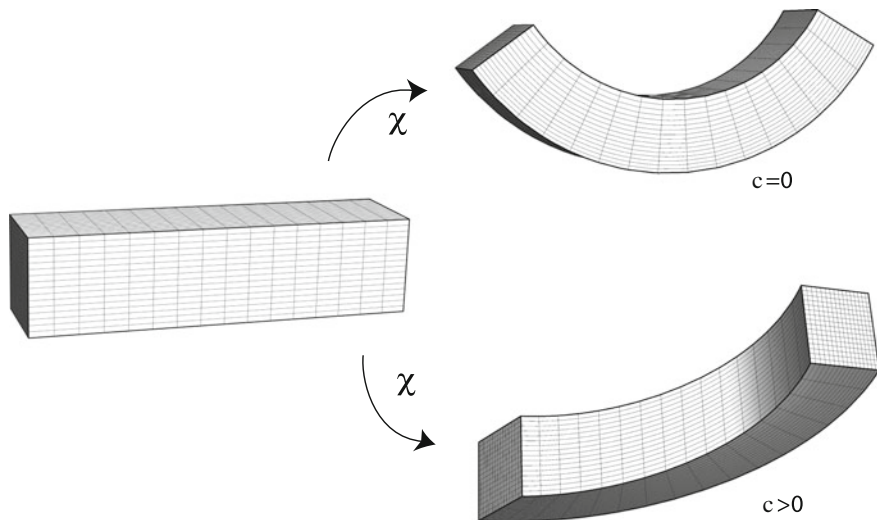


Figure 11.15 Family 1. Bending, stretching, and shearing of a rectangular block. When the parameter c vanishes, the deformation corresponds to the bending/stretching of a block. The parameter c is associated to shearing out of the bending plane.

found by evaluating the Cauchy stress tensor at the boundary. Doing so, one is able to relate the parameters appearing in the solution to the loads required to maintain them.

- **Family 0.** Homogeneous deformations of a rectangular block:

$$x_i = F_{ij}X_j, \quad i = 1, 2, 3, \quad (11.215)$$

where (X_1, X_2, X_3) and (x_1, x_2, x_3) are the Cartesian coordinates of a material point in the reference and current configurations, respectively. The deformation is specified by the nine constants appearing in the deformation gradient $\mathbf{F}$.

- **Family 1.** Bending, stretching, and shearing of a rectangular block as shown in Figure 11.15. This deformation is defined with three arbitrary constants (a, b, c) ($ab \neq 0$) by

$$r = \sqrt{2aX}, \quad \theta = bY, \quad z = \frac{Z}{ab} - bcY, \quad (11.216)$$

where (X, Y, Z) and (r, θ, z) are the Cartesian and cylindrical coordinates of a material point in the reference and current configurations, respectively.

In these coordinates, the matrix of components of the deformation gradient reads (for $a > 0$):

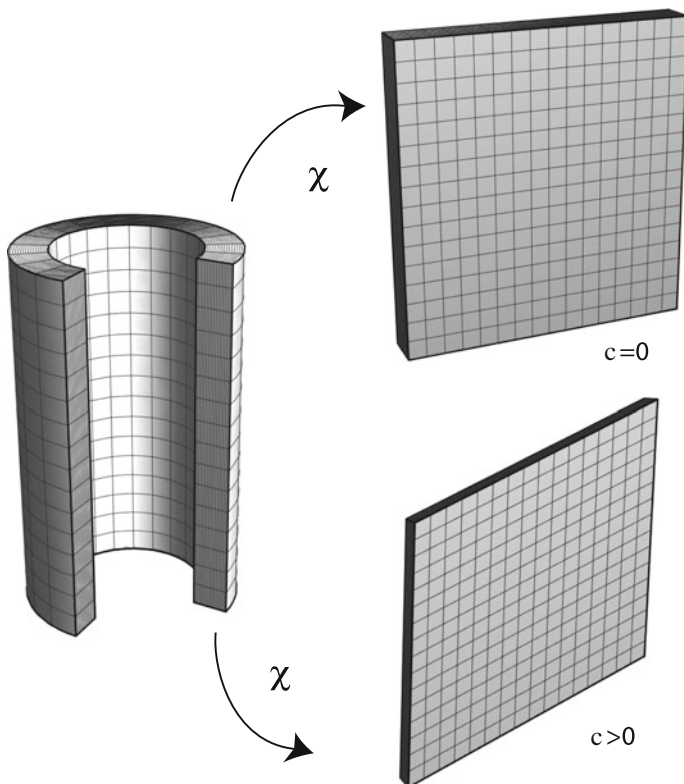


Figure 11.16 Family 2. Straightening, stretching, and shearing of a sector of a cylindrical shell. When the parameter c vanishes, the deformation corresponds to the straightening of the cylinder. The parameter c is associated to extra shearing of the resulting block.

$$[\mathbf{F}] = \begin{bmatrix} \sqrt{a}/\sqrt{2X} & 0 & 0 \\ 0 & b\sqrt{2aX} & 0 \\ 0 & -bc & 1/(ab) \end{bmatrix}. \quad (11.217)$$

- **Family 2.** Straightening, stretching, and shearing of a sector of a cylindrical shell, depicted in Figure 11.16, and defined for three arbitrary constants (a, b, c) ($ab \neq 0$) by

$$x = \frac{1}{2}ab^2R^2, \quad y = \frac{\Theta}{ab}, \quad z = \frac{Z}{b} - c\frac{\Theta}{ab}, \quad (11.218)$$

where (R, Θ, Z) and (x, y, z) are the cylindrical and Cartesian coordinates of a material point in the reference and current configurations, respectively.

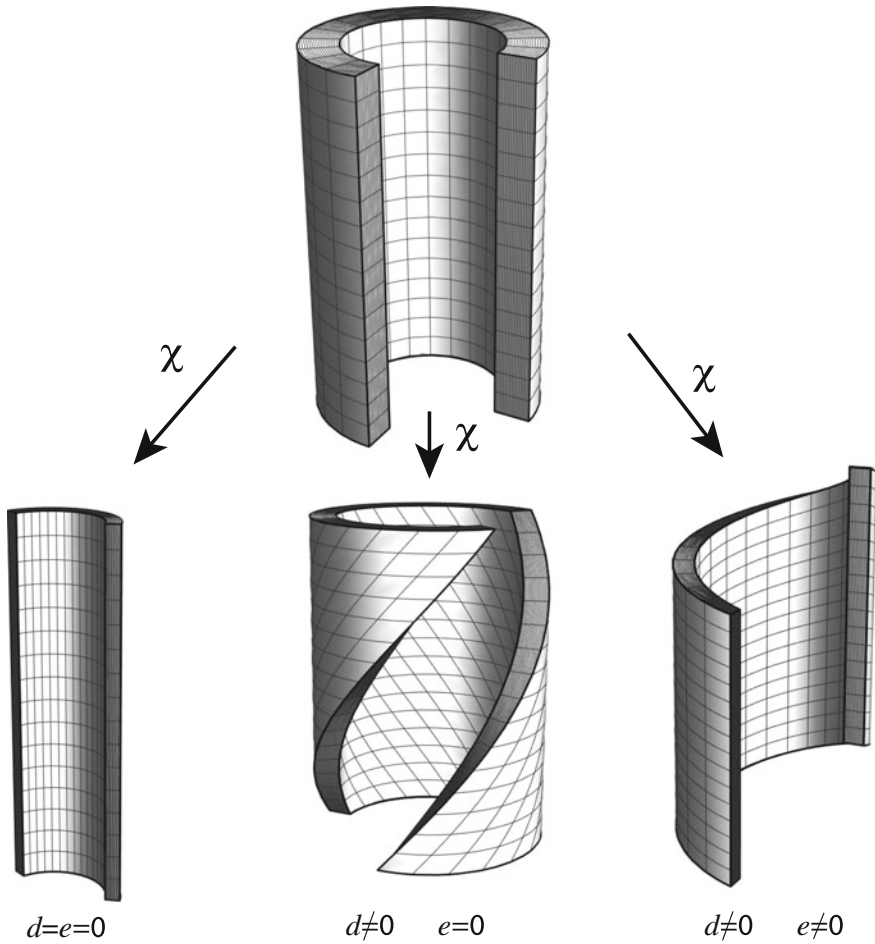


Figure 11.17 Family 3. Inflation, bending, torsion, extension, and shearing of a cylindrical shell. The parameters d and e control the torsion and the shearing along the axis.

In these coordinates, the matrix of components of the deformation gradient is given by

$$[\mathbf{F}] = \begin{bmatrix} ab^2R & 0 & 0 \\ 0 & 1/(abR) & 0 \\ 0 & -c/(abR) & 1/b \end{bmatrix}. \quad (11.219)$$

- **Family 3.** Inflation, bending, torsion, extension, and shearing of a sector of an annular wedge, shown in Figure 11.17, defined by six arbitrary constants (a, b, c, d, e, f) with the constraint $a(cf - de) = 1$:

$$r = \sqrt{aR^2 + b}, \quad \theta = c\Theta + dZ, \quad z = e\Theta + fZ, \quad (11.220)$$

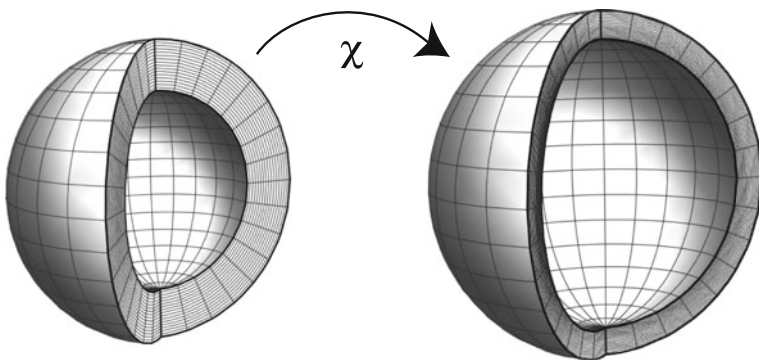


Figure 11.18 Family 4. Inflation of a spherical shell to another spherical shell. The deformation is controlled by a single parameter. A possible choice is the ratio of current to reference inner radii.

where (R, Θ, Z) and (r, θ, z) are the cylindrical coordinates of a material point in the reference and current configurations, respectively. The shearing is both axial (torsional) and azimuthal, that is, the region at constant Z becomes a helicoidal surface.

In these coordinates, the matrix of components of the deformation gradient is given by

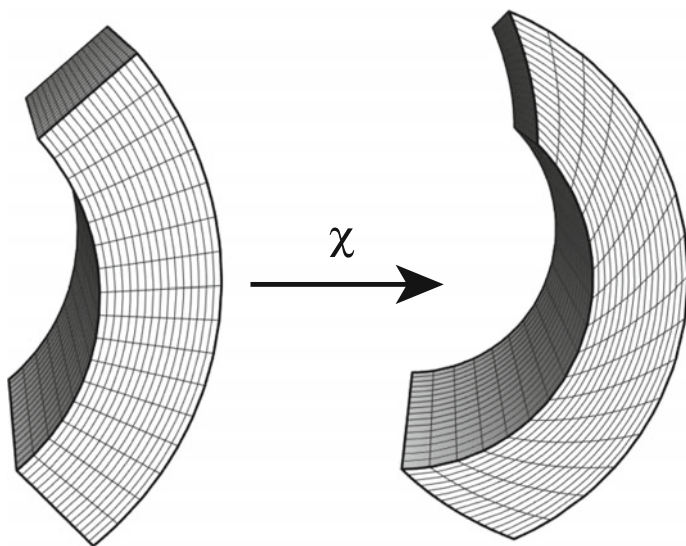


Figure 11.19 Family 5. Inflation, bending, extension, and azimuthal shearing of an annular wedge. Note that the deformation is essentially planar since the deformation in the z -direction is homogeneous.

$$[\mathbf{F}] = \begin{bmatrix} \frac{aR}{\sqrt{aR^2+b}} & 0 & 0 \\ 0 & \frac{c\sqrt{aR^2+b}}{R} & d\sqrt{aR^2+b} \\ 0 & e/R & f \end{bmatrix}. \quad (11.221)$$

- **Family 4.** Inflation (+) or inversion (−) of a sector of a spherical shell, shown in Figure 11.18 with a single constant a :

$$r = \sqrt[3]{\pm R^3 + a}, \quad \theta = \pm \Theta, \quad \phi = \Phi, \quad (11.222)$$

where (R, Θ, Φ) and (r, θ, ϕ) are the spherical coordinates of a material point in the reference and current configurations, respectively.

In these coordinates, the matrix of components of the deformation gradient is given by

$$[\mathbf{F}] = \begin{bmatrix} \pm \frac{R^2}{(R^3+a)^{2/3}} & 0 & 0 \\ 0 & \pm \frac{\sqrt[3]{R^3+a}}{R} & 0 \\ 0 & 0 & \pm \frac{\sqrt[3]{R^3+a}}{R} \end{bmatrix}. \quad (11.223)$$

- **Family 5.** Inflation, bending, extension, and azimuthal shearing of an annular wedge, shown in Figure 11.19, with five constants (a, b, c, d, e) constrained by the condition $a^2ce = 1$:

$$r = aR, \quad \theta = c\Theta + d \log(bR), \quad z = eZ, \quad (11.224)$$

where (R, Θ, Z) and (r, θ, z) are the cylindrical coordinates of a material point in the reference and current configurations, respectively.

In these coordinates, the matrix of components of the deformation gradient is given by

$$[\mathbf{F}] = \begin{bmatrix} a & 0 & 0 \\ ad & ac & 0 \\ 0 & 0 & e \end{bmatrix}. \quad (11.225)$$

11.10 Bifurcation, Buckling, and Instability

For given material and reference configurations with known boundary conditions, the deformations and stresses at equilibrium can be computed, in principle, by solving the system (11.135–11.138). This finite deformation solution represents a mechanical equilibrium whose stability can be probed by the theory of bifurcation. That is, we consider a wider class of deformations and establish the possibility of a bifurcation of a base state by looking for adjacent equilibrium solutions. We note that the

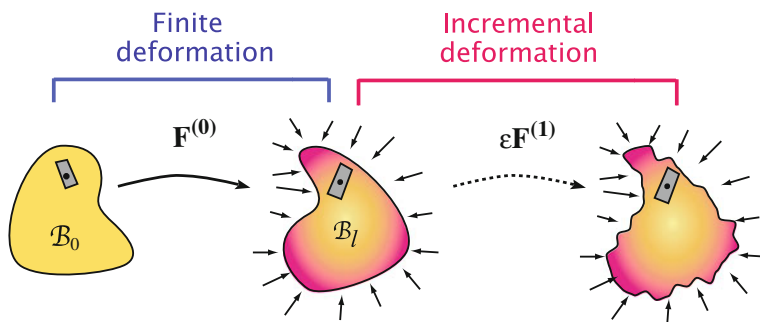


Figure 11.20 Bifurcation: A small incremental deformation is added over a known large-deformation equilibrium solution in order to obtain a new solution valid near the base solution. The dotted line represents an addition on top of the deformation and should be understood as the mapping $1 + \epsilon \mathbf{F}^{(1)}$.

correspondence between mechanical stability and bifurcation is far from trivial as noted by many authors [95, 195, 197, 548]. Here, we take the traditional viewpoint of buckling theory: The existence of a bifurcation offers the possibility of an instability that can be further analyzed either by looking at the dynamics associated with new solutions, as done in the case of rods (Section 6.5), or by analyzing the second variation of the energy, if applicable [257, 713, 785].

In this type of analysis, one starts with a known family of solutions with several parameters. Once the equilibrium homogeneous solution has been obtained, one can study the existence of nearby equilibrium solutions with respect to change in the parameters and identify the value of the parameters where such new solutions first appear.

The general procedure consists in implementing a perturbation expansion in which the new deformations, superimposed on the finite deformation, are assumed to be arbitrarily small as shown in Figure 11.20. This type of deformation in nonlinear elasticity is often referred to as *incremental deformations* [103, 402, 975] or *small-on-large deformations* [555]. Since the incremental deformations are assumed to be small, the full nonlinear system can be linearized and bifurcation points are obtained as the values at which the linearization fails to be injective.

In our setting, we assume that a family of solutions for the Cauchy stress $\mathbf{T}^{(0)}$ and deformations $\chi^{(0)}$ is known for given boundary conditions and is controlled by several parameters. We refer to this solution as the *base solution*. We seek solutions close to the base solution by formally linearizing the governing equations around the base state. Here, for simplicity, we assume that the material is incompressible and hyperelastic and, for this discussion, neglect body force. A detailed discussion of the general bifurcation scheme under arbitrary kinematic constraints and growth is given in Section 14.8. Here, following [465], we present the method by decomposing it into four steps to produce a closed set of linear equations. Then, we illustrate the method on a simple example.

Step 1: Kinematics of incremental deformations. We start with the first-order kinematics by considering a finite deformation $\chi^{(0)}$ on which we superimpose an incremental deformation $\chi^{(1)}$ as

$$\chi = \chi^{(0)} + \epsilon \chi^{(1)}, \quad (11.226)$$

where ϵ is an arbitrary parameter controlling the amplitude of the perturbation. It follows that the deformation gradient is

$$\mathbf{F} = \text{Grad}(\chi) = (\mathbf{1} + \epsilon \mathbf{F}^{(1)}) \mathbf{F}^{(0)}, \quad (11.227)$$

where

$$\mathbf{F}^{(1)} = \text{grad}(\chi^{(1)}), \quad (11.228)$$

is expressed in the current configuration. Explicitly, if we write $\chi^{(0)} = \mathbf{x}(\mathbf{X})$ and $\chi^{(1)} = \mathbf{u}(\mathbf{x}(\mathbf{X}))$, we have

$$\text{Grad} \mathbf{u}(\mathbf{x}(\mathbf{X})) = (\text{grad} \mathbf{u}(\mathbf{x})) \text{Grad} \mathbf{x}(\mathbf{X}) = (\text{grad} \mathbf{u}) \mathbf{F}^{(0)}. \quad (11.229)$$

Step 2: Linearized equations. Second, we obtain the linearized equations of motion by expanding the Cauchy stress tensor to first order:

$$\mathbf{T} = \mathbf{T}^{(0)} + \epsilon \mathbf{T}^{(1)} + \mathcal{O}(\epsilon^2). \quad (11.230)$$

Then, the Cauchy equation (11.136), $\text{div} \mathbf{T} = \mathbf{0}$, written here in the absence of body force, implies both

$$\text{div}(\mathbf{T}^{(0)}) = \mathbf{0}, \quad (11.231)$$

and

$$\text{div}(\mathbf{T}^{(1)}) = \mathbf{0}. \quad (11.232)$$

Step 3: Linearized constitutive equations. Third, we relate the first-order Cauchy stress tensor to the deformation gradient by expanding the constitutive relationship

$$\mathbf{T} = \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{1}, \quad (11.233)$$

to first order:

$$\mathbf{T}^{(0)} = \mathbf{F}^{(0)} W_{\mathbf{F}}^{(0)} - p^{(0)} \mathbf{1}, \quad (11.234)$$

$$\mathbf{T}^{(1)} = \mathcal{L} : \mathbf{F}^{(1)} + \mathbf{F}^{(1)} \mathbf{F}^{(0)} W_{\mathbf{F}}^{(0)} - p^{(1)} \mathbf{1}, \quad (11.235)$$

where $p = p^{(0)} + \epsilon p^{(1)}$, $\mathcal{L}$ is the fourth-order tensor defined by

$$\mathcal{L} : \mathbf{F}^{(1)} = \mathbf{F}^{(0)} \left(W_{\mathbf{FF}}^{(0)} : (\mathbf{F}^{(1)} \mathbf{F}^{(0)}) \right), \quad (11.236)$$

and $W_{\mathbf{F}}^{(0)}$, $W_{\mathbf{FF}}^{(0)}$ are, respectively, the first and second derivatives of W with respect to $\mathbf{F}$ evaluated on $\mathbf{F}^{(0)}$. In Cartesian coordinates, these expressions read

$$\left(W_{\mathbf{F}}^{(0)} \right)_{ij} = \frac{\partial W(\mathbf{F}^{(0)})}{\partial F_{ji}^{(0)}}, \quad (11.237)$$

$$\left(W_{\mathbf{FF}}^{(0)} \right)_{mjnl} = \frac{\partial^2 W(\mathbf{F}^{(0)})}{\partial F_{jm}^{(0)} \partial F_{ln}^{(0)}}, \quad (11.238)$$

and

$$(\mathcal{L} : \mathbf{F}^{(1)})_{ij} = \mathcal{L}_{ijkl} F_{lk}^{(1)} = F_{im}^{(0)} \left(W_{\mathbf{FF}}^{(0)} \right)_{mjnl} F_{lk}^{(1)} F_{kn}^{(0)}. \quad (11.239)$$

The components of the fourth-order tensor $\mathcal{L}$ are the *instantaneous elastic moduli* which are defined as

$$\mathcal{L}_{ijkl} = F_{im}^{(0)} \left(W_{\mathbf{FF}}^{(0)} \right)_{mjnl} F_{kn}^{(0)}. \quad (11.240)$$

These moduli characterize the linear behavior of a material at a finite value of the deformation. For isotropic materials, their form can be given explicitly [975, p. 412]. Let $\{\lambda_1, \lambda_2, \lambda_3\}$ be the principal values of $\mathbf{F}^{(0)}$. Then for an isotropic hyperelastic material the components of $\mathcal{L}$ on the Eulerian principal axes associated with $\mathbf{F}^{(0)}$ are

$$\mathcal{L}_{iijj} = \lambda_i \lambda_j \frac{\partial^2 W}{\partial \lambda_i \partial \lambda_j}, \quad (11.241)$$

$$\mathcal{L}_{ijij} = \left[\lambda_i \frac{\partial W}{\partial \lambda_i} - \lambda_j \frac{\partial W}{\partial \lambda_j} \right] \frac{\lambda_i^2}{(\lambda_i^2 - \lambda_j^2)}, \quad i \neq j, \lambda_i \neq \lambda_j, \quad (11.242)$$

$$\mathcal{L}_{ijji} = \mathcal{L}_{jii j} = \mathcal{L}_{ijij} - \lambda_i \frac{\partial W}{\partial \lambda_i}, \quad i \neq j. \quad (11.243)$$

If $\lambda_i = \lambda_j$ for some $i \neq j$, then

$$\mathcal{L}_{ijij} = \frac{1}{2} \left(\mathcal{L}_{iiii} - \mathcal{L}_{iijj} + \lambda_i \frac{\partial W}{\partial \lambda_i} \right), \quad (11.244)$$

$$\mathcal{L}_{iiii} = \mathcal{L}_{jjjj}, \quad \mathcal{L}_{iikk} = \mathcal{L}_{jjkk}, \quad (11.245)$$

$$\mathcal{L}_{ikik} = \mathcal{L}_{jkjk}, \quad \mathcal{L}_{ikki} = \mathcal{L}_{jk kj}. \quad (11.246)$$

Step 4: The boundary-value problem. The stability analysis proceeds by solving the equation for mechanical equilibrium (11.136) to first order in ϵ , that is,

$$\operatorname{div} \mathbf{T}^{(1)} = \mathbf{0}, \quad (11.247)$$

together with the incompressibility condition to first order. The incompressibility condition is $\det \mathbf{F} = 1$, which, using Jacobi's identity (11.52), reads to first order:

$$\operatorname{tr} \mathbf{F}^{(1)} = \operatorname{div} \mathbf{u} = 0. \quad (11.248)$$

In some cases, the geometry of the problem and the deformations considered are simple enough that the condition for instability related to the existence of solutions for Equation (11.247) can be written in terms of W and the principal stretches $\{\lambda_1, \lambda_2, \lambda_3\}$.

11.10.1 Example: Bifurcation of the Half-Plane

As an example, we consider the problem of a half-plane under compression and look for the possibility of bifurcations. We assume that the half-space is a incompressible hyperelastic half-space with a free surface under pure homogeneous static deformation as studied in Section 11.8.2. The half-space is located in $X_2 > 0$ and λ_2 is the stretch ratio in the direction normal to the free surface. We recall that the principal stretch λ_1 can be used to characterize the deformation so that the components of Cauchy stress tensor can be written as

$$[\mathbf{T}^{(0)}] = \operatorname{diag}(t_1, t_2, t_3), \quad (11.249)$$

and the deformation gradient is

$$[\mathbf{F}^{(0)}] = \operatorname{diag}(\lambda_1, \lambda_2, \lambda_3). \quad (11.250)$$

The three cases of interest are

$$\lambda_2 = \lambda_1^n \quad \text{with} \quad \begin{cases} n = -2 & \text{equibiaxial,} \\ n = -1 & \text{plane strain,} \\ n = -\frac{1}{2} & \text{uniaxial,} \end{cases} \quad (11.251)$$

and $\lambda_3 = \lambda_1^{-n-1}$. Since $t_2 = 0$, we have $p = \lambda_2 W_2$ and

$$t_1 = \lambda_1 W_1 - \lambda_2 W_2, \quad t_3 = \lambda_3 W_3 - \lambda_2 W_2, \quad (11.252)$$

where $W_i = \partial_{\lambda_i} W$. Therefore, all the components of the stress tensor and the deformation gradient tensor are functions of the control parameter λ_1 .

Step 1: Kinematics. We look for values of λ_1 such that the system supports nonhomogeneous solutions in the form of creases that are uniform in the $\mathbf{e}_3$ -direction as shown in Figure 11.21, that is, we look for solutions of the form

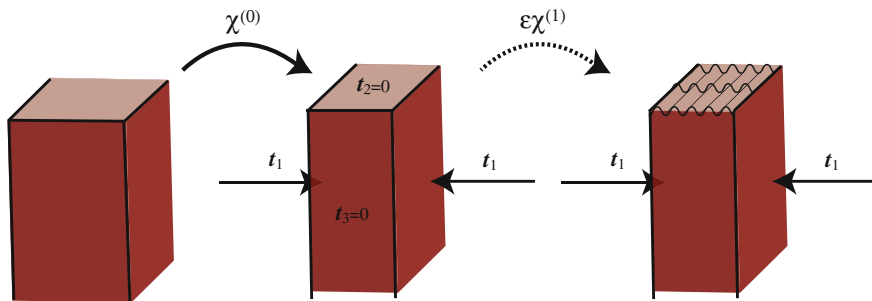


Figure 11.21 Bifurcation of a half-space under uniaxial compression. The finite deformation compresses the half-space. For the same loading, there exists another solution with surface creasing.

$$\mathbf{u} = [u(x_1, x_2), v(x_1, x_2), 0], \quad (11.253)$$

$$p^{(1)} = q(x_1, x_2), \quad (11.254)$$

$$\mathbf{T}^{(1)} = \mathbf{T}^{(1)}(x_1, x_2). \quad (11.255)$$

Step 2: Linearized equations. The two nonvanishing equations of equilibrium and the incompressibility condition form a system of three equations for $\{u, v, q\}$:

$$\frac{\partial T_{11}^{(1)}}{\partial x_1} + \frac{\partial T_{21}^{(1)}}{\partial x_2} = 0, \quad (11.256)$$

$$\frac{\partial T_{12}^{(1)}}{\partial x_1} + \frac{\partial T_{22}^{(1)}}{\partial x_2} = 0, \quad (11.257)$$

$$\frac{\partial u}{\partial x_1} + \frac{\partial v}{\partial x_2} = 0. \quad (11.258)$$

Step 3: Linearized constitutive equations. The components of the linearized stress tensor are

$$T_{11}^{(1)} = \mathcal{L}_{1111} \frac{\partial u}{\partial x_1} + \mathcal{L}_{1122} \frac{\partial v}{\partial x_2} - q + \frac{\partial u}{\partial x_1} (t_1 + p), \quad (11.259)$$

$$T_{12}^{(1)} = \mathcal{L}_{1221} \frac{\partial u}{\partial x_2} + \mathcal{L}_{1212} \frac{\partial v}{\partial x_1} + \frac{\partial u}{\partial x_2} (t_2 + p), \quad (11.260)$$

$$T_{22}^{(1)} = \mathcal{L}_{2211} \frac{\partial u}{\partial x_1} + \mathcal{L}_{2222} \frac{\partial v}{\partial x_2} - q + \frac{\partial v}{\partial x_2} (t_2 + p), \quad (11.261)$$

$$T_{21}^{(1)} = \mathcal{L}_{2121} \frac{\partial u}{\partial x_2} + \mathcal{L}_{2112} \frac{\partial v}{\partial x_1} + \frac{\partial v}{\partial x_1} (t_1 + p). \quad (11.262)$$

Step 4: Solving the boundary-value problem. The stress tensor is constant with respect to (x_1, x_2) . Therefore, System (11.256–11.258) is a linear, homogeneous, system of PDEs with constant coefficients. It can be verified by direct substitution that it admits exponential solutions of the form

$$\{u, v, q\} = e^{ikx_1 + iksx_2} \{U, V, ikQ\}. \quad (11.263)$$

For our problem, the relevant solutions are periodic along x_1 and exponentially decaying for increasing x_2 , that is, we choose

$$k > 0, \operatorname{Im}(s) > 0. \quad (11.264)$$

Substitution of (11.263) in (11.256–11.258) gives a system of three homogeneous linear equations for $\{U, V, Q\}$ and the condition for the existence of a solution is

$$a_0 + 2a_2s^2 + a_4s^4 = 0, \quad (11.265)$$

where

$$a_0 = \mathcal{L}_{1212}, \quad (11.266)$$

$$2a_2 = \mathcal{L}_{1111} + \mathcal{L}_{2222} - 2\mathcal{L}_{1122} - 2\mathcal{L}_{1221}. \quad (11.267)$$

$$a_4 = \mathcal{L}_{2121}. \quad (11.268)$$

In terms of λ_1 , these coefficients are

$$a_0 = \frac{\lambda_1 W_1 - \lambda_2 W_2}{\lambda_1^2 - \lambda_2^2} \lambda_1^2, \quad (11.269)$$

$$2a_2 = \lambda_1^2 W_{11} + \lambda_2^2 W_{22} - 2\lambda_1 \lambda_2 W_{12} - 2\lambda_1 \lambda_2 \frac{\lambda_1 W_1 - \lambda_2 W_2}{\lambda_1^2 - \lambda_2^2}, \quad (11.270)$$

$$a_4 = \frac{\lambda_1 W_1 - \lambda_2 W_2}{\lambda_1^2 - \lambda_2^2} \lambda_2^2, \quad (11.271)$$

where we now regard W as a function of λ_1 and λ_2 , that is, $\bar{W}(\lambda_1, \lambda_2) = W(\lambda_1, \lambda_2, \lambda_3(\lambda_1, \lambda_2))$, $W_i = \partial_{\lambda_i} \bar{W}$ and $W_{ij} = \partial_{\lambda_i \lambda_j}^2 \bar{W}$.

We need conditions on these coefficients to identify the roots of (11.265) that satisfy (11.264). Here, we use the so-called *strong-ellipticity conditions*. These conditions naturally arise when one considers the propagation of a plane homogeneous wave superimposed on the compression of the half-space. If we require that the speed of propagation is real, conditions on the parameters can be obtained [280, 296]. In our case, these conditions are given by

$$a_0 > 0, \quad a_4 > 0, \quad a_2 + \sqrt{a_0 a_4} > 0. \quad (11.272)$$

These conditions imply that there exist two roots of

$$a_0 + 2a_2s^2 + a_4s^4 = 0 \quad (11.273)$$

with $\text{Im}(s) > 0$. Let s_1 and s_2 be these two roots and $\{U_1, V_1, Q_1\}$, $\{U_2, V_2, Q_2\}$, the corresponding solutions. Then, the incremental solution is an arbitrary linear combination of these solutions, that is,

$$u = e^{ikx_1} (C_1 U_1 e^{iks_1 x_2} + C_2 U_2 e^{iks_2 x_2}), \quad (11.274)$$

$$v = e^{ikx_1} (C_1 V_1 e^{iks_1 x_2} + C_2 V_2 e^{iks_2 x_2}), \quad (11.275)$$

$$q = e^{ikx_1} (C_1 Q_1 e^{iks_1 x_2} + C_2 Q_2 e^{iks_2 x_2}). \quad (11.276)$$

The bifurcation condition is obtained by imposing the linearized boundary condition $\mathbf{T}^{(1)} \cdot \mathbf{e}_2 = \mathbf{0}$. The compressed half-space becomes unstable and develops surface instability for critical principal stretch ratio λ_1/λ_2 such that

$$\left(\frac{\lambda_1}{\lambda_2}\right)^2 + 2\left(1 + \frac{a_2}{a_4}\right)\left(\frac{\lambda_1}{\lambda_2}\right) - 1 = 0. \quad (11.277)$$

Explicitly, in terms of W and its derivatives, the bifurcation condition is

$$\lambda_2 \left[W_1 + \left(2 - \frac{\lambda_2}{\lambda_1}\right) W_2 \right] + \lambda_1^2 W_{11} - 2\lambda_1 \lambda_2 W_{12} + \lambda_2^2 W_{22} = 0. \quad (11.278)$$

Next, we look at this condition for various strain-energy functions. We start with the classic elastomer modeled by the Mooney–Rivlin energy W_{mr} from Table 11.1. In this case, the criterion (11.278) leads to a universal condition (independent of μ and ν) [280]:

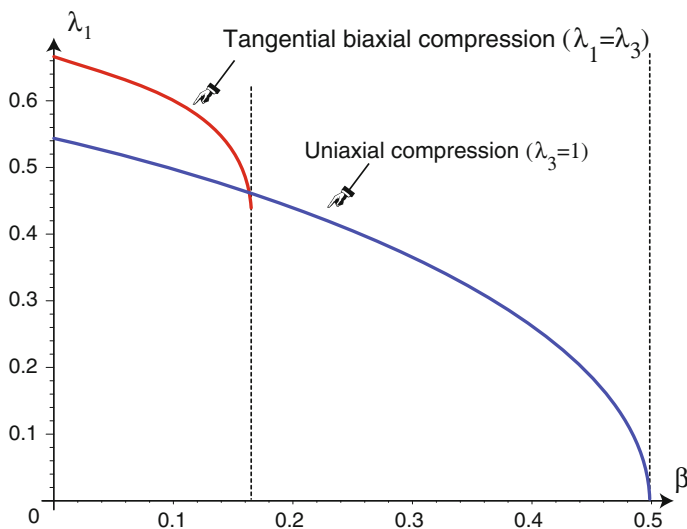


Figure 11.22 Critical values of the stretch ratio λ_1 for the instability of a Fung elastic half-space characterized by a strain-hardening parameter β .

$$\lambda_1^{n+2} + 3\lambda_1^{2n+1} - \lambda_1^{3n} + \lambda_1^3 = 0. \quad (11.279)$$

Depending on n , we obtain the classic values for the critical compression ratio of instability for a half-plane made of a material with the Mooney–Rivlin (or neo-Hookean) strain-energy function. Green and Zerna [504] found $(\lambda_1)_{\text{cr}} = 0.66614$ under biaxial compression ($n = -2$); Biot [102] found $(\lambda_1)_{\text{cr}} = 0.54369$ under plane strain ($n = -1$) and $(\lambda_1)_{\text{cr}} = 0.44375$ under uniaxial compression ($n = -1/2$).

Next, we turn to the popular Fung strain-energy function for soft tissues. We take $W = W_{\text{fu}}$ in (11.278) and obtain after simplification the following bifurcation condition:

$$\lambda_1^{n+2} + 3\lambda_1^{2n+1} - \lambda_1^{3n} + \lambda_1^3 + 2\beta(\lambda_1^5 - 2\lambda_1^{3+2n} + \lambda_1^{4n+1}) = 0. \quad (11.280)$$

For $n = -1$ or $n = -2$, there is a critical value $\alpha_{-1} = 1/2$, $\alpha_{-2} \approx 0.1644$ after which the bifurcation criterion has no positive real root, see Figure 11.22. We conclude that a Fung elastic half-plane under either axial or tangential compression is *always stable* for realistic physiological values of the parameters. For $n = -1/2$ (normal biaxial compression), the criterion has a positive real root for all α , which however decreases rapidly toward zero. Hence, for $\beta > 3$, the half-space can be compressed by more than 97% before the bifurcation criterion is met. Next, we consider the Gent strain-energy function, originally proposed for rubber [432], but also used for the modeling of strain-hardening soft tissues. We take $W = W_{\text{ge}}$ in (11.278) and obtain after simplification of the following bifurcation condition:

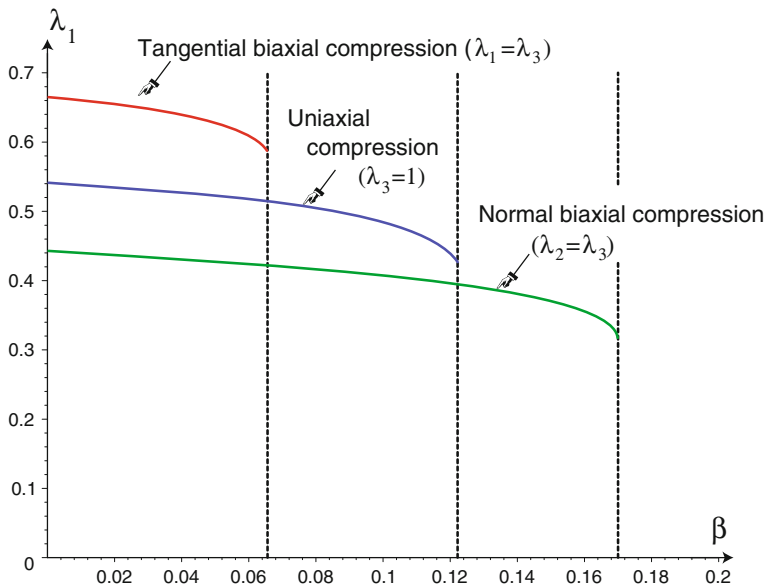


Figure 11.23 Critical values of the stretch ratio λ_1 for the surface instability of a Gent elastic half-space characterized by a strain-hardening parameter β .

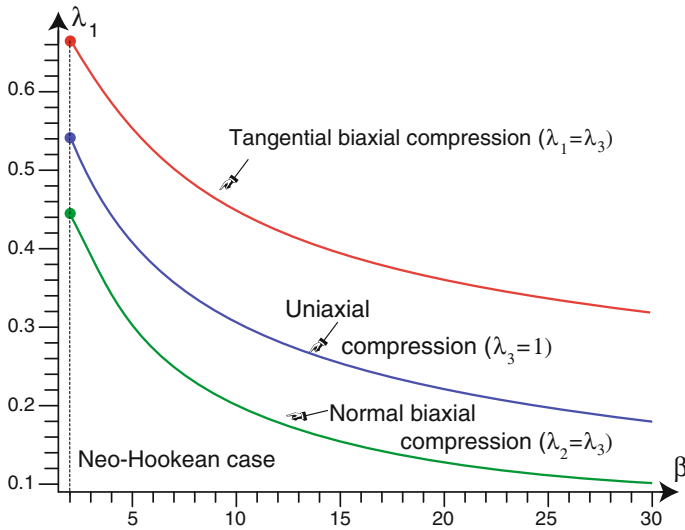


Figure 11.24 Critical values of the stretch ratio λ_1 for the instability of a Ogden elastic half-space characterized by a strain-hardening parameter β .

$$\beta(3\lambda_1^{n-1} - 2\lambda_1^{n+1} - 11\lambda_1^{2n} - \lambda_1^{4n-2} + 9\lambda_1^{2n-2} + \lambda_1^{5n-3} + \lambda_1^{3n-1} - 3\lambda_1^{3n-3} + 3) + \lambda_1^{n-1} + 3\lambda_1^{2n-2} - \lambda_1^{3n-3} + 1 = 0. \quad (11.281)$$

For $n = -1$, $n = -2$, and $n = -1/2$, there is a critical value $\beta_{-1} \approx 0.122$, $\beta_{-2} \approx 0.066$, and $\beta_{-1/2} \approx 0.170$ after which the bifurcation criterion has no positive real root, see Figure 11.23. We conclude that a Gent elastic half-plane under axial, tangential, or normal compression is *always stable* for realistic physiological values of the parameters.

Finally, we use the one-term Ogden model, for which the bifurcation condition reads

$$\lambda_1^{n+\beta} + \lambda_1^{n\beta+1} - \lambda_1^{n(1+\beta)} - \lambda_1^{1+\beta} + \beta(\lambda_1^{1+\beta} + \lambda_1^{n\beta+1}) = 0. \quad (11.282)$$

The left-hand side of this equation is equal to -1 for $\lambda_1 = 0$ and to 2β for $\lambda_1 = 1$. Therefore, it admits a real root for all positive values of β and for all values of n . The bifurcation curves are shown in Figure 11.24.

We comment that no finite body is a half-space. The instability found in the half-space is relevant when finite size effects can be ignored. Otherwise, we expect a body to become unstable through other deformation modes such as the ones found in buckling or barreling. We will encounter such instabilities when we study the deformations of cylinder and spheres induced by growth.

11.11 Anisotropic Materials

Many elastic biological tissues have highly anisotropic mechanical properties [408, p. 500]. These anisotropic properties are determined primarily by the presence of fibers [386, 1368]. For instance, for soft tissues such as tendons, arterial wall, aortic valve, myocardium, and pericardium, anisotropy is determined in the first place by the arrangement of the collagen fibers [408, 599, 635, 686, 769] in a mostly isotropic elastin matrix.

Collagen is a fibrous protein, which comprises 25% of the total protein mass in mammals [15, p. 1184] and is the most abundant protein in vertebrates. Collagen is present in tissues in various forms, in particular, in the form of fibrils, which consist of many cross-linked collagen molecules, that are from 50 to 500 nm in diameter and can further organize into fascicles. Special collagen type, geometry, density, and arrangement endow tissues with anisotropic mechanical properties. Collagen fibers in tendons are parallel and aligned in the direction of loading, while in the arterial wall, a significant fiber dispersion around two preferred fiber directions is observed. It also provides the tissue with strongly nonlinear mechanical responses as illustrated by the phenomenon of *stretch locking* in rabbit skin [769] shown in Figure 11.25.

In plant tissues the same mechanical role is played by cellulose microfibrils based on sugar chains, and with Young's modulus around 130 GPa, reinforcing an isotropic matrix composed of hemicellulose and lignin molecules with respective Young's modulus around 40 MPa and 2 GPa [148]. It is the fine control of fiber geometry

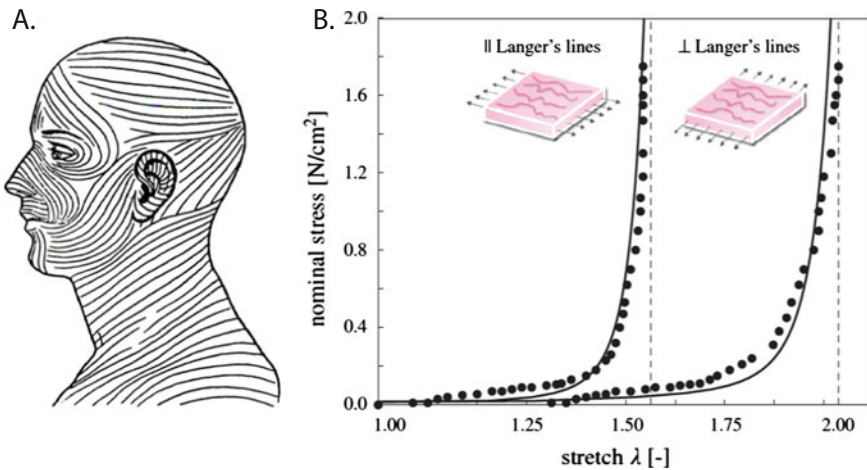


Figure 11.25 A. Langer's lines showing line of anisotropy in the skin. B. Uniaxial tension test on rabbit skin shows different behaviors in direction along or across Langer's lines (reproduced from [144], based on data [769]). Solid lines represent the computational simulation based on an eight-chain model [40]. The dotted lines are the so-called *locking stretches* after which no further stretch is possible (picture courtesy of Ellen Kuhl).

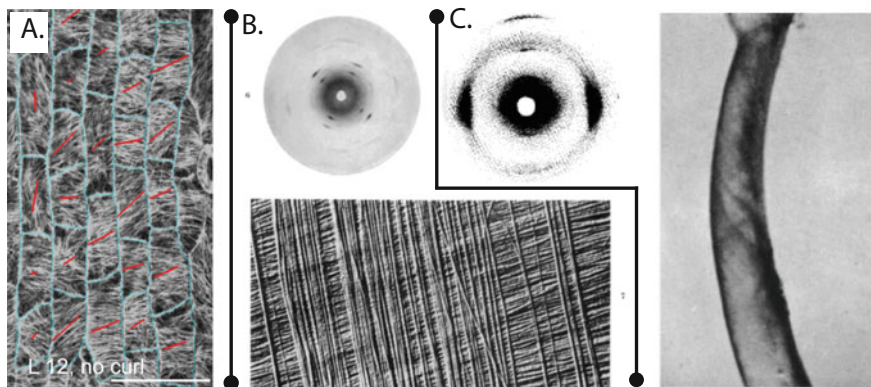


Figure 11.26 Examples of fiber reinforcement in biological tissues. A. Microtubule alignment in the exocarp cells of *Cardamine hirsuta*. The microtubules wind helically around the cells (picture courtesy of Angela Hay [582]). B. Microfibrils in green algae. The X-ray analysis shows the characteristic X structure indicating a mostly helical fiber [389]. C. Fiber wall structure of the sporangiophore of the fungus *Phycomyces* showing spiraling fibers in the cytoplasm together with the same characteristic X-ray signature [886].

and density that provides plants with their mechanical property and their ability to interact with their environment [317, 387, 797].

Similarly, in the fungal kingdom, the cell wall is, typically, constructed of chitin microfibrils embedded in an elastic matrix of amorphous material composed of chitosan and chitin [178, 625]. Such a composite material naturally lends itself to modeling in terms of an elastic matrix with fiber reinforcements [483] (Figure 11.26).

As the internal structure of a tissue determines its mechanical properties, it is reasonable to include it in a constitutive model. The theory of nonlinear fiber-reinforced elastic composites, developed by Rivlin, Spencer and others [9, 1183, 1184, 1248], asserts that the strain-energy function is in general expressed through a set of deformation invariants, whose number depends on the symmetry exhibited by the material. In this theory, fibers are modeled by continuous fields, that is, they are represented by local directions of anisotropy rather than actual physical fibers. A popular, *a priori*, assumption in constitutive models is that the total stress generated by the whole tissue is the sum of stresses generated by its constituents [604, 767, 768]. This assumption can be used to incorporate quantitative data characterizing a tissue's structure directly into the constitutive relation, e.g., fiber volume fraction or orientation-dependent density can be included as multiplicative factors in the appropriate term. In addition, structural approaches allow for a formulation of phenomenological laws for fiber remodeling and the study of the dynamics of mechanically induced fiber reorientation [303, 540, 865, 870].

11.11.1 One Fiber

A material reinforced by fibers that are perfectly aligned in one direction is an example of a *transversely isotropic material*, i.e., a material with one distinguished direction. The fiber direction is specified by a unit vector $\mathbf{M}$ in the reference configuration as shown in Figure 11.27. For this fiber, we define the *structure tensor*

$$\mathbf{H} = \mathbf{M} \otimes \mathbf{M}, \quad (11.283)$$

which contains all information about material anisotropy. We assume that the strain-energy function of the fiber-reinforced material depends on $\mathbf{H}$, and as a consequence, the requirement of isotropy $W(\mathbf{Q}^T \mathbf{C} \mathbf{Q}) = W(\mathbf{C})$ is not identically satisfied for an arbitrary proper orthogonal second-order tensor $\mathbf{Q}$. Instead, it must be satisfied for all proper orthogonal tensors $\mathbf{Q}$ such that $\mathbf{Q}\mathbf{M} = \pm\mathbf{M}$. This condition is enforced by considering that the strain-energy function is a function of both $\mathbf{C}$ and $\mathbf{H}$, that is $W = W(\mathbf{C}, \mathbf{H})$, and demanding that

$$W(\mathbf{C}, \mathbf{H}) = W(\mathbf{Q}^T \mathbf{C} \mathbf{Q}, \mathbf{Q}^T \mathbf{H} \mathbf{Q}), \quad \forall \mathbf{Q} \in SO(3). \quad (11.284)$$

A strain-energy function for such materials depends in general on a deformation tensor through five scalars, which consists of the three usual isotropic deformation invariants I_1 , I_2 , and I_3 defined by

$$I_1 = \text{tr } \mathbf{B}, \quad I_2 = \frac{1}{2}[I_1^2 - \text{tr}(\mathbf{B}^2)], \quad I_3 = \det \mathbf{B} = J^2. \quad (11.285)$$

and two extra *pseudo-invariants*, which are related to the strains in the fibers when deformed.

$$I_4 = \mathbf{M} \cdot (\mathbf{C}\mathbf{M}) = \mathbf{C} : \mathbf{H}, \quad I_5 = \mathbf{M} \cdot (\mathbf{C}^2 \mathbf{M}) = \mathbf{C}^2 : \mathbf{H}, \quad (11.286)$$

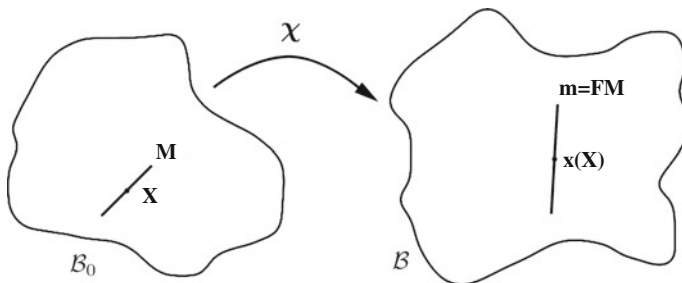


Figure 11.27 A one-fiber material. In an anisotropic one-fiber material, the response of the material depends on the deformation gradient $\mathbf{F}$ and the direction of a distinguished material line represented by a unit vector $\mathbf{M}$. In a deformation, this direction is mapped to a vector $\mathbf{m} = \mathbf{F}\mathbf{M}$.

where we used the double contraction between second-order tensors

$$\mathbf{A} : \mathbf{B} = \text{tr}(\mathbf{AB}) = A_{ij}B_{ji}. \quad (11.287)$$

The invariant I_4 has a natural interpretation as the square of the fiber stretch in the current configuration, that is, the norm of $\mathbf{m} = \mathbf{FM}$.

The general form for the Cauchy stress tensor (11.134) in terms of W remains valid. Using the identities

$$\mathbf{F} \frac{\partial I_4}{\partial \mathbf{F}} = 2\mathbf{FM} \otimes \mathbf{FM} = 2\mathbf{m} \otimes \mathbf{m}, \quad (11.288)$$

$$\begin{aligned} \mathbf{F} \frac{\partial I_5}{\partial \mathbf{F}} &= 2\mathbf{F}(\mathbf{M} \otimes \mathbf{FCM} + \mathbf{CM} \otimes \mathbf{FM}) \\ &= 2(\mathbf{m} \otimes \mathbf{Bm} + \mathbf{Bm} \otimes \mathbf{m}), \end{aligned} \quad (11.289)$$

we obtain an explicit expression for the Cauchy stress tensor:

$$\begin{aligned} \mathbf{T} = J^{-1} [&-p\mathbf{I} + 2W_1\mathbf{B} + 2W_2(I_1\mathbf{B} - \mathbf{B}^2) + 2I_3W_3 \\ &+ 2W_4\mathbf{m} \otimes \mathbf{m} + 2W_5(\mathbf{m} \otimes \mathbf{Bm} + \mathbf{Bm} \otimes \mathbf{m})], \end{aligned} \quad (11.290)$$

where $W_i = \partial W / \partial I_i$, $i = 1, \dots, 5$.

11.11.2 Two Fibers

Many biological tissues are reinforced in two directions and, accordingly, can be modeled by a material with two fibers. The mechanical advantage of a tissue with two fibers appears when the tissue is in tension. With a single fiber, an extension in any direction away from the fiber always produces shear. With two fibers, the shear produced by each fiber can be balanced by the other fiber when they have the same material response and their average direction matches the maximal principal direction. Further, the angle between the two fibers can be tuned to change the overall stiffness of the material.

Reinforcing by an additional family of fibers further reduces the symmetry of the material, but it extends the set of invariants from five to nine. These four extra scalars account for the strains in the second family and the coupling between the two fiber families [1184]. We use the unit vectors $\mathbf{M}$ and $\mathbf{M}'$ to define two preferred directions in the reference configuration $\mathcal{B}_0$. The energy for an unconstrained material with two families of fibers is a function of eight invariants. These are the principal invariants I_1, I_2, I_3 together with two pseudo-invariants I_4, I_5 that depend on $\mathbf{M}$, two pseudo-invariants I_6, I_7 that depend on $\mathbf{M}'$ and two coupling terms I_8, I_9 defined by

$$\begin{aligned}
I_4 &= \mathbf{M} \cdot (\mathbf{CM}), & I_5 &= \mathbf{M} \cdot (\mathbf{C}^2 \mathbf{M}), \\
I_6 &= \mathbf{M}' \cdot (\mathbf{CM}'), & I_7 &= \mathbf{M}' \cdot (\mathbf{C}^2 \mathbf{M}'), \\
I_8 &= (\mathbf{M} \cdot \mathbf{M}') \mathbf{M} \cdot (\mathbf{CM}'), & I_9 &= (\mathbf{M} \cdot \mathbf{M}')^2.
\end{aligned} \tag{11.291}$$

Note that the last invariant is not a function of the deformation and will only appear as a constant in the strain-energy function. It will therefore be ignored from the analysis at the expense of a possible redefinition of the strain-energy function. The strain-energy function W is now a function of all first eight invariants so that we write

$$W = W(I_1, I_2, I_3, I_4, I_5, I_6, I_7, I_8). \tag{11.292}$$

For an incompressible material we have $I_3 = 1$, and the explicit expression for the Cauchy stress tensor is

$$\begin{aligned}
\mathbf{T} &= -p\mathbf{I} + 2W_1\mathbf{B} + 2W_2(I_1\mathbf{B} - \mathbf{B}^2) \\
&\quad + 2W_4\mathbf{m} \otimes \mathbf{m} + 2W_6\mathbf{m}' \otimes \mathbf{m}' \\
&\quad + 2W_5(\mathbf{m} \otimes \mathbf{Bm} + \mathbf{Bm} \otimes \mathbf{m}) + 2W_7(\mathbf{m}' \otimes \mathbf{Bm}' + \mathbf{Bm}' \otimes \mathbf{m}') \\
&\quad + W_8(\mathbf{m} \otimes \mathbf{m}' + \mathbf{m}' \otimes \mathbf{m})(\mathbf{M} \cdot \mathbf{M}'),
\end{aligned} \tag{11.293}$$

where $\mathbf{m} = \mathbf{FM}$, $\mathbf{m}' = \mathbf{FM}'$, and $W_i = \partial W / \partial I_i$ for $i = 1, \dots, 8$.

11.11.3 Example: The Fiber-Reinforced Cuboid

We consider the homogeneous deformation of a hyperelastic, incompressible cuboid $\mathcal{B}_0 = [0, L_1] \times [0, L_2] \times [0, L_3]$, subjected to constant normal external loads t_1, t_2, t_3 measured as force per unit area in the deformed configuration. The cuboid is made out of a homogeneous material reinforced by two families of fibers, which are aligned symmetrically in the $\mathbf{E}_1 - \mathbf{E}_2$ plane, as shown in Figure 11.28. The directions of the fiber families are $\mathbf{M} = (\cos \Theta, \sin \Theta, 0)$, $\mathbf{M}' = (\cos \Theta, -\sin \Theta, 0)$.

We further restrict our attention to a simple form for the isotropic and anisotropic responses, the so-called *standard fiber-reinforcing model* [272, 615, 877–879, 1052, 1248]

$$W = W_{\text{iso}} + W_{\text{aniso}} = \frac{\mu}{2}(I_1 - 3) + \frac{\mu\gamma}{2}[(I_4 - 1)^2 + (I_6 - 1)^2]. \tag{11.294}$$

The constitutive equation (11.293) for this strain-energy function is

$$\mathbf{T} = -p\mathbf{I} + \mu\mathbf{F}[\mathbf{1} + 2\gamma(I_4 - 1)\mathbf{M} \otimes \mathbf{M} + 2\gamma(I_6 - 1)\mathbf{M}' \otimes \mathbf{M}']\mathbf{F}^T. \tag{11.295}$$

Due to the particular choice of fiber alignment and strength, the two equal and opposite fibers with angle $\pm\Theta$ in the $\mathbf{E}_1 - \mathbf{E}_2$ plane are mapped into two equal and

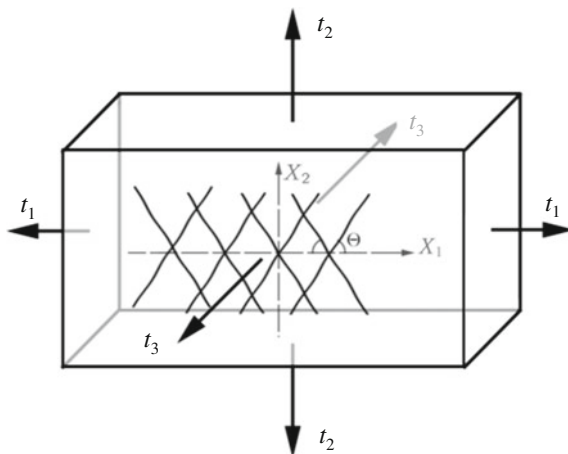


Figure 11.28 A cuboid is subjected to external hydrostatic loading, maintaining constant normal stress on each face of the cuboid. The material is reinforced by two families of fibers, which are in-plane, aligned symmetrically, and make an angle Θ with the $\mathbf{E}_1$ direction.

opposite fibers with angle $\pm\theta$ as shown in Figure 11.29. We also have $I_4 = I_6 = \lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta$, where λ_i is the stretch in the X_i direction, and

$$[\mathbf{M} \otimes \mathbf{M} + \mathbf{M}' \otimes \mathbf{M}'] = 2\text{diag}(\cos^2 \Theta, \sin^2 \Theta, 0). \quad (11.296)$$

Hence, we have

$$\mathbf{T} = -p\mathbf{1} + \mu\mathbf{B} [1 + 4\gamma(\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)\text{diag}(\cos^2 \Theta, \sin^2 \Theta, 0)].$$

For a homogeneous deformation, the Cauchy stress is homogeneous as well and the Cauchy equation is identically satisfied. The particular form of the fiber stiffness and alignment and the boundary conditions

$$\mathbf{T}(X_i = 0) = \mathbf{T}(X_i = L_i) = t_i \mathbf{e}_i, \quad (11.297)$$

imply that $[\mathbf{T}] = \text{diag}(t_1, t_2, t_3)$. From (11.11.3), we see that $\mathbf{F}$, in these coordinates, must also be diagonal, that is, $[\mathbf{F}] = \text{diag}(\lambda_1, \lambda_2, \lambda_3)$. Thus, (11.295) together with the incompressibility condition become

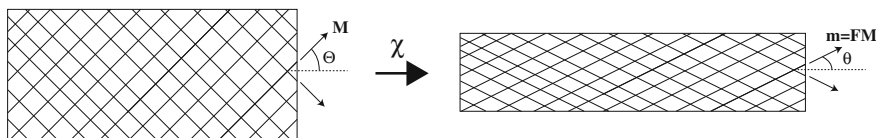


Figure 11.29 Deformation of two equal and opposite fibers.

$$t_1 = -p + \mu (\lambda_1^2 + 4\gamma(\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)\lambda_1^2 \cos^2 \Theta), \quad (11.298)$$

$$t_2 = -p + \mu (\lambda_2^2 + 4\gamma(\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)\lambda_2^2 \sin^2 \Theta), \quad (11.299)$$

$$t_3 = -p + \mu \lambda_3^2, \quad (11.300)$$

$$\lambda_1 \lambda_2 \lambda_3 = 1, \quad (11.301)$$

where the four unknowns λ_i and p can be determined from the loads t_i and the fiber orientation angle Θ . The last two relations (11.300) and (11.301) give $\lambda_3 = \lambda_2^{-1} \lambda_1^{-1}$ and $p = \mu \lambda_3^2 - t_3$, so that, after substitution in the first two equations, the problem can be reduced to finding (λ_1, λ_2) as a function of t_1, t_2, t_3 , that is,

$$A = \frac{\lambda_1^2 - \lambda_2^2}{4\gamma} + (\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)(\lambda_1^2 \cos^2 \Theta - \lambda_2^2 \sin^2 \Theta), \quad (11.302)$$

$$B = \frac{-1}{2\gamma \lambda_1^2 \lambda_2^2} + \frac{\lambda_1^2 + \lambda_2^2}{4\gamma} + (\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)(\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta), \quad (11.303)$$

where

$$A = \frac{t_1 - t_2}{4\gamma\mu}, \quad B = \frac{t_1 + t_2 - 2t_3}{4\gamma\mu}. \quad (11.304)$$

Geometrically, Equations (11.302–11.303) define, for given A and B , two level sets, and the solution lies at their intersection.

In many situations, fibers embedded in a matrix may not support compressive loads as they would buckle under compression [604, 1189]. Therefore, we further restrict the study of our model to the *fiber-tensile region*, defined by

$$\lambda_f = \lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta > 1, \quad \Theta \in [0, \pi/2]. \quad (11.305)$$

Fibers are unstrained on the boundary of the region (11.305), and are in compression when $\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta < 1$.

We first compute the effect of fiber alignment and stiffness by computing an effective Young's modulus. Young's modulus is only defined for isotropic materials, but in a given direction, one can define a modulus as the ratio of the uniaxial tension N by the stretch in the same direction in the limit of small deformations, that is, the *effective Young's modulus* in a direction is defined as the gradient of N in that direction evaluated at the stress-free state. For example, for an uniaxial tension in the $\mathbf{e}_1$ direction $t_1 = N, t_2 = t_3 = 0$, we define

$$E_{\text{eff}} \equiv \left. \frac{\partial N}{\partial \lambda_1} \right|_{\lambda_1=1}, \quad (11.306)$$

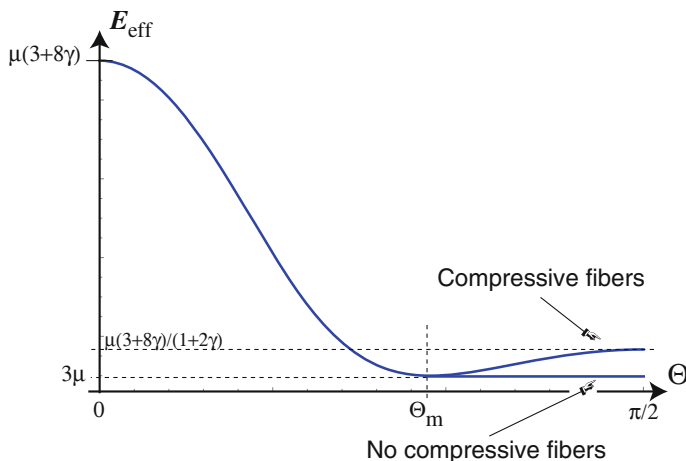


Figure 11.30 Effective Young's modulus for a fiber-reinforced sheet as a function of the fiber angle.

and, after linearizing (11.302–11.303) around the unstressed configuration, we find

$$E_{\text{eff}} = \mu \frac{4[3 + 5\gamma + 3\gamma \cos(4\Theta)]}{4 + 3\gamma - 4\gamma \cos(2\Theta) + \gamma \cos(4\Theta)}. \quad (11.307)$$

As shown in Figure 11.30, the effective Young's modulus has a maximum for $\Theta = 0$ when the fibers are aligned with the axis:

$$E_{\text{eff}}(\Theta = 0) = (3 + 8\gamma)\mu. \quad (11.308)$$

The minimum effective Young's modulus $E_{\text{eff}}(\Theta = \Theta_m) = 3\mu$ is attained for

$$\Theta_m = \tan^{-1} \sqrt{2} = \Phi_m \approx 54.74^\circ, \quad (11.309)$$

where Φ_m is the *magic angle* that appears in several interesting applications. It will be discussed in detail in Section 11.11.5.

For $\Theta_m < \Theta < \pi/2$, $I_4 < 1$ and the fibers are in compression. If we allow for compressive fibers, E_{eff} increases to the locally maximal value of

$$E_{\text{eff}}(\Theta = \pi/2) = \mu \frac{3 + 8\gamma}{1 + 2\gamma}. \quad (11.310)$$

In the absence of compressive fibers, the material behaves isotropically and the effective modulus remains at 3μ .

Remarkably, we see that the apparent stiffness of a material in a given direction can be tuned to any value between the matrix stiffness and the fiber stiffness by

choosing the appropriate fiber angle Θ and fiber density. The modulus ratio between the two extremal values is $1 + 3\gamma/8$ and a typical ratio of γ is between 10 and 1000. This simple effect is at work in fungi, plants, and animal tissues where, typically, the isotropic elastic matrix remains mostly unchanged while fibers are constantly turned over to maintain the appropriate level of homeostatic stress, the tissue stiffness or for healing [303, 540, 635, 871].

As an example, in the aorta an elastin matrix reinforced with two equal and opposite fibers helically wrapping around a cylindrical geometry, the effective Young's modulus is around 90 kPa at the ascending aorta and 10 kPa at the femoral bifurcation, which correlates with the elastin content [137].

In the nonlinear regime, we observe an interesting behavior. As expected, the stretch along the tensile stress always increases as shown in Figure 11.31. Similarly, the stretch perpendicular to the direction of the applied load in the fiber plane always decreases as we would expect for an isotropic material. However, in the direction normal to the fibers, the material thickness determined by λ_3 can increase, decrease, or first decrease then increase. This non-monotonic behavior depends on the balance between the nonlinear material response and the anisotropy.

We identify in the parameter space, $(1/\gamma, \Theta)$, these different behaviors by solving Equations (11.302–11.303) under the condition $\lambda_3 = 1$, that is, $\lambda_1 = \lambda_2$. This extra condition leads to two curves in the plane $(1/\gamma, \Theta)$ given by [864]

$$\frac{1}{\gamma} = \sin^2(2\Theta), \quad \frac{1}{\gamma} = \sin^2(2\Theta) - 4 \sin^4 \Theta. \quad (11.311)$$

These curves are shown in Figure 11.32 together with the corresponding points of Figure 11.31.

11.11.4 Example: The Fiber-Reinforced Cylinder

We consider a tube made out of an incompressible material with initial inner radius $A = 1$, outer radius $B > A$, and height H deformed into a tube with radii a and b and height h . We assume that the tube is allowed to inflate, extend, and twist while remaining cylindrical at all time. This problem is the classic inflation–extension–torsion problem for the cylinder. It is a particular case of Family 3 of semi-inverse problems (11.220). In the usual cylindrical coordinates $\{r, \theta, z\}$ and $\{R, \Theta, Z\}$ the deformation is given by

$$r = \sqrt{a^2 + \frac{R^2 - A^2}{\zeta}}, \quad (11.312)$$

$$\theta = \Theta + \tau \zeta Z, \quad (11.313)$$

$$z = \zeta Z, \quad (11.314)$$

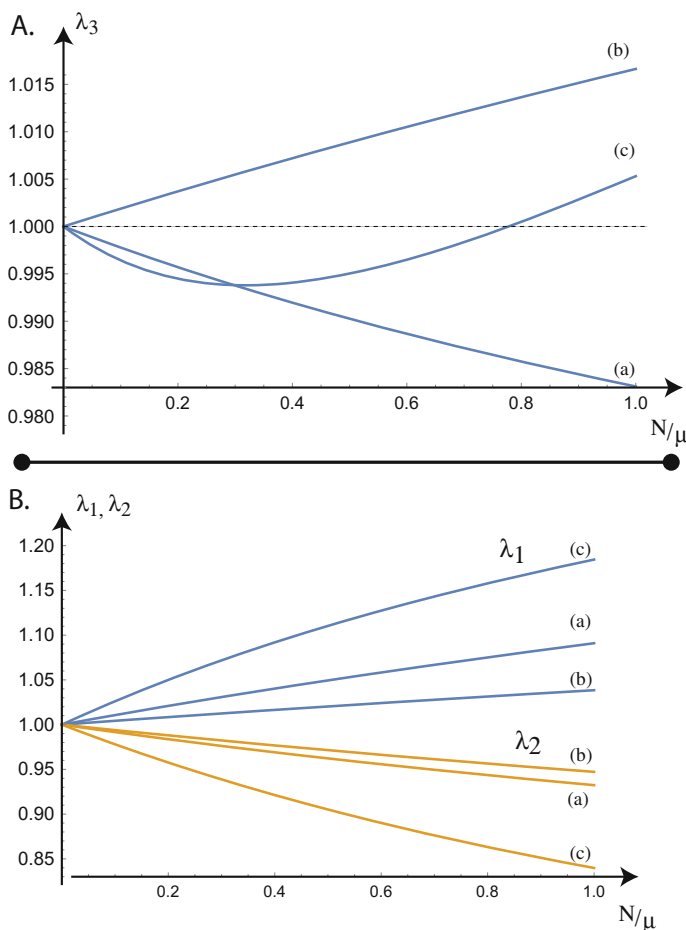


Figure 11.31 The three principal stretches as a function of the tension. For some values of γ and Θ , the thickness of the cuboid always decreases, always increases, or first decreases, then increases. Parameter values: (a): $\Theta = \pi/8$, $\gamma = 4/3$; (b): $\Theta = \pi/8$, $\gamma = 4$; (c): $\Theta = \pi/4$, $\gamma = 4$.

where the axial stretch ζ and the twist τ are constant.

The position vectors are, respectively,

$$\mathbf{X} = R\mathbf{E}_R + Z\mathbf{E}_Z, \quad (11.315)$$

$$\mathbf{x} = \lambda R\mathbf{e}_r + \zeta Z\mathbf{e}_z. \quad (11.316)$$

Using identity (11.60), the deformation gradient, $\mathbf{F} = \text{Grad } \mathbf{x}$, in cylindrical coordinates is given by

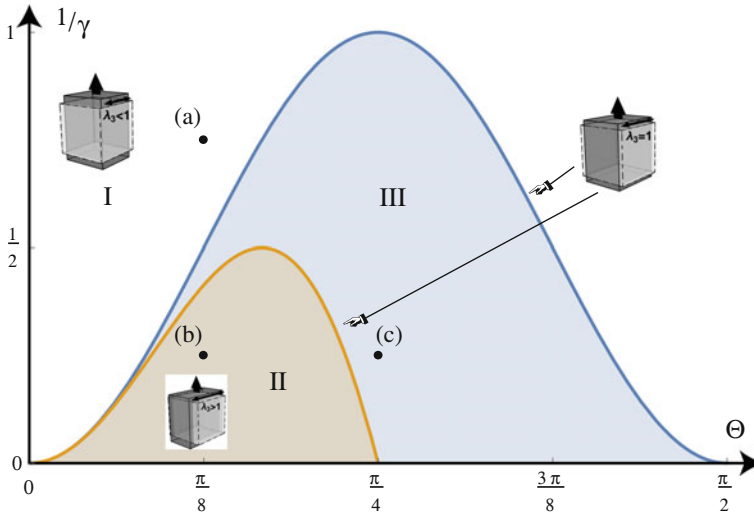


Figure 11.32 Parameter space for inversion: Depending on the relative fiber stiffness γ and the fiber direction Θ , in tension, the thickness of a fiber either decreases (Zone I), increases (Zone II), or first decreases, then increases (Zone III). Insert shown for different values of the tension. The stretch profiles as a function of the tension for specific points (a, b, c) are given in Figure 11.31.

$$[\mathbf{F}] = \begin{bmatrix} \frac{1}{\lambda\zeta} & 0 & 0 \\ 0 & \lambda & \zeta\tau r \\ 0 & 0 & \zeta \end{bmatrix}, \quad (11.317)$$

where we have used the incompressibility condition $\det \mathbf{F} = 1$ and

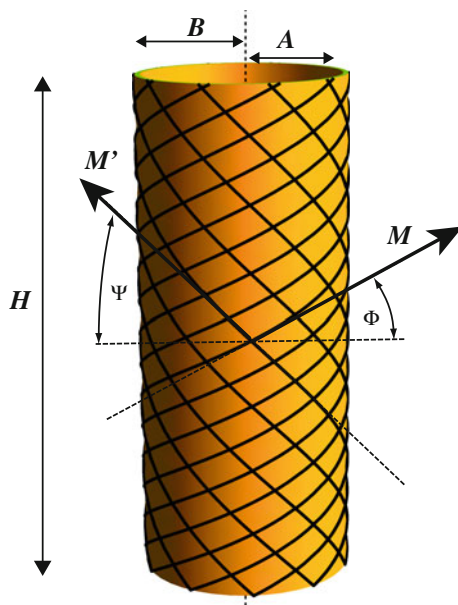
$$\lambda = \frac{r}{R} = \frac{1}{R} \sqrt{a^2 + \frac{R^2 - A^2}{\zeta}}. \quad (11.318)$$

Therefore, a single parameter fully describes the radial profile of the deformation. Setting $\lambda_a = a/A$, it follows that

$$\lambda_b = \frac{b}{B} = \frac{1}{\zeta} \sqrt{1 + \frac{A^2}{B^2} (\zeta\lambda_a^2 - 1)}. \quad (11.319)$$

The anisotropic response of the cylinder is modeled by two families of embedded fibers $\mathbf{M}$ and $\mathbf{M}'$. For simplicity, we will refer to a family of distributed fibers simply as a *fiber*. Both fibers wind helically around the axis and may induce a rotation of the cylinder under extension depending on their strengths and angles. The components of the direction vectors with respect to the basis $(\mathbf{E}_R, \mathbf{E}_\Theta, \mathbf{E}_Z)$ are

Figure 11.33 Geometry of the fibers. The angle Φ denote the direction of the first fiber with respect to the cross section (counted counter-clockwise) and the angle Ψ is the angle of the second fiber (counted clockwise).



$$\begin{bmatrix} M_R \\ M_\Theta \\ M_Z \end{bmatrix} = \begin{bmatrix} 0 \\ \cos \Phi \\ \sin \Phi \end{bmatrix}, \quad \begin{bmatrix} M'_R \\ M'_\Theta \\ M'_Z \end{bmatrix} = \begin{bmatrix} 0 \\ -\cos \Psi \\ \sin \Psi \end{bmatrix}. \quad (11.320)$$

Here we have assumed that the fibers remain locally tangent to the cylinder. Following Figure 11.33, the angles between the fibers and the circumferential direction are denoted by Φ and Ψ . Note that we have chosen the angle Ψ so that when the angles are equal $\Phi = \Psi$, the two fibers make the same angle with the axis, and are said to be *opposite*. Opposite fibers are a common occurrence and they are found, for instance, in the popular toys shown in Figure 11.34.

Under a deformation $\mathbf{F}$, the orientation of the fiber characterized by a vector $\mathbf{M}$ with angle Φ in the reference configuration is mapped, in the current configuration, to the vector

$$\mathbf{m} = \begin{bmatrix} m_r \\ m_\theta \\ m_z \end{bmatrix} = \mathbf{F}\mathbf{M} = \begin{bmatrix} 0 \\ \lambda \cos \Phi + r\zeta\tau \sin \Phi \\ \zeta \sin \Phi \end{bmatrix}. \quad (11.321)$$

Therefore, the new fiber angle is

$$\phi = \arctan \left(\frac{\zeta \sin \Phi}{\lambda \cos \Phi + r\zeta\tau \sin \Phi} \right). \quad (11.322)$$

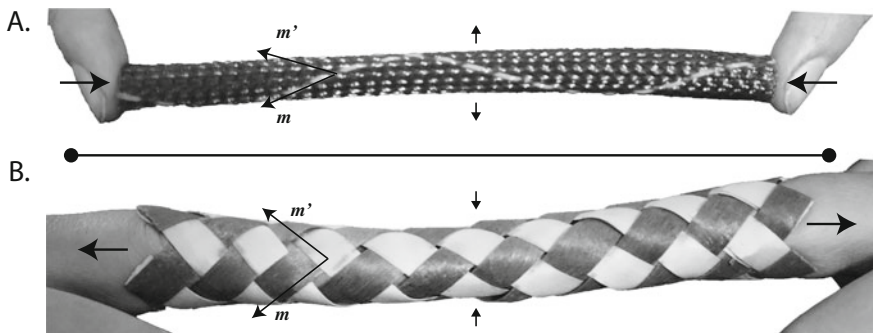


Figure 11.34 Two simple toys demonstrate the principle of opposite fibers and the change in fiber orientation in compression and tension. Top: The boing-boing rocket stores elastic energy under compression by changing the fiber angle. The rocket can be released by quickly removing one finger. Bottom: The finger trap. In extension, the cylinder radius decreases and traps the fingers.

For these deformations, the only nonvanishing component of the Cauchy equation $\text{div } \mathbf{T} = \mathbf{0}$ is

$$\frac{dT_{rr}}{dr} + \frac{1}{r}(T_{rr} - T_{\theta\theta}) = 0. \quad (11.323)$$

This equation can be integrated once over r to obtain

$$T_{rr}(r) = \int_r^b \frac{T_{rr} - T_{\theta\theta}}{r} dr, \quad a \leq r \leq b. \quad (11.324)$$

We consider a simple thought experiment in which the tube is capped at both ends and subject to an axial extension ζ due to an internal pressure P and to a total axial load N on the top cap. The tube is also subject to an external moment M leading to a twist represented by τ .

First, we express the boundary condition in the radial direction. Taking the radial component of the Cauchy stress tensor $\mathbf{T}$ to vanish at the outer boundary, we have $T_{rr}(r = b) = 0$. On the inner wall, the boundary condition associated with the pressure is $T_{rr}(r = a) = -P$. Therefore, the two conditions on the pressure can be used to simplify (11.324) to

$$P = \int_a^b \frac{T_{\theta\theta} - T_{rr}}{r} dr. \quad (11.325)$$

Second, the condition on the two end caps is a combination of an external axial stress superimposed on the pointwise stress due to the internal pressure acting on the end cap:

$$T_{zz}(z = 0) = N_z, \quad T_{zz}(z = h) = N_z. \quad (11.326)$$

Following the discussion of Section 11.8.3, we replace these pointwise conditions by an integral condition relating the total application of forces and moments on the caps of the cylinder:

$$2\pi \int_a^b T_{zz} r \, dr = N = F + \chi P \pi a^2, \quad (11.327)$$

where the total axial load N is decomposed into an external applied load F and the load created by the internal pressure acting over the cap. Following the argument in Section 11.8.3, this last condition can be replaced by

$$\pi \int_a^b (2T_{zz} - T_{rr} - T_{\theta\theta}) r \, dr = F + (\chi - 1) P \pi a^2, \quad (11.328)$$

and the last term vanishes for a capped cylinder, the case considered here.

Third, when $\tau \neq 0$, we have to take into account the possibility of applying a moment on the ends. This loading can be expressed also as an integral condition relating the total moment acting on the tube axis to the axial stress. That is,

$$\int_a^b T_{\theta z} r^2 \, dr = M. \quad (11.329)$$

Therefore, the three boundary conditions are

$$C_1 : \int_a^b \frac{T_{\theta\theta} - T_{rr}}{r} \, dr = P, \quad (11.330)$$

$$C_2 : \pi \int_a^b (2T_{zz} - T_{rr} - T_{\theta\theta}) r \, dr = F, \quad (11.331)$$

$$C_3 : 2\pi \int_a^b T_{\theta z} r^2 \, dr = M. \quad (11.332)$$

The semi-inverse problem consists in finding the values of (λ_a, ζ, τ) corresponding to the three external loads (F, M, P) through the analysis of equilibria.

The standard fiber-reinforcing model with fiber extension. We further restrict our attention to the *standard fiber-reinforcing model*, $W = W_{\text{iso}} + W_{\text{fib}}$, with

$$W_{\text{iso}} = \frac{\mu_1}{2} (I_1 - 3), \quad (11.333)$$

$$W_{\text{fib}}(I_4, I_6) = \frac{\mu_4}{4} (I_4 - 1)^2 + \frac{\mu_6}{4} (I_6 - 1)^2, \quad (11.334)$$

where the material parameters $\mu_i > 0$ have the dimension of a pressure.

From the strain-energy function, we compute the Cauchy stress tensor

$$\mathbf{T} = \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{1}, \quad (11.335)$$

where p is the Lagrangian multiplier associated with incompressibility. In our case, these equations simplify to

$$\mathbf{T} = 2W_1 \mathbf{B} + 2W_4 \mathbf{m} \otimes \mathbf{m} + 2W_6 \mathbf{m}' \otimes \mathbf{m}' - p \mathbf{1}, \quad (11.336)$$

with $W_i = \partial_{I_i} W$. The nonvanishing components of the Cauchy stress tensor are given by

$$\begin{aligned} T_{rr} &= -p + 2W_1 \zeta^{-2} \lambda^{-2}, \\ T_{\theta\theta} &= -p + 2(\lambda^2 + r^2 \zeta^2 \tau^2) W_1 \\ &\quad + 2(\lambda \cos \Phi + r \zeta \tau \sin \Phi)^2 W_4 - 2(\lambda \cos \Psi - r \zeta \tau \sin \Psi)^2 W_6, \\ T_{zz} &= -p + 2\zeta^2 W_1 + 2\zeta^2 \sin^2 \Phi W_4 + 2\zeta^2 \sin^2 \Psi W_6, \\ T_{z\theta} = T_{\theta z} &= 2\zeta [r \zeta \tau W_1 + \sin \Phi (\lambda \cos \Phi + r \zeta \tau \sin \Phi) W_4 \\ &\quad - \sin \Psi (\lambda \cos \Psi - r \zeta \tau \sin \Psi) W_6]. \end{aligned}$$

Since the constitutive relationships are written in terms of $\{\lambda, \zeta, \tau\}$, we rewrite the three boundary conditions in terms of integrals over λ using the identity

$$\frac{dr}{d\lambda} = A \frac{(1 - \zeta \lambda_a^2)^{1/2}}{(1 - \zeta \lambda^2)^{3/2}}, \quad (11.337)$$

which yields the equivalent boundary conditions

$$C_1 : \int_{\lambda_a}^{\lambda_b} \frac{T_{rr} - T_{\theta\theta}}{\lambda(\lambda^2 \zeta - 1)} d\lambda = P, \quad (11.338)$$

$$C_2 : \pi A^2 \int_{\lambda_a}^{\lambda_b} \frac{1 - \zeta \lambda_a^2}{(1 - \zeta \lambda^2)^2} \lambda (2T_{zz} - T_{rr} - T_{\theta\theta}) d\lambda = F, \quad (11.339)$$

$$C_3 : 2\pi A^3 \int_{\lambda_a}^{\lambda_b} \frac{(1 - \zeta \lambda_a^2)^{3/2}}{(1 - \zeta \lambda^2)^{5/2}} \lambda^2 T_{z\theta} d\lambda = M. \quad (11.340)$$

While explicit expression for the three integrals for (M, N, P) for the particular choice (11.333–11.334) can be obtained, they are far too cumbersome to be useful.

Membrane limit. We can take advantage of the assumption that the tube is thin and expand the three integrals (M, N, P) in the thickness of the tube. Without loss of generality, we measure all lengths with respect to the inner reference radius, that is, we set $A = 1$. Then, we introduce ϵ by $B = 1 + \epsilon$ and expand

$$M = M^{(1)}\epsilon + M^{(2)}\epsilon^2 + \dots, \quad (11.341)$$

$$F = F^{(1)}\epsilon + F^{(2)}\epsilon^2 + \dots, \quad (11.342)$$

$$P = P^{(1)}\epsilon + P^{(2)}\epsilon^2 + \dots \quad (11.343)$$

Explicitly, to first order these expressions read

$$M^{(1)} = 2\pi\lambda [\zeta\lambda\mu_1\tau + \mu_4 J_4 \sin(\Phi)(\zeta\lambda\tau \sin(\Phi) + \lambda \cos(\Phi)) + \mu_6 J_6 \sin(\Psi)(\zeta\lambda\tau \sin(\Psi) - \lambda \cos(\Psi))], \quad (11.344)$$

$$F^{(1)} = -\frac{\pi}{\zeta} \left[\frac{\mu_1}{\zeta^2\lambda^2} (1 + \zeta^4\lambda^2 (\lambda^2\tau^2 - 2) + \zeta^2\lambda^4) + \mu_4 J_4 (\zeta \sin(\Phi) (\zeta (\lambda^2\tau^2 - 2) \sin(\Phi) + 2\lambda^2\tau \cos(\Phi)) + \lambda^2 \cos^2(\Phi)) + \mu_6 J_6 (\zeta^2 (\lambda^2\tau^2 - 2) \sin^2(\Psi) - 2\zeta\lambda^2\tau \sin(\Psi) \cos(\Psi) + \lambda^2 \cos^2(\Psi)) \right], \quad (11.345)$$

$$P^{(1)} = \frac{1}{\zeta} \left[\frac{\mu_1}{\zeta^2\lambda^4} (\zeta^4\lambda^4\tau^2 + \zeta^2\lambda^4 - 1) + \mu_4 J_4 (\zeta\tau \sin(\Phi) + \cos(\Phi))^2 + \mu_6 J_6 (\cos(\Psi) - \zeta\tau \sin(\Psi))^2 \right], \quad (11.346)$$

where

$$\begin{aligned} J_4 &= (I_4 - 1) \\ &= \zeta \sin(\Phi) (\zeta (\lambda^2\tau^2 + 1) \sin(\Phi) + 2\lambda^2\tau \cos(\Phi)) + \lambda^2 \cos^2(\Phi) - 1, \\ J_6 &= (I_6 - 1) \\ &= \zeta^2 (\lambda^2\tau^2 + 1) \sin^2(\Psi) - 2\zeta\lambda^2\tau \sin(\Psi) \cos(\Psi) + \lambda^2 \cos^2(\Psi) - 1. \end{aligned}$$

11.11.4.1 A Cylinder with Equal Fibers but Different Orientations

As a first example of the possible behaviors in this system, we consider the problem of rotation under pressure in a tube with two fibers with equal strength, $\mu_6 = \mu_4$, but of varying angle. If we fix one fiber, we can vary the angle of the other fiber and ask whether a change in pressure will lead to a reversal in rotation from a left-handed rotation to a right-handed rotation. The condition for inversion is obtained by considering the change of twist τ with respect to pressure $\tau = \tau(P)$ and identifying the points at which this relationship is stationary. The condition $\tau'(P) = 0$ leads to

$$\mu_4 \sin(\Phi - \Psi) [6\mu_1 (2 \cos(\Phi + \Psi) + \cos(3\Phi + \Psi) + \cos(\Phi + 3\Psi)) + 8\mu_4 \sin^2(\Phi + \Psi)(\cos(\Phi) \cos(\Psi) - 2 \sin(\Phi) \sin(\Psi))] = 0. \quad (11.347)$$

We show in Figure 11.35 the inversion curves in the parameter space (Φ, Ψ) , for $\mu_1 \ll \mu_4$ and $\mu_4 \ll \mu_1$. The two limits are easily obtained analytically from (11.347) by taking $\mu_1 = 0$ or $\mu_4 = 0$. We see the role of the magic angle introduced in Section 11.11.3 and discussed below, as being the distinguished value at which an

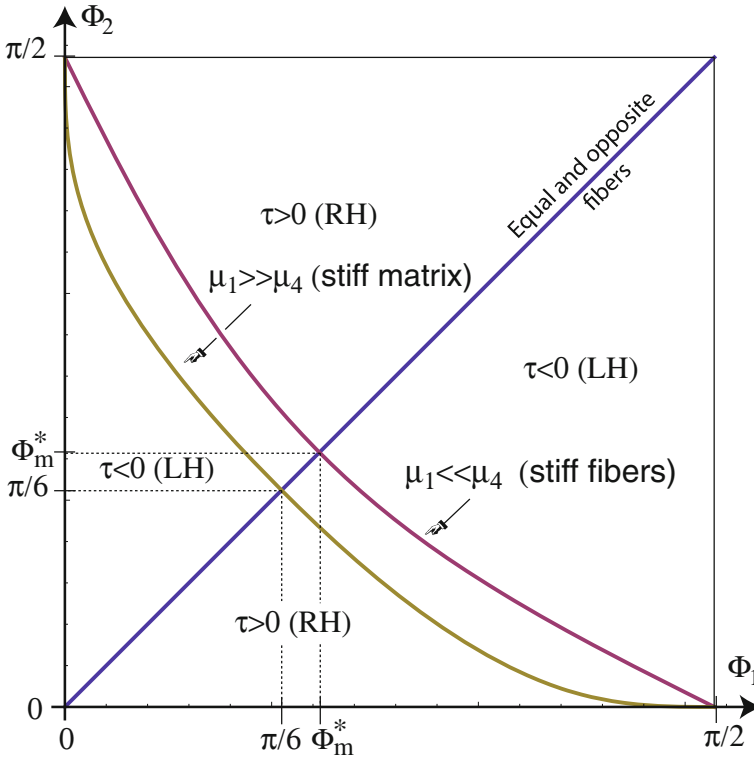


Figure 11.35 Twist induced by inflation for a cylindrical membrane in small deformations as a function of the orientation of the two fibers.

inversion of rotation appears for systems with stiff fibers. In this case, if we start with one fiber oriented at the magic angle and vary the other one there will just be a single inversion of rotation (when the two are equal). For other values, there will be two inversions, one when the two angles are equal and the second at different values of the angle, showing the interesting property of no net rotation (in small deformations) despite the tube being clearly anisotropic.

11.11.5 Application: The Hydrostatic Skeleton

A simple cylindrical structure, known as a *cylindrical hydrostatic skeleton* with reinforced fibers is found in many ectothermic and soft-bodied organisms such as nemertean and turbellarian worms. Of particular note is the work of Harris and Crofton [543] and Clark and Cowey [214]. Building on the concept of a hydrostatic skeleton [690, 691, 1104], they model the worm body as a cylindrical membrane

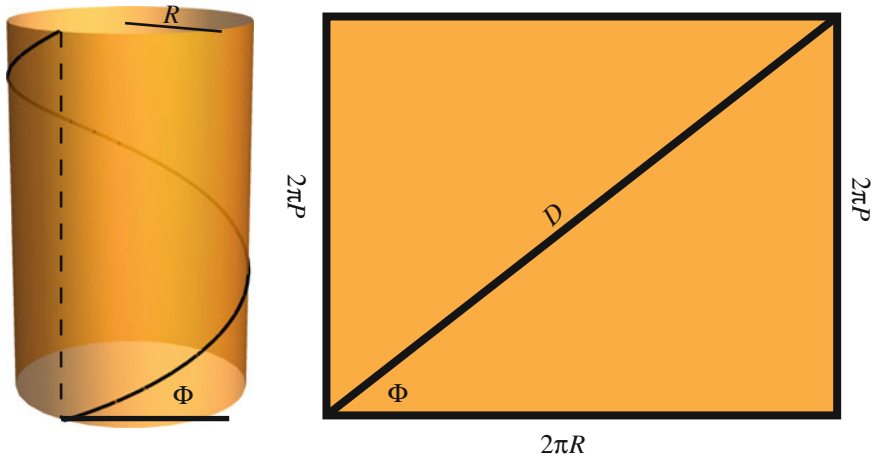


Figure 11.36 A geometric model of hydrostatic skeleton obtained by assuming that the skeleton can have a cylindrical shape, with inextensible fibers winding helically around the cylinder.

reinforced with a lattice of crossed, inextensible, fibers winding around the membrane with helical geometry, and they characterize the possible extension and retraction of the lattice network as being analogous to that of lazy tongs or a trellis. Their mathematical model, which is purely geometric, proved to be remarkably successful in explaining their detailed experimental studies of the locomotion and flattening of worms.

Consider a cylinder of height $2\pi P$ and radius R with a helical inextensible fiber of fixed length D as shown in Figure 11.36. The volume enclosed is simply

$$V = 2\pi^2 R^2 P = \frac{D^3}{4\pi} \sin^2 \Phi \cos \Phi. \quad (11.348)$$

The maximal volume is attained when $\partial_\Phi V = 0$, that is, for

$$\Phi_m^* = \frac{\pi}{2} - \tan^{-1} \sqrt{2} \approx 35.26^\circ, \quad (11.349)$$

as shown in Figure 11.37. For any given volume $0 < V_1 < V_{\max}$, there exist two angles Φ_1 and Φ_2 in $(0, \pi/2)$ that give rise to a cylinder of volume V_1 . Therefore, in principle, a worm could change its extension from $H_1 = D \cos \Phi_1$ to $H_2 = D \cos \Phi_2 > H_1$ at constant volume. This change in extension can be obtained by contracting fiber muscles, a transformation that can take place by flattening the cross section to conserve the volume. In the initial and final configurations, the fibers have length D and are at rest. Therefore, in this range of parameters, the hydrostatic skeleton can adopt two shapes of different lengths and maintain these shapes without muscular contraction.

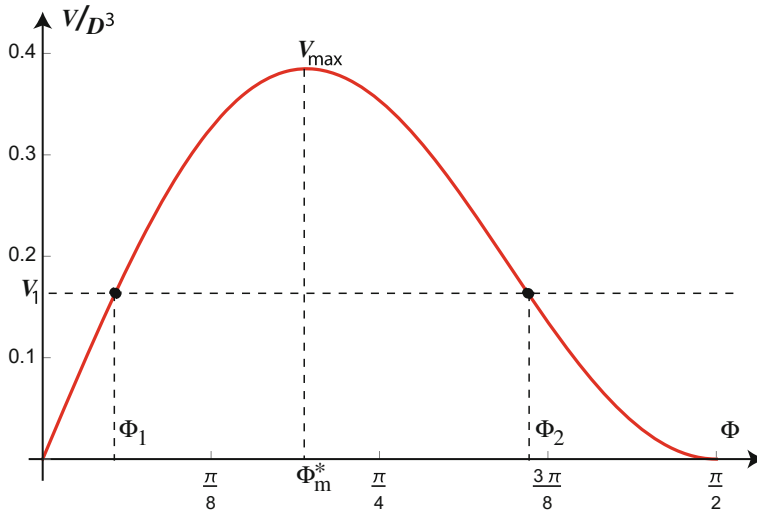


Figure 11.37 The magic angle gives the maximal enclosed volume of a cylinder reinforced by inextensible fibers of fixed length D . For $V < V_{\max}$ there exist two angles at fixed volume.

We refer to the reciprocal of this angle, $\Phi_m = \pi/2 - \Phi_m^*$, as the *magic angle* since it seems to appear, as if by magic, in many different settings in mechanics and in solid-state nuclear magnetic resonance [484, 569, 600, 1117]. For instance, this angle is believed to be key in understanding the elongation of notochords [6, 716, 717]. Further, an inanimate analog of the model of Clark and Cowey can be found in the McKibben actuator which consists of a flexible tube surrounded by a sheath of braided families of inextensible fibers helically wound in opposing directions. This design is the basis for so-called *pneumatic artificial muscles* used in robotics, prosthetics, and orthotics [256, 796]. These actuators are typically pressure controlled and their precise functionality is determined by the weave of the fibers. As with the Clark and Cowey model, the fiber winding angle of 35.26° plays a special role in the actuator design.

We will now show that the magic angle also appears naturally as a special limiting case of a nonlinear elastic model. We start our analysis with the simple case of a cylinder with two families of fibers of equal strength ($\mu_6 = \mu_4$) and opposite orientation ($\Psi = \Phi$). This corresponds to the classic case of the McKibben actuators, arteries, and other hydrostats. Under extension or inflation, the couples created by the two fibers cancel out and there is no net couple associated with the deformation and thus no rotation or twist ($\tau = 0$).

We are particularly interested in identifying inversion due to internal change of pressure. We look at the condition under which the radial strain does not vary under a change a pressure. A local analysis for small strains [484] leads to the condition

$$3\mu_1 + \mu_4 \sin^2(\Phi)(1 - 3\cos(2\Phi)) = 0. \quad (11.350)$$

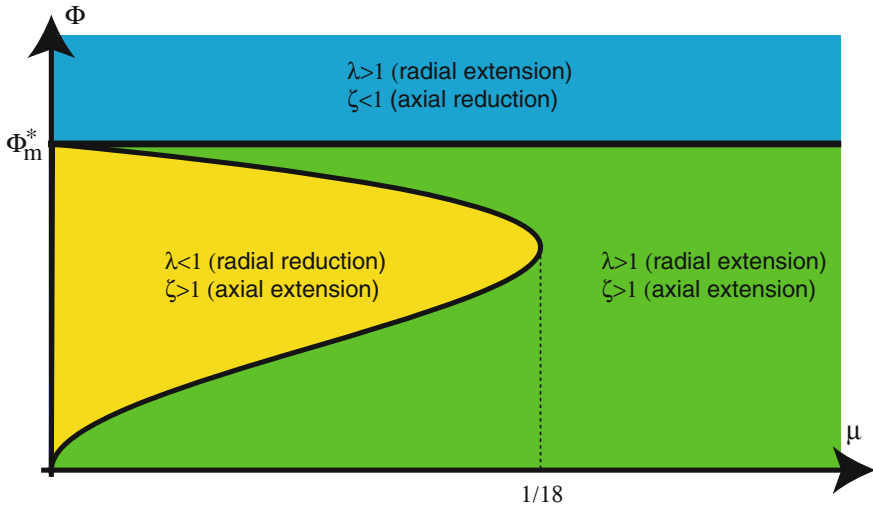


Figure 11.38 Parameter space for the radial and axial expansion of a thin tube under pressure. Depending on the relative stiffness of the fiber versus the matrix and the fiber angle, a capped tube under pressure can extend radially and axially (bottom left), extend radially but shrink axially (top), or extend axially but shrink radially (bottom right).

The condition for an inversion in the axial strain is $\Phi = \Phi_m^*$

By denoting $\mu = \mu_1/\mu_4$ as the ratio of matrix modulus to the fiber modulus, we obtain a complete description of the possible inversions under a change in pressure in the parameter space (μ, Φ) as shown in Figure 11.38.

Depending on the design criterion, one can consider different tube constructions by varying the fiber angle. For fiber angles larger than Φ_m^* the tube contracts under increased pressure and this behavior provides a model for pneumatic muscles. For tubes with fiber angle close to Φ_m^* , the deformation of the tube in the axial direction is minimal. For fiber angles less than Φ_m^* , the tube extends maximally. Note that this analysis is only valid for small enough P . For larger pressure, we expect the tube to increase eventually in length and radius.

11.11.6 Fiber Dispersion

In addition to having strong anisotropy dictated by several fiber directions, many tissues also exhibit a fair amount of dispersion around these principal directions. For instance, collagen fibers in the arterial wall show a significant fiber dispersion around two preferred fiber directions as demonstrated experimentally [164] by polarized light microscopy. It is therefore necessary to consider continuous distributions of fiber direction as first proposed by Lanir [767] who computed the total stress generated by fibers as an integral over a range of fiber angles. This model was further simplified [388, 426] by the introduction of the notion of generalized structure tensors. Models

based on this simplified approach were applied to many soft tissues, including the human aortic valve [388], the arterial wall [604], the cornea [518, 1010], the articulate cartilage [358], and the bat wing membrane [1296].

First, we consider the case of a single principal direction around which mechanically equivalent fibers are dispersed. We further assume that the strain-energy function can be split into an isotropic component and an anisotropic contribution due to the fibers [864] so that

$$W = W_{\text{iso}} + W_{\text{fib}}, \quad (11.351)$$

with

$$W_{\text{fib}} = \oint_{\mathbb{U}^2} \rho(\mathbf{M}) w_{\text{fib}}(I_{\mathbf{f}}(\mathbf{M})) d\omega, \quad (11.352)$$

where $\mathbb{U}^2 = \{\mathbf{M} \in \mathbb{R}^3, \text{ s.t. } |\mathbf{M}| = 1\}$ is the unit sphere, $d\omega$ is the surface element area in the reference direction, $I_{\mathbf{M}} = \mathbf{M} \otimes \mathbf{M} : \mathbf{C}$ is the squared stretch in the direction $\mathbf{M}$, and $\rho(\mathbf{M})$ is an *orientation density function* defined as a probability distribution with the usual normalization condition

$$\oint_{\mathbb{U}^2} \rho d\omega = 1. \quad (11.353)$$

Note, however, that other authors have used different conventions [426, 1011]. Without loss of generality, it is assumed that $\rho(\mathbf{M}) = \rho(-\mathbf{M})$ holds, since $\mathbf{M}$ and $-\mathbf{M}$ define the same fiber.

In the case of m families of distributed fibers, the fiber contribution to the strain-energy function is

$$W_{\text{fib}} = \sum_{i=1}^m \oint_{\mathbb{U}^2} \rho^{(i)}(\mathbf{M}) w_{\text{fib}}^{(i)}(I_{\mathbf{f}}(\mathbf{M})) d\omega, \quad (11.354)$$

where the i th fiber family is characterized by a strain-energy function $w_{\text{fib}}^{(i)}(\mathbf{M})$ and an orientation density function $\rho^{(i)} = \rho^{(i)}(\mathbf{M})$. The Cauchy stress is then given by

$$\mathbf{T} = -p\mathbf{1} + \mathbf{T}_{\text{iso}} + \mathbf{T}_{\text{fib}} = -p\mathbf{1} + 2\mathbf{F} \frac{\partial W_{\text{iso}}}{\partial \mathbf{C}} \mathbf{F}^T + 2\mathbf{F} \frac{\partial W_{\text{fib}}}{\partial \mathbf{C}} \mathbf{F}^T. \quad (11.355)$$

For the strain-energy function (11.354), we obtain

$$\mathbf{T}_{\text{fib}} = 2\mathbf{F} \left(\sum_{i=1}^m \oint_{\mathbb{U}^2} \rho^{(i)}(\mathbf{M}) \frac{\partial w_{\text{fib}}^{(i)}(I_{\mathbf{f}})}{\partial I_{\mathbf{f}}} \mathbf{M} \otimes \mathbf{M} d\omega \right) \mathbf{F}^T. \quad (11.356)$$

This *angular integration method* [228, 1011, 1170] is a rather cumbersome approach from a computational point of view as a full angular integration has to be performed at each material point to obtain the Cauchy stress tensor.

The main idea to simplify this computation is to perform an angular averaging. We define the averaging operator

$$\langle \bullet \rangle_\rho = \oint_{\mathbb{U}^2} \rho(\mathbf{M}) \bullet \, d\omega, \quad (11.357)$$

where $\bullet$ denotes any tensorial quantity. Its normalized counterpart is

$$[\bullet]_\rho = \frac{\langle \bullet \rangle_\rho}{\langle 1 \rangle_\rho} = \frac{\oint_{\mathbb{U}^2} \rho(\mathbf{M}) \bullet \, d\omega}{\oint_{\mathbb{U}^2} \rho(\mathbf{M}) \, d\omega}. \quad (11.358)$$

Next, we compute the Taylor expansion of $w_{\text{fib}}(I_f)$ about $I_f = [I_f]_\rho$

$$w_{\text{fib}}(I_f) = w_{\text{fib}}([I_f]_\rho) + w'_{\text{fib}}([I_f]_\rho)(I_f - [I_f]_\rho) + \mathcal{O}((I_f - [I_f]_\rho)^2). \quad (11.359)$$

By omitting higher order terms and by applying $[\bullet]_\rho$ to both sides we obtain

$$[w_{\text{fib}}(I_f)]_\rho \approx w_{\text{fib}}([I_f]_\rho)[1]_\rho + w'_{\text{fib}}([I_f]_\rho)[(I_f - [I_f]_\rho)]_\rho. \quad (11.360)$$

Using $[1]_\rho = 1$ and $[I_f - [I_f]_\rho]_\rho = 0$, we obtain

$$\langle w_{\text{fib}}(I_f) \rangle_\rho \approx \langle 1 \rangle_\rho w_{\text{fib}}\left(\frac{\langle I_f \rangle_\rho}{\langle 1 \rangle_\rho}\right). \quad (11.361)$$

This approximation forms the basis of the generalized structure tensor approach. The *generalized structure tensor* is defined as

$$\mathbf{H} = \langle \mathbf{M} \otimes \mathbf{M} \rangle_\rho. \quad (11.362)$$

The right-hand side of (11.361) can then be written as

$$\langle 1 \rangle_\rho w_{\text{fib}}\left(\frac{\langle I_f \rangle_\rho}{\langle 1 \rangle_\rho}\right) = \text{tr}(\mathbf{H}) w_{\text{fib}}\left(\frac{\mathbf{H} : \mathbf{C}}{\text{tr}(\mathbf{H})}\right),$$

whereas the left-hand side of (11.361) equals $\oint_{\mathbb{U}^2} \rho w_{\text{fib}}(I_f) \, d\omega$. Therefore, (11.361) approximates the total angularly integrated fiber strain-energy function by a strain-energy function depending directly on $\mathbf{H}$.

In a material reinforced by fiber families with strain-energy functions $w_{\text{fib}}^{(i)}$ and orientation density functions $\rho^{(i)}$, we define for each fiber family, $\mathbf{H}^{(i)} = \langle \mathbf{M} \otimes \mathbf{M} \rangle_{\rho^{(i)}}$. These generalized structure tensors are objective and symmetric tensors. They do not depend on the deformation and serve as an alternative representation of structural data. The total contribution of the fibers to the strain-energy function is then

$$W_{\text{fib}} = \sum_i \text{tr}(\mathbf{H}^{(i)}) w_{\text{fib}}^{(i)} \left(\frac{\mathbf{H}^{(i)} : \mathbf{C}}{\text{tr}(\mathbf{H}^{(i)})} \right), \quad (11.363)$$

and the Cauchy stress is

$$\mathbf{T}_f = 2\mathbf{F} \left(\sum_i \mathbf{H}^{(i)} w_{\text{fib}}^{(i)'} \left(\frac{\mathbf{H}^{(i)} : \mathbf{C}}{\text{tr}(\mathbf{H}^{(i)})} \right) \right) \mathbf{F}^T. \quad (11.364)$$

The approach that uses (11.362) together with (11.363–11.364) is the *generalized structure tensor method*. Note that if the orientation density functions $\rho^{(i)}$ satisfy (11.353), the term $\text{tr} \mathbf{H}^{(i)} = 1$ can be omitted.

The angular integration and the generalized structure tensor methods are equivalent in the case of spherical deformations and in the absence of dispersion (i.e., perfect fiber alignment) [228]. From a computational point of view, the generalized structure tensor method is vastly superior since the angular integration has to be performed only once, to compute $\mathbf{H}$, which is independent of the deformations, as long as ρ does not change. Further, the derivative of the fiber strain-energy function w_{fib}' needs to be evaluated only once for a given value of the deformation tensor $\mathbf{C}$.

Transversely isotropic fiber density functions. Of particular interest are transversely isotropic, or axisymmetric, orientation density function where for each fiber, we have

$$\rho(\mathbf{M}) = \tilde{\rho}(\theta) = \tilde{\rho}(-\theta), \quad \theta = \arccos(\mathbf{M} \cdot \bar{\mathbf{M}}), \quad (11.365)$$

which defines a fiber dispersion around the mean fiber directions $\bar{\mathbf{M}}$. An example of this fiber distribution is shown in Figure 11.39A, where there are two main mean fiber distributions around which there is a transversely isotropic orientation density. The generalized structure tensor for such an orientation density function is

$$\mathbf{H} = \kappa \mathbf{1} + (1 - 3\kappa) \bar{\mathbf{M}} \otimes \bar{\mathbf{M}}, \quad (11.366)$$

where

$$\kappa = \pi \int_0^\pi \tilde{\rho}(\theta) \sin^3 \theta \, d\theta \in [0, \frac{1}{2}], \quad (11.367)$$

is the *dispersion parameter* [426]. The complete alignment in the direction $\bar{\mathbf{M}}$, the isotropic distribution, and the complete alignment in the plane perpendicular to $\bar{\mathbf{M}}$ correspond to the values $\kappa = 0, 1/3, 1/2$, respectively [604].

Apart from the case $\kappa = 0$ and $1/2$ different distributions may lead to the same parameter κ . For example, the value $\kappa = 1/3$ corresponds to the case when the fiber distribution forms a cone, whose generatrix and axis make an angle

$$\Theta^* = \arctan \sqrt{2}, \quad (11.368)$$

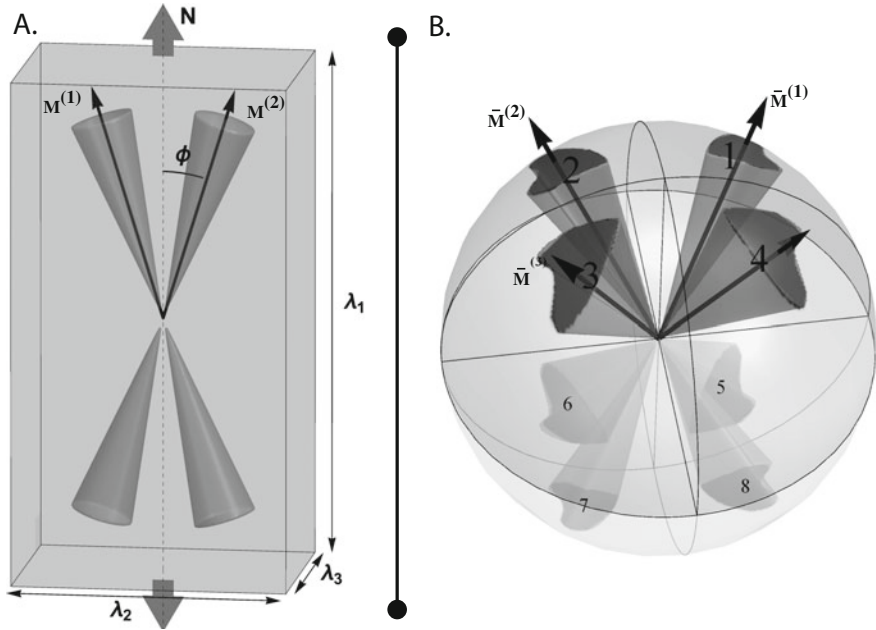


Figure 11.39 A. A material reinforced by two families of mechanically equivalent fibers is in uniaxial tension, subject to the axial load N . Both fiber families are transversely isotropic and described by the von Mises distribution. The mean fiber directions $\mathbf{M}^{(i)}$ are aligned symmetrically with respect to the principal directions. If $\phi \neq 0, \pi/2$, the material is orthotropic. B. Orthotropically symmetric fiber-reinforcement in a material with four families of fibers. Each family has a reference direction $\bar{\mathbf{M}}^{(i)}$ and orientation density function $\rho^{(i)}$.

i.e., $\tilde{\rho}(\theta) = \delta(\Theta^* - \theta)$, where we recognize again the ubiquitous magic angle Φ_m discussed in the previous sections.

The simple form of the generalized structure tensor in (11.366) allows us to express the mean square of fiber stretch through the invariants of a transversely reinforced material, $I_1 = \text{tr} \mathbf{C}$, $I_4 = \bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C}$,

$$\langle I_f \rangle_\rho = \mathbf{H} : \mathbf{C} = (1 - 3\kappa)I_4 + \kappa I_1. \quad (11.369)$$

Therefore, the standard reinforced model for transverse isotropic fiber distribution can be obtained by the following replacement $I_4 \rightarrow \kappa I_1 + (1 - 3\kappa)I_4$, and $I_6 \rightarrow \kappa I_1 + (1 - 3\kappa)I_6$, that is,

$$\begin{aligned} W = & \frac{\mu_1}{2}(I_1 - 3) \\ & + \frac{\mu_4}{2} [(\kappa I_1 + (1 - 3\kappa)I_4)^2 - 1]^2 \\ & + \frac{\mu_6}{2} [(\kappa I_1 + (1 - 3\kappa)I_6)^2 - 1]^2, \end{aligned} \quad (11.370)$$

and we see that the fibers now also contribute to the isotropic part of the strain-energy function.

Fiber exclusion. The generalized structure tensor provides a simple way to model the exclusion of compressed fiber by annihilating the anisotropic part of $\mathbf{H}$ if the stretch in the main direction is compressive ($\bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C} - 1 < 0$), as suggested by Gasser et al. [426, 604]. That is, for each fiber we define

$$\mathbf{H} = \begin{cases} \kappa \mathbf{1} + (1 - 3\kappa) \bar{\mathbf{M}} \otimes \bar{\mathbf{M}}, & \bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C} > 1, \\ \kappa \mathbf{1}, & \bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C} \leq 1, \end{cases} \quad (11.371)$$

and Equations (11.363) and (11.364) should be used as before.

Holzapfel and Ogden [604] observed that values of κ from $(1/3, 1/2)$ yield negative pressure in an inflated thin-walled tube and concluded that these values are therefore nonphysical.

This problem can be circumvented by defining the generalized structure tensor for transversely isotropic fiber distribution as follows [864]:

$$\mathbf{H} = \begin{cases} \kappa \mathbf{1} + (1 - 3\kappa) \bar{\mathbf{M}} \otimes \bar{\mathbf{M}}, & (1 - 3\kappa) (\bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C} - 1) > 0, \\ \kappa \mathbf{1}, & \kappa \leq \frac{1}{3}, \quad \bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C} \leq 1, \\ (1 - 2\kappa) \mathbf{1}, & \kappa > \frac{1}{3}, \quad \bar{\mathbf{M}} \otimes \bar{\mathbf{M}} : \mathbf{C} > 1. \end{cases} \quad (11.372)$$

This modified generalized structure tensor has now all the desired properties. In particular, it provides a mechanism of exclusion of compressed fibers, so that an isochoric deformation always results in an average extension of fibers ($\mathbf{H}^{(i)} : \mathbf{C} \geq 1$) for any values of κ . With this definition, it is not necessary to perform an integration for each deformation. The integration can be performed only once to compute the dispersion parameter κ .

Chapter 12

The Kinematics of Growth



In the previous chapter, we have defined general kinematics for the deformations of three-dimensional bodies in Euclidean spaces. We can generalize and adapt these methods to describe growth processes changing the shape and volume of a body and quantify the stresses generated through these processes.

We saw in Section 1.1.3 that a kinematic description of volumetric growth can be achieved by specifying at each point of a body how an infinitesimal sphere is transformed into an infinitesimal ellipsoid as shown in Figure 12.1.

The problem of growth is that neighboring points in the body may grow in a way that is incompatible for the body to retain its integrity. Due to growth, parts of the body may overlap or be torn apart. In an elastic body, as points are pushed together, or pulled apart, they develop elastic strains to maintain the body's continuity and integrity.

One of the central ideas of morphoelasticity is that the body keeps its integrity in growth by developing elastic strains. Elastic growth can be thought of as a two-step process. The first step is a purely geometric deformation, prescribing how each point of the body is affected by growth. The second step is an elastic accommodation necessary to maintain both the integrity of the body as a continuum and its mechanical equilibrium in the current configuration.

The focus of this chapter is the geometric description of growth deformations. In particular, we define the notion of incompatibility and different tensorial objects

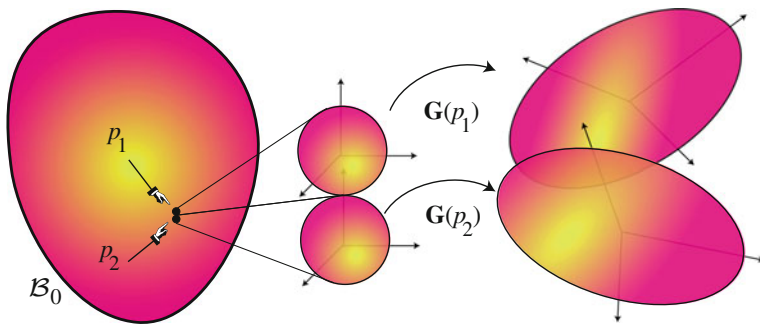


Figure 12.1 A local element inside a body can expand or shrink anisotropically. This process is characterized locally by a growth tensor $\mathbf{G}$, transforming a sphere into an ellipsoid. Two neighboring points may grow such that they would overlap after growth creating incompatibility.

needed to quantify incompatibility in a growing body. We first show how growth tensors naturally arise from the description of residual stresses.

12.1 A Thought Experiment

In order to understand the nature of stresses generated through growth, we first perform a thought experiment on an elastic body in a three-dimensional space. This body could be part of a soft organ such as an artery or a heart, it could be the branch of a tree, a solid tumor, or any other body that could be reasonably modeled as an elastic continuum. For simplicity, we assume that it is not currently growing or moving: The body is in state of static equilibrium and has been brought to our thought laboratory ready for a thought experiment that will allow us to describe its stress state and its material response. We have two problems. First, we need to quantify these internal stresses. Second, recalling that the basic assumptions of nonlinear elasticity is to define a constitutive relationship by considering the strains away from a stress-free configuration, we need to obtain a state where all stresses have been removed. The two problems are closely related.

First, we remove all possible external applied loads and body forces by releasing attachments, removing pressure fields, and turning off gravitation. Gravitation can be removed by either sending our thought experiment in space, by placing it in a neutrally buoyant enclosure, or by realizing that the typical stresses generated by the gravitational field can be neglected in comparison to other stresses acting on the body.

The second step consists in evaluating the internal stresses that may have arisen as a consequence of growth. Indeed, in the absence of applied loads and body forces, our body may still experience *residual stresses*. Without knowledge of the elastic properties of our elastic material, the existence of residual stress can be demonstrated

by a destructive experiment that consists in cutting the body and realizing that, in the process, pieces of the material change shape as elastic stresses are relieved. For instance, residual stresses are observed by slicing arteries or rhubarbs as discussed in Section 2.2. The hope here is that by successive slicing, we obtain a configuration where all residual stresses have been removed. This stress-free configuration could then be used to obtain a constitutive law and by carefully tracking all changes in shape, we could then compute the residual stresses in the material.

To demonstrate the existence of residual stress, we consider the following simple physical experiment. Take an unstressed elastic tube and turn it inside out to transform it into a different tube. Even in the absence of external loads, this new tube is stressed. The residual stresses can be easily relieved by a single longitudinal cut that would allow the tube, after relaxation, to regain its original unstressed tubular shape. However, without a priori knowledge of how the residual stress was built in the structure, it is not clear how we should cut the tube as to relieve all stresses. For instance, an alternative way of cutting the tube would be to slice it into many rings. At each cut the internal diameter of the ring would change indicating again the presence of residual stress. But these rings are still stressed. We could then slice each ring along a circle as to create two new rings. Each new ring could be divided again into two new rings and so on. After each cut, we would observe some variation in the diameters of the rings indicating the release of residual stress. The cutting process would need to be repeated indefinitely since each new cut reveals the existence of residual stress. We conclude from this simple example that even, in the case where a single cut may be enough, without prior knowledge of the residual stress field, a destructive experiment, if not performed judiciously, may require infinitely many cuts to relieve all stresses.

There may be also cases where a finite number of well-placed cuts may not be sufficient to relieve all stresses, even with a perfect knowledge of the residual stress field. In these cases, we would need to repeat the cutting process indefinitely, until we reach a state where all material pieces are completely stress-free. This state which is determined by a collection of pieces or points is particularly important as the elastic properties of our material are defined with respect to a stress-free configuration. Performing suitable mechanical experiments on each piece would yield a constitutive law relating stresses to strains. These pieces or material points can then be put back into the original body by first elastically straining each piece so that they fit together and then by reapplying loads and body forces.

Rather than starting with the grown body, a different approach for the problem of growth is to go back in time and assume that, before growth takes place, the body is in a stress-free configuration. In this initial configuration, all constitutive laws can be defined. Then the grown configuration is obtained from the collection of stress-free pieces by changing their size through growth, shrinking, and rigid-body motion. As we will see, the action of growth defined a new state that can be used to compute the residual stresses.

Our first goal in this chapter is to show that this process of repeated slicing will converge and that we can reach a state where each individual, possibly infinitesimal, piece is stress-free. Our second goal is to make sense of the configuration obtained

by this repeated process. The third goal is to understand the geometry associated with these different configurations and understand the differences between the case of *global incompatibility* where a finite number of cuts may completely relieve all residual stresses, and the case of *local incompatibility*, where an infinite number of cuts are needed. Finally, we will complete this picture by defining the configuration obtained by growth and shrinking of each individual piece to reconstruct a stress-free body. That is, we will demonstrate that the process responsible for incompatibility can be described by a growth tensor and that there exists an initial stress-free reference configuration from which the current state of the body can be described through a combination of growth and elastic deformations. The view in this chapter is purely static. That is, the body is assumed to be in an *elastic* static equilibrium and any *growth dynamics* has been frozen.

12.2 Relieving Stresses

We now formalize the process of unloading a stressed body as described in the previous section. We consider a body B in a configuration $\mathcal{B}$ in the three-dimensional Euclidean space $\mathbb{E}^3$. The body is composed of hyperelastic nonpolar material presently in a state of elastic equilibrium, that is, in balance with body forces $\mathbf{b}$ and applied loads. The stresses are characterized by the Cauchy stress tensor $\mathbf{T} = \mathbf{T}(\mathbf{x})$, $\mathbf{x} \in \mathcal{B}$, that obeys the equations of motion in the current configuration

$$\operatorname{div} \mathbf{T} + \rho \mathbf{b} = \mathbf{0}, \quad \mathbf{T}^\top = \mathbf{T}, \quad (12.1)$$

where, as before, $\mathbf{x}$ denotes a position in the body of a material point $p \in B$, and $\rho = \rho(\mathbf{x})$ is the current mass density. The boundary conditions are specified by a combination of displacement $\mathbf{x}_b$ and surface tractions $\mathbf{t}_b$ as explained in Section 11.5.

We wish to analyze the nature of the stresses in this body and how they were generated. The first step is to remove all applied loads, displacements and body forces so that $\mathbf{b} = \mathbf{0}$ in $\mathcal{B}$ and $\mathbf{t}_n = \mathbf{0}$ everywhere on $\partial\mathcal{B}$. By removing loads and tractions, the body is elastically deformed into a *residually stressed* configuration $\mathcal{B}_r$, where the subscript r refers to the residually stressed configuration with Cauchy stress $\mathbf{T}_r$ that satisfies

$$\operatorname{div}_r \mathbf{T}_r = \mathbf{0}, \quad \mathbf{T}_r^\top = \mathbf{T}_r, \quad (12.2)$$

where div_r is the divergence with respect to $\mathbf{x}_r \in \mathcal{B}_r$. The stress further satisfies the condition that no surface traction is applied on the body

$$\mathbf{T}_r(\mathbf{x}_r)\mathbf{n}(\mathbf{x}_r) = \mathbf{0}, \quad \forall \mathbf{x}_r \in \partial\mathcal{B}_r, \quad (12.3)$$

where $\mathbf{n}(\mathbf{x}_r)$ is the normal vector at a material point p located at $\mathbf{x}_r$ on the boundary of $\mathcal{B}_r$ (Figure 12.2).

The loading process is the reverse deformation, that is a deformation from $\mathcal{B}_r$ to $\mathcal{B}$ denoted by χ_1 so that $\mathbf{x}_1 = \chi_1(\mathbf{x}_r)$. The deformation gradient tensor from $\mathcal{B}_r$ to $\mathcal{B}$ is

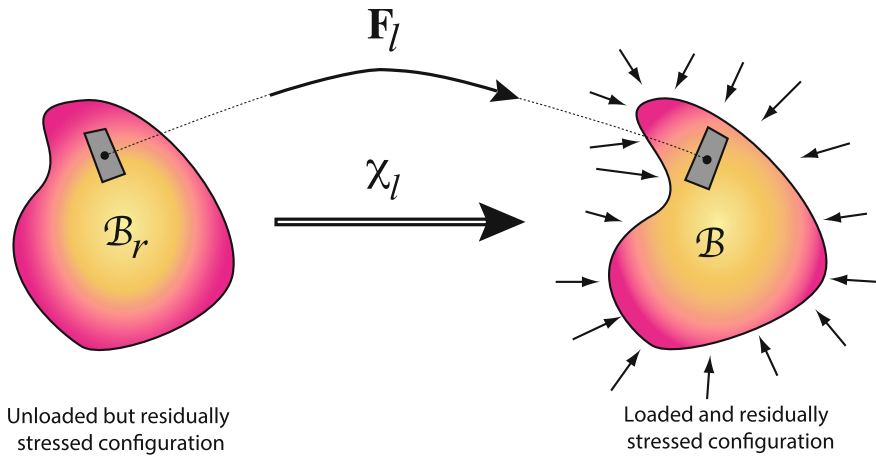


Figure 12.2 The removal of the traction forces and body forces is a deformation from $\mathcal{B}_l$ to $\mathcal{B}_r$. The inverse deformation is the unloading process and is characterized by the invertible map χ_l with gradient tensor $\mathbf{F}_l(\mathbf{x}_r)$.

$$\mathbf{F}_l(\mathbf{x}_r) = \text{grad}_r \chi_l(\mathbf{x}_r). \quad (12.4)$$

If this unloaded configuration is stress-free, then we have a reference configuration from which all geometric and physical quantities can be evaluated as described in the previous chapter. Instead, we will assume that the new unloaded configuration still exhibits stress. There are two fundamental questions related to the residually stressed configuration. First, assuming that the *residual stress* $\mathbf{T}_r$ and the elastic response of the unstressed elastic material are known, how can we compute the current state of the body for given loads and body forces? The main problem comes in the formulation of a constitutive law that would enable us to compute the Cauchy stress from (12.1). This constitutive relationship would naturally depend on the residual stress $\mathbf{T}_r$ and on the deformation. That is, it must take the form

$$\mathbf{T}_r = \mathcal{H}(\mathbf{F}_l, \mathbf{T}_r). \quad (12.5)$$

For particular configurations [522] or in the limit of small deformations, this constitutive relationship for a stressed material is given by a linear superposition of the stress related to the loads and body forces, and the residual stress. However, for large deformations, the constitutive relationship that describes the relationship between the Cauchy stress $\mathbf{T}$ and the deformation gradient $\mathbf{F}_l$ cannot be easily obtained [669]. Here, the theory of invariants can be used to obtain a general form of this constitutive relationship in the same spirit that leads to the formulation, in Section 11.7, of strain-energy functions in terms of the invariants of the right Cauchy–Green tensor [880,

881, 962]. However, this formulation includes many new invariants and unknown functions that are difficult to specify without prior knowledge of the stresses. In particular, it requires knowledge of the residual stress, which is precisely the object that we are trying to relate to a microscopic growth process.

An alternative method to obtain a constitutive law is to unload the body along the principal direction of stresses to obtain a stress-free configuration from which the total elastic strains can be computed [669]. Therefore, it relies on the existence of a stress-free configuration. But, the existence of such a configuration has not yet been established.

The second question is then, how do we obtain a stress-free state from the residually stressed configuration? If such a configuration could be obtained, then the traditional methods of elasticity would apply.

The existence of such a state through the repeated slicing of the body relies on *Signorini's mean-stress theorem* [456, p. 100]: *In a simply connected body $\mathcal{B}$ of volume V , in mechanical equilibrium, subject to an applied load $\mathbf{t}_b$ and body force $\mathbf{b}$, we define the mean-stress $\bar{\mathbf{T}}$ to be*

$$\bar{\mathbf{T}} = V^{-1} \int_{\mathcal{B}} \mathbf{T} dv. \quad (12.6)$$

If the stress $\mathbf{T}$ is differentiable, then

$$\bar{\mathbf{T}} = \frac{1}{2} V^{-1} \left[\int_{\mathcal{B}} \rho (\mathbf{b} \otimes \mathbf{x} + \mathbf{x} \otimes \mathbf{b}) dv + \int_{\partial \mathcal{B}} (\mathbf{t}_b \otimes \mathbf{x} + \mathbf{x} \otimes \mathbf{t}_b) da \right]. \quad (12.7)$$

Therefore, in the absence of body force and traction, the mean stress on a body vanishes identically. In particular, if we follow a point $\mathbf{x} \in \mathcal{B}_r$, through repeated cuts, the volume of the sub-bodies decreases. Since the Cauchy stress is continuous and differentiable at $\mathbf{x}$, it converges, in the limit of infinitely small bodies, toward the null average. In this limit, the stress vanishes identically.

Therefore by a repeated series of cuts sketched in Figure 12.3, the initial body is divided into a collection, possibly infinite, of sub-bodies on which the Cauchy stress vanishes identically.

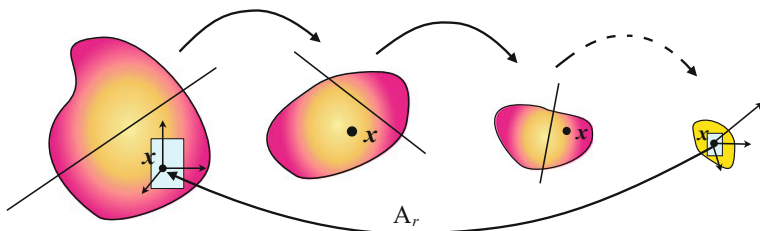
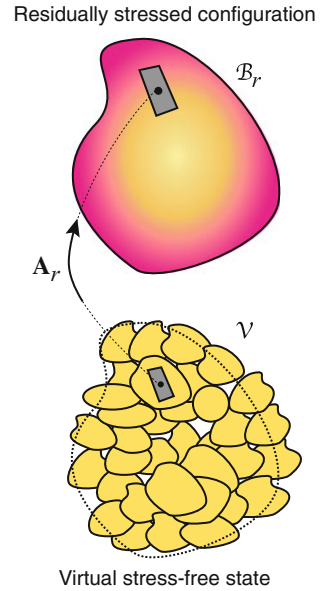


Figure 12.3 The residually stressed body $\mathcal{B}_r$ is repeatedly cut, relieving stress. As the number of cuts $n \rightarrow \infty$, the Cauchy stress at a point $\mathbf{x}$ converges towards the average stress.

Figure 12.4 In the unstressing procedure, the residually stressed body is cut in sub-bodies which are stress-free. At each point, the deformation tensor $\mathbf{A}_r$ characterizes the strains relieved by cutting. The resulting state is a stress-free dislocated body.



After every cut, stress is relieved and the evolution of a basis of tangent vectors in the tangent space can be followed. The change in these bases are defined by the strain relieved at each step and it can be used to define a deformation tensor. More precisely, the change in strain is defined locally by a two-point tensor that maps tangent vectors at p to tangent vectors in the new unstressed configuration. We denote by $\mathbf{A}_r^{-1}$ the *local elastic deformation tensor* mapping the tangent space $T_p \mathcal{B}_r$ at a material point $p \in B$ to the tangent space of the same material point in a stress-free configuration as depicted in Figure 12.4. The union of all images of the tangent spaces of $\mathcal{B}_r$ under $\mathbf{A}_r^{-1}$ forms a tangent bundle $T\mathcal{V}$, that is,

$$\mathbf{A}_r : T\mathcal{V} \rightarrow T\mathcal{B}_r. \quad (12.8)$$

At each point, this mapping is between tangent spaces. If the configuration $\mathcal{B}_r$ is not stress-free, then $\mathbf{A}_r$ cannot be obtained as the gradient of a deformation over the entire body, otherwise, by contradiction, all stresses would have been removed during unloading. Therefore, the actual position in space of a point whose tangent space is $T_p \mathcal{V}$ cannot be defined by the mapping $\mathbf{A}_r$.

Two possible equivalent definitions can be adopted here. The first possibility is to consider that the tangent bundle $T\mathcal{V}$ is the tangent bundle to a global differentiable manifold $\mathcal{V}$. The nonexistence of a global invertible differentiable map from $\mathcal{B}_r$ to $\mathcal{V}$ implies that $\mathcal{V}$ is not an Euclidean manifold and its geometry can be described through the standard quantifiers of differential geometry. This point of view will be further explored in Section 12.5.

The second possibility is to identify the placement of points p in the two states. Then, the *virtual state* $\mathcal{V}$ in the Euclidean space can be seen as a *dislocated body*, that is, an *incompatible state* defined by a collection of stress-free, possibly infinitesimal, sub-bodies with possible overlaps or gaps. For the remainder of this section, we adopt this point of view and consider the virtual state $\mathcal{V}$ as a dislocated body. The virtual state is not realized as a configuration in Euclidean space, but a state on which kinematic measures such as strains can be defined. More importantly, $\mathcal{V}$ is a stress-free state of a hyperelastic material suitable for the computation of stresses in both the residual and final configurations.

We recall that a *deformation* is a global differentiable one-to-one map between the tangent bundle of two body manifolds. Whereas the virtual state is not defined as a configuration, its tangent bundle $T\mathcal{V}$ is well defined. We use the letter $\mathbf{A}$ to denote elastic deformations that may be incompatible and we use $\mathbf{F}$ to denote a compatible deformation, that is, deformations that can be written as the gradient of a mapping.

It is important to note that the deformation tensor $\mathbf{A}$ is not necessarily unique or defined independently of the cutting procedure. Assume that two different cutting procedures lead to two different configurations $\mathcal{V}_1$ and $\mathcal{V}_2$ defined by two different deformation tensors $\mathbf{A}_1, \mathbf{A}_2$. We restrict our attention to strictly convex strain-energy functions $W = W(\mathbf{C})$ with respect to the right Cauchy–Green tensor $\mathbf{C}$. A scalar function W is *strictly convex* with respect to C if

$$2(W(\mathbf{C}_2) - W(\mathbf{C}_1)) > (W_{\mathbf{C}} + W_{\mathbf{C}}^T)(\mathbf{C}_2 - \mathbf{C}_1), \quad \forall \mathbf{C}_2 \neq \mathbf{C}_1. \quad (12.9)$$

This condition implies that the material can only have a single stress-free state. Therefore, it can be shown [524] that for a hyperelastic material with a strictly convex strain-energy function $W = W(\mathbf{C})$, the two deformation tensors $\mathbf{A}_1$ and $\mathbf{A}_2$ are related by

$$\mathbf{A}_1 = \mathbf{A}_2 \mathbf{Q}, \quad \mathbf{Q} \in SO(3). \quad (12.10)$$

Therefore, in the unstressing process, the two right Cauchy–Green tensors

$$\mathbf{C}_1 = \mathbf{A}_1^T \mathbf{A}_1, \quad \mathbf{C}_2 = \mathbf{A}_2^T \mathbf{A}_2, \quad (12.11)$$

are related by

$$\mathbf{C}_2 = \mathbf{Q}^T \mathbf{C}_1 \mathbf{Q}. \quad (12.12)$$

Furthermore, if there exists a mapping ξ between the two states $\mathcal{V}_1$ and $\mathcal{V}_2$ such that $\mathbf{Q} = \nabla \xi$, then it must be a rigid-body deformation, that is, a rotation followed by a translation [525, p. 49]. This observation allows us to define the virtual state as a class of equivalence, where any two members in the same class are related by a proper rotation.

A natural problem regarding the non-Euclidean manifold $\mathcal{V}$ and the incompatible deformation tensor $\mathbf{A}_r$ is to characterize how these objects fail to be, respectively, flat and compatible. Before doing so we introduce another configuration that will be used to connect explicitly the existence of a residual stress field to a growth mechanism.

12.3 The Conceptual Hypothesis of Morphoelasticity

The existence of residual stress in biological materials is closely associated to growth or to an internal reorganization of the reference configuration. As different elements of a body change in size or relative position, they create stresses even in the absence of applied loads. So far, we have assumed that the body B under consideration has a residual stress field. This assumption led us to the definition of a virtual state $\mathcal{V}$.

The central postulate of *morphoelasticity* is that the residual stresses are solely created by a local growth deformation tensor. That is, the deformation gradient can be decomposed multiplicatively as

$$\mathbf{F} = \mathbf{A}\mathbf{G}, \quad (12.13)$$

where the tensor $\mathbf{G}$ describes the change of shape and volume at all points in the body due to growth.

The corresponding conceptual hypothesis, that anelastic contribution can be taken into account through a *multiplicative decomposition of the deformation gradient*, follows from early work in different communities [1111]: In polymer swelling it was first discussed by Flory (1956) [368]; in the theory of defects by Bilby, Gardner, and Stroh (1957) [98]; in elastoplasticity by Kröner (1958) [729], [732, p. 100] [730, p. 286]; and later popularized by Lee [777] (1969). In the theory of thermoelasticity, it was properly formalized by Stojanović et al. (1964) [1196, 1197] and in the context of biological tissues, the multiplicative decomposition was independently proposed in Russia by Kondaurov and Nikitin (1987) [721] and in Japan by Takamizawa et al. (1987) [1216–1218] who used it to characterize residual stresses in arteries. The same conceptual ideas can also be found in the work of Tranquillo and Murray on wound healing [1243, 1244].

However, this approach only became a central concept of biomechanics following the seminal work of Rodriguez, McCulloch, and Hoger (1994) [1091] who showed how to translate growth processes in terms of the tensor $\mathbf{G}$.

The general principle states that growth in an elastic tissue can be modeled by an anelastic process which is the result of a combination of a local growth deformation from a compatible configuration followed by a local elastic deformation.

A configuration of a body B is said to be *compatible* if there exists an isometric embedding of the body B in $\mathbb{E}^3$. That is, we postulate the existence of an initial compatible reference configuration $\mathcal{B}_0 \subset \mathbb{E}^3$ and a growth tensor $\mathbf{G}(\mathbf{X}_0, t)$ defined at every material point $p \in B$ with coordinates $\mathbf{X}_0 \in \mathcal{B}_0$ at time t , as shown in Figure 12.5. The growth tensor maps the tangent space $T_p \mathcal{B}_0$ at every point p to the linear space $T_p \mathcal{V}$ of a virtual state $\mathcal{V}$ for the same material point: that is, we have

$$\mathbf{G} : T\mathcal{B}_0 \rightarrow T\mathcal{V}. \quad (12.14)$$

We note that for a given virtual state $\mathcal{V}$, the growth tensor $\mathbf{G}$ and the initial configuration $\mathcal{B}_0$ are not unique. For instance, it is easy to picture that a rectangle

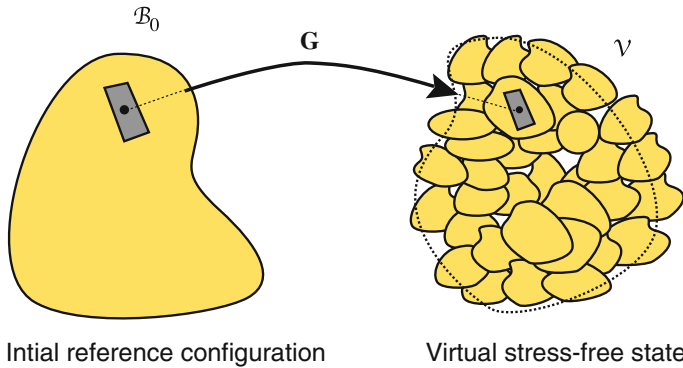


Figure 12.5 The action of the growth tensor. The growth tensor maps vectors in the tangent space of the initial configuration to vectors in the tangent space of the virtual state. The initial configuration and the virtual state are stress-free.

can be obtained as the isotropic growth of a smaller rectangle, or the anisotropic growth of a square along one direction. Nevertheless, the Cauchy stress and shape of the body in the current configuration is independent of the choice of both the initial configuration and growth tensor as long as their tangent bundle can be identified.

We now consider the product of the two deformations taking the initial reference configuration to the residually stressed configuration as shown in Figure 12.6:

$$\mathbf{F}_r(\mathbf{X}_0, t) = \mathbf{A}_r(\mathbf{X}_0, t)\mathbf{G}(\mathbf{X}_0, t). \quad (12.15)$$

Since $\mathbf{F}_r$ is a local deformation tensor between two compatible configurations of the same body B , it is the gradient of an invertible differentiable map between the initial reference configuration and the final configuration:

$$\mathbf{x}_r = \chi_r(\mathbf{X}_0, t), \quad (12.16)$$

where $\mathbf{x}_r$ denotes the position of a point p in the current unloaded configuration with position $\mathbf{X}_0$ in the initial reference configuration, as shown in Figure 12.6. Physically, the inverse of the growth process can be thought of as the local shrinking, growing, and rigid-body motion of the dislocated sub-bodies associated with $\mathcal{V}$ so that they again form a compatible configuration.

We can now slightly shift our point of view. Initially, we started with a body with residual stress and, by a series of thought experiments, first unloaded it, then unstressed it to define a virtual stress-free state amenable to a treatment in nonlinear elasticity. The next step was to postulate that this virtual state is itself the result of a local growth process defining the tangent bundle $\mathcal{TV}$. Doing so, we went backward in the process that created the shape and stresses in the current configuration.

Now, to respect causality, we look at the forward growth process: We start with an initial body and study its evolution through growth by specifying a growth law.

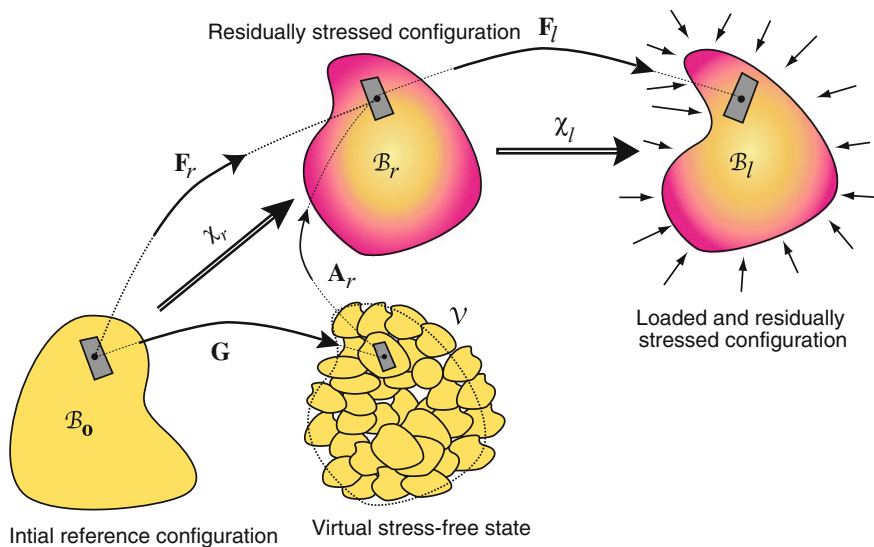


Figure 12.6 The creation of residual stress is obtained by considering a growth process followed by an elastic response. The last deformation consists in loading the body with traction and body forces.

Accordingly, we start from a known initial stress-free configuration $\mathcal{B}_0$ of a body B in $\mathbb{E}^3$ and study those growth processes in an elastic body that can be expressed as the result of a growth deformation followed by an elastic deformation. The growth tensor $\mathbf{G}$ takes the initial configuration to a virtual stress-free state that may be incompatible. Then, a local elastic tensor $\mathbf{A}$ restores compatibility of the body and enforces the boundary conditions and body forces so that the body is in a compatible configuration in mechanical equilibrium, that is, we have

$$\mathbf{F}(\mathbf{X}_0, t) = \mathbf{A}(\mathbf{X}_0, t)\mathbf{G}(\mathbf{X}_0, t), \quad (12.17)$$

as shown in Figure 12.7. Note that both $\mathbf{A}$ and $\mathbf{G}$ have positive determinants. With respect to the previous discussion it should be clear that $\mathbf{A} = \mathbf{F}_l\mathbf{A}_r$.

12.4 Example: The Growing Ring

As a paradigm, we consider the simple, but illuminating problem of a growing circular ring with diagonal growth. The growing ring is modeled as the section of three-dimensional tube. In cylindrical coordinates, the growth tensor is

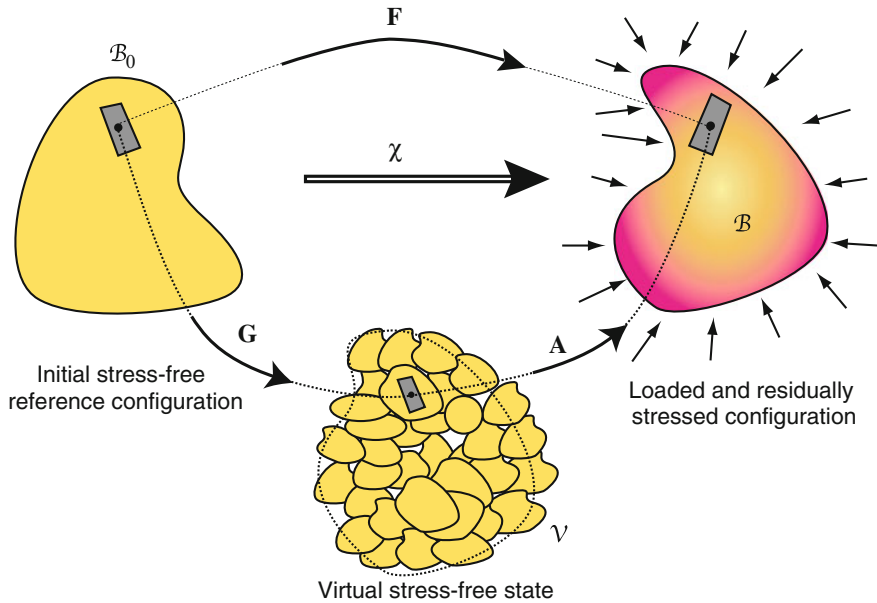


Figure 12.7 The multiplicative-decomposition: Starting from an initial stress-free configuration in Euclidean space, a local deformation $\mathbf{G}$ is applied to each material point, creating a virtual stress-free state which is further deformed by $\mathbf{A}$, to recover integrity of the body, into a residually stressed configuration in Euclidean space. The intermediate virtual state is needed for the definition of constitutive laws.

$$\mathbf{G} = \gamma_r \mathbf{E}_R \otimes \mathbf{E}_{0,R} + \gamma_\Theta \mathbf{E}_\Theta \otimes \mathbf{E}_{0,\Theta} + \gamma_z \mathbf{E}_Z \otimes \mathbf{E}_{0,Z}, \quad (12.18)$$

where γ_r , γ_θ , and γ_z are strictly positive and function of the radial variable R_0 only. If we further restrict growth so that $\gamma_z = 1$, each cross section of the tube are subject to the same deformation. Therefore, we can identify the two bases at each point so that $\mathbf{E}_R = \mathbf{E}_{0,R}$, $\mathbf{E}_{0,\Theta} = \mathbf{E}_\Theta$, $\mathbf{E}_{0,Z} = \mathbf{E}_Z$.

To understand the effect of growth, we first consider the case where γ_r, γ_θ constant. If $\gamma_\theta = 1$ and $\gamma_r \neq 1$, then growth is purely in the radial direction, with each radial fiber expanding if $\gamma_r > 1$ and contracting if $\gamma_r < 1$. We will refer to this case as *radial growth*. Similarly, the case of *hoop growth* defined when $\gamma_r = 1, \gamma_\theta \neq 1$ corresponds to circumferential fibers gaining or losing mass, as shown in Figure 12.8.

If growth is chosen to be transversely isotropic, $\gamma_r = \gamma_\theta$, the new ring is a pure dilation of the original one, that is, $R = \gamma_r R_0$ and $\Theta = \Theta_0$. The tensor $\mathbf{G}$ is therefore the gradient of a deformation and, following the reasoning of the previous section, no residual stress is created in the growth process.

If we consider anisotropic homogeneous growth ($\gamma_r \neq \gamma_\theta$), then residual stresses are created in a ring, but the actual values of these stresses will depend on the equations of equilibrium. We will establish these equations in the next chapter and compute the stresses generated by constant growth coefficients in Section 13.8.3.

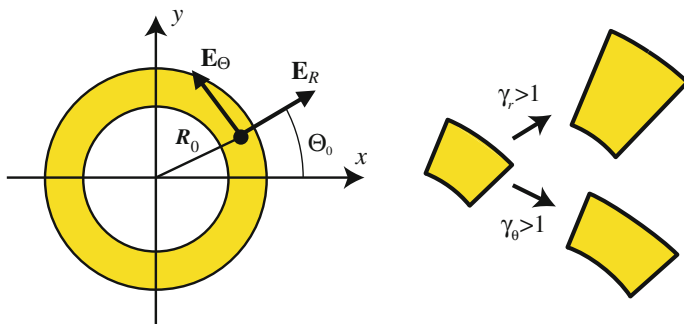


Figure 12.8 Growth of ring elements. A ring sector remains a ring sector when either grown through hoop only growth and/or radial growth.

The residual stress generated during the growth of a ring can be directly observed by cutting the ring and observing that it relaxes to a sector as shown schematically in Figure 12.9. In the present case, we assume that the body is homogeneous and that there is no deformation in the axial direction. We further assume that the open body has the shape of a ring sector and that it is stress-free. Then, the residual stress can be fully described by the geometry of this open configuration and a suitable growth tensor can be identified up to a multiplicative constant. Indeed, in this case the virtual state is locally compatible and is, for positive opening angles, globally compatible too. Therefore, we can find a set of coordinates describing the body and an invertible mapping between the initial and virtual state given by

$$R = R_0, \quad \Theta = (1 - \varphi/\pi)\Theta_0, \quad Z = Z_0, \quad (12.19)$$

and choose, without loss of generality, $A = A_0$, $B = B_0$. As discussed above, a given residually stressed material can be obtained through different growth processes starting with a different initial configuration. The choice $A = A_0$ and $B = B_0$ is one of such possibilities.

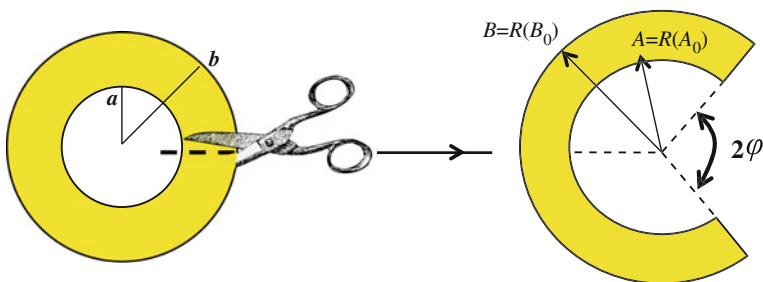


Figure 12.9 Schematic of a radial cut in a ring and the corresponding opening angle φ .

The growth tensor is then easily identified, in cylindrical coordinates, as

$$[\mathbf{G}] = [\mathbf{R}] \operatorname{diag}(1, \varphi/\pi, 1). \quad (12.20)$$

where $\mathbf{R}$ is the rotation matrix around the Z -axis of angle φ/π . Once the growth tensor is known, the stress field of the closed ring under load can be calculated from the equilibrium equations.

The existence of a locally compatible stress-free grown configuration allows for an explicit construction of the residually stressed state based on explicit mapping obtained through a series of cutting and gluing moves that are reminiscent of Volterra's dislocation theory [175, 1175]. From this perspective, the problem of residual stress consists in finding an appropriate locally compatible stress-free configuration. Equivalently this stress-free configuration can be obtained by a deformation whose growth tensor is compatible. For instance, in the simple case of the ring studied here, the open ring can be obtained from the current configuration by a single cut or from an initial configuration by the growth tensor (12.20).

12.5 The Problem of Incompatibility

The unloading and unstressing process creates a virtual state characterized, locally, by a linear space $T_p\mathcal{V}$ at a material point $p \in B$. This decomposition can easily be performed in terms of deformation tensors. However, a difficulty emerges when one tries to associate a deformation to these deformation tensors so that they are deformation gradient tensors *bona fide*. The impossibility to define such mappings, globally or locally, is the problem of incompatibility. We wish to quantify this incompatibility both geometrically and analytically. Geometrically, it means that we need to define a measure of how $\mathcal{V}$ fails to be Euclidean. Analytically, we need to quantify the lack of existence of a mapping whose gradient would be $\mathbf{A}$.

A tensor $\mathbf{G}(\mathbf{X})$ is said to be *locally compatible* if it is the gradient of a deformation, that is, if there exists a smooth mapping $\mathbf{y} = \mathbf{y}(\mathbf{X})$ such that $\mathbf{G} = \operatorname{Grad} \mathbf{y}$. It is *globally compatible* if it is a diffeomorphism over the body $\mathcal{B}_0$ defined as an open set in $\mathbb{E}^3$. A natural question is to establish whether a given growth tensor is locally compatible as it would ensure the existence of a local set of coordinates on the virtual state that can be used to solve the elastic problem and compute the residual stress. Here, we assume that the body $\mathcal{B}_0$ is simply connected. An excellent generalization to the case of non-simply connected bodies has been developed by Yavari [1351]. We draw from results in the theory of continuous dislocations [180], elasto-plasticity [524], and the geometry of differentiable manifolds [259] to establish the main results.

12.5.1 A Differential Geometry Perspective

We first discuss the geometry of Euclidean and Riemannian manifolds to describe the virtual state. The basic idea is to quantify the geometry in the virtual state $\mathcal{V}$ based on geometric quantifiers defined on the initial configuration $\mathcal{B}_0$. Since many of the expressions in this section are best defined in component form, we will use some of the standard notation of differential geometry, assume summation over repeated indices. In this chapter, we distinguish between upper and lower indices, so that any geometric quantity can be written in an arbitrary basis.

12.5.1.1 The Growth Metric and the Riemannian Curvature Tensor

The growth tensor $\mathbf{G} : T\mathcal{B}_0 \rightarrow T\mathcal{V}$ maps, at each point p , the tangent space of the initial configuration to the tangent space of the virtual state at the same material point p . We assume that the initial configuration is a simply connected Euclidean manifold with the usual definition of a Euclidean metric. That is, for a given set of Cartesian coordinates $\{x^i\}$ in a basis $\{\mathbf{E}_i\}$ the initial position vector is $\mathbf{X}_0 = \mathbf{X}_{0,i}\mathbf{E}_{0,i}$. The metric tensor $\mathbf{M}_0$ has components

$$[\mathbf{M}_0]_{ij} = \mathbf{E}_{0,i} \cdot \mathbf{E}_{0,j} = \delta_{ij}, \quad (12.21)$$

where, we have assumed the standard inner product.

At a given point p , we wish to introduce a notion of distance and angle between vectors on $T_p\mathcal{V}$. One way to do so is to consider the right Cauchy–Green tensor associated with $\mathbf{G}$, that is,

$$\mathbf{M} = \mathbf{G}^T \mathbf{G}. \quad (12.22)$$

The tensor $\mathbf{M}$ provides a measure of distance and angle between vectors that are the image of vectors in the initial configuration, as explained in Section 11.1.6. Explicitly, if $\mathbf{V}_0 = V_0^i \mathbf{E}_i$ is a vector in $T\mathcal{B}_0$, its image is $\mathbf{V} = \mathbf{G} \mathbf{V}_0$ and its lengths after deformation is

$$|\mathbf{V}| = |\mathbf{G} \mathbf{V}| = \sqrt{M_{ij} V_0^i V_0^j}. \quad (12.23)$$

We see that the quadratic form $M_{ij} V_0^i V_0^j$ characterizes the natural lengths and angles of vectors defined in the tangent plane of a point in the virtual state in terms of quantities defined in the initial configuration. That is, the metric $\mathbf{M}$ is the *pull-back* of the initial configuration metric associated with the tensor $\mathbf{G}$ [216]. This quadratic form, defines on $\mathcal{V}$, a metric referred to as the *growth metric*.

An important characterization of a metric is its flatness. A metric is said to be *flat* if there exists a local system of coordinates where the metric tensor reduces to the identity, otherwise, the metric is *non-flat*.

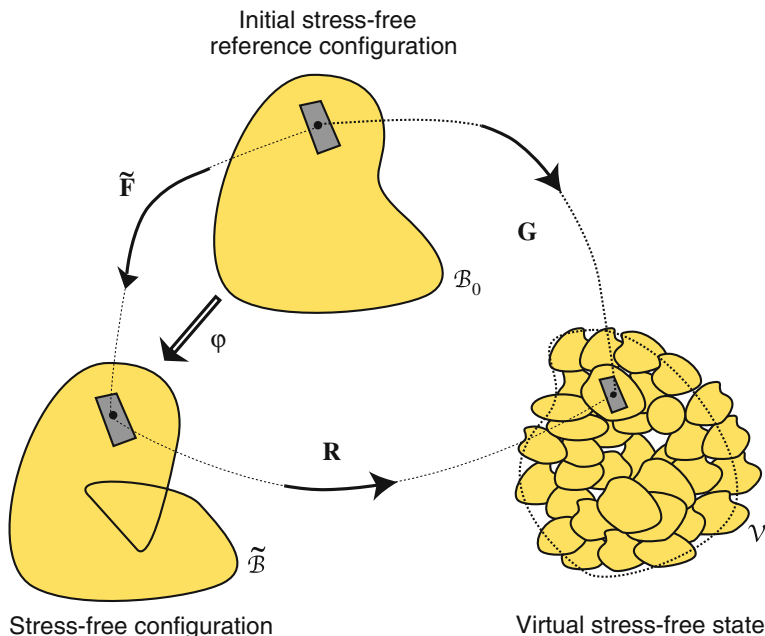


Figure 12.10 If the metric is flat there exists a stress-free configuration $\tilde{\mathcal{B}}$ such that the map $\tilde{\mathbf{F}}^{-1}\mathbf{G}$ is locally a rotation.

We first consider the case of a flat metric shown in Figure 12.10. That is, there exists a mapping $\varphi : \mathcal{B}_0 \rightarrow \tilde{\mathcal{B}} \subset \mathbb{E}^3$ from the initial configuration to a new stress-free configuration $\tilde{\mathcal{B}}$ such that the associated metric in this new configuration reduces to the identity,

$$\tilde{\mathbf{F}}^{-\mathrm{T}}\mathbf{M}\tilde{\mathbf{F}}^{-1} = \mathbf{1}. \quad (12.24)$$

where $\tilde{\mathbf{F}} = \text{Grad}_0(\varphi)$. This last relation can be written as

$$\mathbf{M} = \tilde{\mathbf{F}}^{\mathrm{T}}\tilde{\mathbf{F}}, \quad (12.25)$$

which implies that the growth metric is the right Cauchy–Green tensor of a smooth deformation. Since, by definition we have $\mathbf{M} = \mathbf{G}^{\mathrm{T}}\mathbf{G}$, the identity $\mathbf{G}^{\mathrm{T}}\mathbf{G} = \tilde{\mathbf{F}}^{\mathrm{T}}\tilde{\mathbf{F}}$ implies that the tensors $\mathbf{G}$ and $\tilde{\mathbf{F}}$ differ at most by a rotation at each point as can easily be established by using the polar decomposition of $\tilde{\mathbf{F}}$. Therefore at each point $p \in B$, we have

$$\mathbf{G}(p) = \mathbf{R}(p)\tilde{\mathbf{F}}(p), \quad (12.26)$$

where $\mathbf{R} \in SO(3)$. A few comments are in order.

- When the metric tensor $\mathbf{M}$ is flat, the tensor $\mathbf{M}$ is a *compatible strain tensor*: $\mathbf{M}$ is equal to the right Cauchy–Green strain tensor of a smooth deformation.
- The existence of a compatible strain tensor $\mathbf{M}$ does not imply that the growth tensor $\mathbf{G}$ is compatible. Indeed, if the rotation $\mathbf{R}$ is not a rigid-body rotation, then the compatibility of the map $\mathbf{G}$ does not follow from the compatibility of $\tilde{\mathbf{F}}$. If $\mathbf{M}$ is compatible, and $\mathbf{G}$ incompatible, then the body is in a state of *contorted aleotropy* in the nomenclature of Noll [963]. See also [331, 336, 337] for examples and interesting discussions.
- The mapping φ is an *immersion*, that is, the mapping is differentiable and its gradient is invertible at all points. An immersion ensures the existence of $\tilde{\mathbf{F}}$ and its inverse at all points, but it does not guarantee the existence of a globally invertible map φ . Consider for instance the growing ring studied in Section 12.4. In the case of positive constant hoop growth $\gamma_r = 1$, $\gamma_\theta > 0$, the growth tensor can be written locally as a deformation gradient of a mapping, but this mapping is not globally invertible.
- By construction the state $\mathcal{V}$ is stress-free. Since the configuration $\tilde{\mathcal{B}}$ is related to $\mathcal{V}$ by a local rotation and stress is insensitive to rotation, the configuration $\tilde{\mathcal{B}}$ is also stress-free.

We conclude that if the growth metric is flat, there exists a configuration $\tilde{\mathcal{B}}$ from which stresses can be evaluated. The next question is to find an effective method to determine whether a given growth metric is flat. The answer is provided by a basic theorem from differential geometry that relates the flatness of the metric to the vanishing of the associated Riemannian curvature tensor. Curvature tensors are fourth-order tensors that play a central role in the description and properties of Riemannian manifolds. They are defined in general through the concept of connections studied in the next section. However, there is a particular curvature tensor, the *Riemannian curvature tensor*, that can be defined directly from the metric tensor. First, we define the *Christoffel symbols* associated with the metric $\mathbf{M}$:

$$\overset{\circ}{\Gamma}_{ijk} = \frac{1}{2} (\partial_j M_{ik} + \partial_i M_{jk} - \partial_k M_{ij}), \quad (12.27)$$

$$\overset{\circ}{\Gamma}_{ij}^k = M^{kl} \overset{\circ}{\Gamma}_{ijl}, \quad (12.28)$$

where $\partial_j = \frac{\partial}{\partial X_{0,j}}$ and $[M^{kl}] = [M_{ij}]^{-1}$ is the inverse of the metric $\mathbf{M}$ in component form. Then the *Riemannian curvature tensor associated with the metric $\mathbf{M}$* is

$$\overset{\circ}{\mathcal{R}}_{lijk} = \partial_j \overset{\circ}{\Gamma}_{ikl} - \partial_k \overset{\circ}{\Gamma}_{ijl} + \overset{\circ}{\Gamma}_{ij}^m \overset{\circ}{\Gamma}_{klm} - \overset{\circ}{\Gamma}_{ik}^m \overset{\circ}{\Gamma}_{jlm}. \quad (12.29)$$

We can now state the fundamental theorem related to the Riemannian curvature tensor [211]: *Let Ω be a connected and simply-connected set in $\mathbb{R}^3$ equipped with*

a metric $\mathbf{M} \in C^2(\Omega)$. The metric $\mathbf{M}$ is flat if and only if its Riemannian curvature tensor vanishes identically, that is,

$$\overset{\circ}{\mathcal{R}}_{lijk} = 0, \quad \forall i, j, k, l. \quad (12.30)$$

Note that due to symmetries with respect to indices, only six components of the Riemann curvature tensor are independent in three dimensions. These six independent components can be extracted from the curvature tensor by constructing either the Ricci curvature tensor or, equivalently, the second-order symmetric *Einstein tensor* or *incompatibility tensor*

$$\overset{\circ}{S}^{ij} = \frac{1}{4} \epsilon^{ikl} \overset{\circ}{\mathcal{R}}_{klmn} \epsilon^{jmn}, \quad (12.31)$$

where ϵ^{ijk} denotes the usual *Levi-Civita or permutation symbols*, that is, $\epsilon^{ijk} = 1$ if (i, j, k) is an even permutation of $(1, 2, 3)$, -1 if it is an odd permutation, and 0 if any index is repeated. Condition (12.30) for flatness can then be written as $\overset{\circ}{S} = \mathbf{0}$.

This last result gives us a simple algorithmic way to test the flatness of the growth metric without the need to construct an immersion φ : Given a growth tensor $\mathbf{G}$, compute $\mathbf{M}$ and $\overset{\circ}{S}$. If $\overset{\circ}{S} = \mathbf{0}$, then the metric is flat and $\mathbf{M}$ is a compatible strain tensor. Otherwise, the metric is non-flat. In such a case, no immersion exists but the virtual state can be described as a Riemannian manifold with metric $\mathbf{M}$.

Our geometric analysis identifies two different sources of residual stresses. In the first case, the growth tensor defines a growth metric that is flat. The nonexistence of a mapping between the initial configuration and the grown configuration is due to a global constraint. Putting aside for the time being the situation where the body could be in a state of contorted aleotropy, the growth tensor is locally integrable, but there is no global mapping such that it is a gradient and therefore it fails to be globally integrable.

In the second case, the deformation gradient is not locally integrable and the growth metric is non-flat. There is no local mapping that will immerse the grown stress-free body in the Euclidean space. That is, there are regions of the stressed body where infinitely many cuts will be necessary to relieve all stresses.

Historical note. Within the theory of elasticity, the problem of incompatibility can be seen as the nonlinear version of the Saint-Venant compatibility problem in linear elasticity. In 1864, Saint-Venant derived six independent conditions for the linear strains to be the symmetric part of the gradient of a displacement field. More, precisely, given a second-order linear strain tensor $\mathbf{E}$, the Saint-Venant equations provide conditions for the existence of a displacement field $\mathbf{u}$ such that

$$\mathbf{E} = \frac{1}{2} (\nabla \mathbf{u} + \nabla \mathbf{u}^T). \quad (12.32)$$

These conditions were subsequently derived by Beltrami in 1886 in the context of differential geometry [30, 321]. The connection between differential geometry and

anelasticity has been first put forward by Eckart in 1948 [321] and by Kondo in 1949 [722] who writes: “*The Riemannian curvature has however been introduced into the theory of elasticity in connection with incompatibilities and we can realize without difficulty the existence of a Riemannian state of the elastic body, observing that the essential properties of elastic bodies with initial stresses can best be described by means of Riemannian geometry.*” These ideas were further formalized by Kondo [723], Bilby *et al.* [97] and Kröner [730, 731] and first applied in the context of biomechanics in [1218] (see also [418, 702, 703, 1350]).

12.5.1.2 Growth Metric and Curvature for a Growing Ring

We consider a growing ring as a section of a growing tube. Since we do not consider deformations in the axial direction, the problem is two-dimensional, but all formulas can be readily adapted to this case. We describe the stress-free configuration $\mathcal{B}_0$ with respect to the cylindrical coordinates $\{R_0, \Theta_0, Z_0\}$ so that, a material point has coordinates

$$\mathbf{X}_0 = R_0 \mathbf{E}_{R_0} = (R_0 \cos \Theta_0) \mathbf{E}_1 + (R_0 \sin \Theta_0) \mathbf{E}_2 + Z_0 \mathbf{E}_3. \quad (12.33)$$

The basis vectors are $\mathbf{E}_{R_0} = \partial_{R_0} \mathbf{X}_0$, $\mathbf{E}_{\Theta_0} = \partial_{\Theta_0} \mathbf{X}_0$, and $\mathbf{E}_{Z_0}$. Accordingly, the matrix of the metric tensor $\mathbf{M}_0 = M_{0,\alpha\beta} \mathbf{E}_\alpha \otimes \mathbf{E}_\beta$ in these coordinates is simply given by

$$[\mathbf{M}_0] = \begin{bmatrix} \mathbf{E}_{R_0} \cdot \mathbf{E}_{R_0} & \mathbf{E}_{R_0} \cdot \mathbf{E}_{\Theta_0} & \mathbf{E}_{R_0} \cdot \mathbf{E}_{Z_0} \\ \mathbf{E}_{\Theta_0} \cdot \mathbf{E}_{R_0} & \mathbf{E}_{\Theta_0} \cdot \mathbf{E}_{\Theta_0} & \mathbf{E}_{\Theta_0} \cdot \mathbf{E}_{Z_0} \\ \mathbf{E}_{Z_0} \cdot \mathbf{E}_{R_0} & \mathbf{E}_{Z_0} \cdot \mathbf{E}_{\Theta_0} & \mathbf{E}_{Z_0} \cdot \mathbf{E}_{Z_0} \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & R_0^2 & 0 \\ 0 & 0 & 1 \end{bmatrix}. \quad (12.34)$$

We consider the particular case where the growth tensor is diagonal and only a function of the radial variable, that is,

$$[\mathbf{G}] = \begin{bmatrix} \gamma_r(R_0) & 0 & 0 \\ 0 & \gamma_\theta(R_0) & 0 \\ 0 & 0 & \gamma_z(R_0) \end{bmatrix}. \quad (12.35)$$

The growth metric is the right Cauchy–Green tensor associated with $\mathbf{G}$ and is given by $\mathbf{M} = \mathbf{G}^T \mathbf{G}$ which, in components, reads

$$[\mathbf{M}] = [\mathbf{G}]^T [\mathbf{M}_0] [\mathbf{G}] = \begin{bmatrix} \gamma_r^2 & 0 & 0 \\ 0 & R_0^2 \gamma_\theta^2 & 0 \\ 0 & 0 & \gamma_z^2 \end{bmatrix}. \quad (12.36)$$

Once the components of the metric tensor are known, it is a tedious, but easy exercise to compute a table of the 27 possible Christoffel symbols. In our case, the only nonvanishing components are

$$\overset{\circ}{\Gamma}_{11}^1 = \frac{\gamma'_r}{\gamma_r}, \quad \overset{\circ}{\Gamma}_{22}^1 = \frac{-R_0\gamma_\theta(\gamma_\theta + R_0\gamma'_\theta)}{\gamma_r^2}, \quad (12.37)$$

$$\overset{\circ}{\Gamma}_{12}^2 = \overset{\circ}{\Gamma}_{21}^2 = \frac{1}{R_0} + \frac{\gamma'_\theta}{\gamma_\theta}, \quad (12.38)$$

$$\overset{\circ}{\Gamma}_{31}^3 = \overset{\circ}{\Gamma}_{33}^1 = \frac{\gamma'_z}{\gamma_z}, \quad (12.39)$$

$$\overset{\circ}{\Gamma}_{13}^3 = -\frac{\gamma'_z\gamma_z}{\gamma_r}. \quad (12.40)$$

It is now straightforward to generate the 81 components of the curvature tensor. Doing so, we realize that the only nonvanishing components of the Riemann curvature tensors are

$$\overset{\circ}{\mathcal{R}}_{2112} = R_0 \frac{\gamma_\theta}{\gamma_r} (\gamma_r(2\gamma'_\theta + R_0\gamma''_\theta) - \gamma_\theta\gamma'_r - R_0\gamma'_\theta\gamma'_r), \quad (12.41)$$

$$\overset{\circ}{\mathcal{R}}_{1212} = \overset{\circ}{\mathcal{R}}_{2121} = -\overset{\circ}{\mathcal{R}}_{1221} = -\overset{\circ}{\mathcal{R}}_{2112}, \quad (12.42)$$

$$\overset{\circ}{\mathcal{R}}_{1313} = \frac{\gamma_z}{\gamma_r} (\gamma'_r\gamma'_z - \gamma''_z\gamma_r), \quad (12.43)$$

$$\overset{\circ}{\mathcal{R}}_{1331} = \overset{\circ}{\mathcal{R}}_{3113} = -\overset{\circ}{\mathcal{R}}_{3131} = -\overset{\circ}{\mathcal{R}}_{1313}, \quad (12.44)$$

$$\overset{\circ}{\mathcal{R}}_{2332} = R_0 \frac{\gamma_\theta\gamma_z}{\gamma_r^2} \gamma'_z(\gamma_\theta + R_0\gamma'_\theta), \quad (12.45)$$

$$\overset{\circ}{\mathcal{R}}_{2323} = \overset{\circ}{\mathcal{R}}_{3232} = -\overset{\circ}{\mathcal{R}}_{3223} = -\overset{\circ}{\mathcal{R}}_{2332}. \quad (12.46)$$

The condition $\overset{\circ}{\mathcal{R}} = 0$ leads to

$$R_0\gamma'_\theta = C\gamma_r - \gamma_\theta, \quad (12.47)$$

$$\gamma'_z(\gamma_\theta + R_0\gamma'_\theta) = 0, \quad (12.48)$$

$$\gamma'_r\gamma'_z - \gamma''_z\gamma_r = 0, \quad (12.49)$$

where C is an arbitrary constant. The second equation leads either to $\gamma'_z = 0$ or $\gamma_\theta + R_0\gamma'_\theta = 0$.

In the first case, the third equation is identically satisfied and the condition for local compatibility is

$$R_0\gamma'_\theta = C\gamma_r - \gamma_\theta. \quad (12.50)$$

If, for instance, we choose $\gamma_r = \gamma_\theta$, this condition leads to $\gamma_r = \gamma_\theta = \mu R^\nu$ with μ, ν constant and the corresponding growth tensor does not create locally residual stress.

In the second case, $\gamma_\theta + R_0\gamma'_\theta = 0$ and $C = 0$. We have

$$\gamma_\theta = C_1/R_0 \quad \text{and} \quad \gamma'_r\gamma'_z = \gamma''_z\gamma_r, \quad (12.51)$$

that is, $\gamma'_z = C\gamma_r$ for a new arbitrary constant C . If we choose, for instance $\gamma_r = \gamma_z$, we have $\gamma_r = K \exp(CR_0)$. Again, this profile of growth will not create residual stress unless global constraints, such as the closure of the ring, are applied.

In these examples, if there is global incompatibility due to the material overlapping on itself during growth, a finite number of cuts would relieve all stresses. Similar examples of continuous distributions of defects leading to so-called *impotent stresses* can be found in [1352, 1354].

12.5.1.3 A Heuristic Definition of the Growth Connection

The vanishing of the Riemannian curvature tensor guarantees the compatibility of the strain tensor, but it does not guarantee that $\mathbf{G}$ is the gradient of a deformation, merely that there exists a rotation matrix $\mathbf{R}$ at each point $p \in B$ such that $\mathbf{R}\mathbf{G}$ is compatible. Therefore, the analysis of the Riemannian curvature is not sufficient to establish the compatibility of the growth tensor. However, we can associate the growth tensor with other geometric quantities that will enable us to provide a finer description of compatibility.

The growth metric gives us a way to characterize lengths and angles between vectors at a given point in the virtual state and identify the flatness, or lack thereof, of $\mathcal{V}$. We now wish to compare vectors at different points in $\mathcal{V}$ which, in turn, leads to the idea of parallel transport, derivatives, and connections. Connections provide a way to take derivatives of vector fields over manifolds and can be defined intrinsically on manifolds. We first restrict our attention to a particular connection associated with a deformation tensor. In our case, the growth tensor gives us a natural way to compare vectors and define a derivative. We say that two vectors in $T\mathcal{V}$ at two different points are equivalent if they are the images of the same vectors. More precisely, as shown in Figure 12.11, equivalence for a vector field $\mathbf{v}$ at two different points p and q with coordinates $\mathbf{X}$ and $\mathbf{Y}$ in $\mathcal{B}_0$ implies that

$$\mathbf{G}(\mathbf{X}_0)\mathbf{v}(\mathbf{X}_0) = \mathbf{G}(\mathbf{Y}_0)\mathbf{v}(\mathbf{Y}_0). \quad (12.52)$$

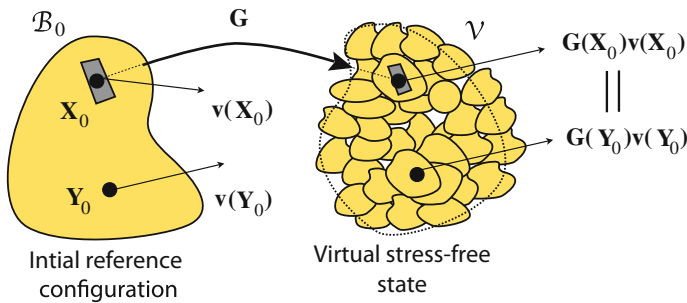
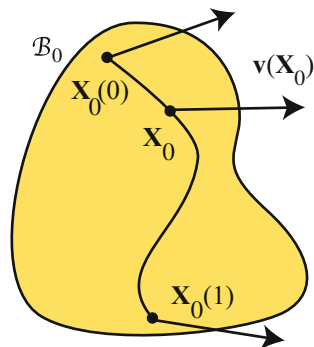


Figure 12.11 Defining a notion of equivalence for vector fields in $\mathcal{V}$ at different points in $\mathcal{V}$.

Figure 12.12 The parallel transport of a vector on $\mathcal{V}$ can be performed by using the initial configuration $\mathcal{B}_0$. A vector field $\mathbf{v}(\mathbf{X}_0)$ is parallel transported on all points from $\mathbf{G}(\mathbf{X}_0(0))$ to $\mathbf{G}(\mathbf{X}_0(1))$ on $\mathcal{V}$ if it satisfies Equation (12.53) along the path in $\mathcal{B}_0$.



If this equality holds for every pair of material points in the body B , the vector field $\mathbf{v}$ should be regarded as constant on $\mathcal{V}$. In particular, for q close to p , we can localize the equivalence relation and write the differential condition for a vector field to be constant, namely:

$$\text{Grad}_0 \mathbf{v}(\mathbf{X}_0) + (\mathbf{G}^{-1} \text{Grad}_0 \mathbf{G}) \mathbf{v}(\mathbf{X}_0) = \mathbf{0}. \quad (12.53)$$

This last relation can be used to define a notion of *parallel transport* of a vector: Starting at a point with coordinates $\mathbf{X}_0(0) \in \mathcal{B}_0$, a vector $\mathbf{v}(\mathbf{X}_0)$ is *parallel transported* to a point $\mathbf{X}_0(1) \in \mathcal{B}_0$ along a path if the differential equation (12.53) is satisfied on this path (Figure 12.12).

The notion of parallel transport is central to the theory of differential geometry as it provides a natural notion of equivalence between vector fields. In our heuristic construction, the tensor $\mathbf{G}$ endows $\mathcal{V}$ with a structure that allows us to compare vectors at different points. The central quantity associated with this construction is the *growth connection* defined by

$$\mathbf{\Gamma} = \mathbf{G}^{-1} \text{Grad } \mathbf{G}. \quad (12.54)$$

The connection is not coordinate independent, but tensorial quantities can be extracted from its components. To do so, we now turn to a formal description of the Riemannian and affine geometry of the virtual state.

12.5.1.4 Riemann–Cartan Manifolds

Connections are fundamental quantities defined on manifolds that allow for the proper definition of derivatives. It is appropriate at this point to give a full definition of basic geometric quantities associated with manifolds. A *linear affine connection* on a manifold $\mathcal{V}$ is an operation $\nabla : (\mathbf{u}, \mathbf{v}) \in \mathcal{X}(\mathcal{V}) \times \mathcal{X}(\mathcal{V}) \rightarrow \nabla_{\mathbf{u}} \mathbf{v} \in \mathcal{X}(\mathcal{V})$, where $\mathcal{X}(\mathcal{V})$ is the set of vector fields on $\mathcal{V}$, and such that $\forall f, f_1, f_2 \in C^\infty(\mathcal{V}), \forall a_1, a_2 \in \mathbb{R}$:

$$i) \quad \nabla_{f_1 \mathbf{u}_1 + f_2 \mathbf{u}_2} \mathbf{v} = f_1 \nabla_{\mathbf{u}_1} \mathbf{v} + f_2 \nabla_{\mathbf{u}_2} \mathbf{v}, \quad (12.55)$$

$$ii) \quad \nabla_{\mathbf{u}}(a_1 \mathbf{v}_1 + a_2 \mathbf{v}_2) = a_1 \nabla_{\mathbf{u}}(\mathbf{v}_1) + a_2 \nabla_{\mathbf{u}}(\mathbf{v}_2), \quad (12.56)$$

$$iii) \quad \nabla_{\mathbf{u}}(f \mathbf{v}) = f \nabla_{\mathbf{u}} \mathbf{v} + (\mathbf{u} f) \mathbf{v}. \quad (12.57)$$

We call $\nabla_{\mathbf{u}} \mathbf{v}$, the *covariant derivative* of $\mathbf{v}$ along $\mathbf{u}$. A *parallel transport* of the vector field $\mathbf{v}$ is obtained along $\mathbf{u}$ if $\nabla_{\mathbf{u}} \mathbf{v} = 0$. In a local set of coordinates $\{X_i\}$, we can give an explicit form to the connection

$$\nabla_{\partial_i} \partial_j = \Gamma^k_{ij} \partial_k, \quad (12.58)$$

in terms of Γ^k_{ij} , the *Christoffel symbols of the connection* and where $\partial_i = \frac{\partial}{\partial X_i}$ form a natural basis for the tangent space corresponding to the choice of coordinates $\{X_i\}$. A linear connection is said to be *compatible with a metric* $\mathbf{M}$ of the manifold if

$$\nabla_{\mathbf{u}} (\mathbf{v} \cdot \mathbf{M} \mathbf{w}) = \nabla_{\mathbf{u}} \mathbf{v} \cdot (\mathbf{M} \mathbf{w}) + \mathbf{v} \cdot (\mathbf{M} \nabla_{\mathbf{u}} \mathbf{w}). \quad (12.59)$$

In general, the geometry of a manifold $\mathcal{V}$ is fully specified by a metric $\mathbf{M}$ and a connection ∇ . Here, we restrict our attention to *Riemann–Cartan manifolds* $(\mathcal{V}, \nabla, \mathbf{M})$ which have the properties of being *metric-compatible*, that is $\nabla \mathbf{M} = 0$. In components this condition reads

$$\frac{\partial M_{ij}}{\partial X_k} - \Gamma^l_{ki} M_{lj} - \Gamma^l_{kj} M_{il} = 0. \quad (12.60)$$

The general case where the metric is not compatible with the connection is related to the notion of point defects in the theory of dislocation [458, 1353]. We can attach to a manifold equipped with a connection two fundamental quantities the *torsion tensor* $\mathcal{T} : \mathcal{X}(\mathcal{V}) \times \mathcal{X}(\mathcal{V}) \rightarrow \mathcal{X}(\mathcal{V})$ and the *curvature tensor* $\mathcal{R} : \mathcal{X}(\mathcal{V}) \times \mathcal{X}(\mathcal{V}) \times \mathcal{X}(\mathcal{V}) \rightarrow \mathcal{X}(\mathcal{V})$. They are defined as

$$\mathcal{T}(\mathbf{u}, \mathbf{v}) = \nabla_{\mathbf{u}} \mathbf{v} - \nabla_{\mathbf{v}} \mathbf{u} - [\mathbf{u}, \mathbf{v}], \quad (12.61)$$

$$\mathcal{R}(\mathbf{u}, \mathbf{v}) \mathbf{w} = \nabla_{\mathbf{u}} \nabla_{\mathbf{v}} \mathbf{w} - \nabla_{\mathbf{v}} \nabla_{\mathbf{u}} \mathbf{w} - \nabla_{[\mathbf{v}, \mathbf{u}]} \mathbf{w}. \quad (12.62)$$

A geometric interpretation of the torsion tensor is given in Figure 12.13. In components with respect to the local coordinates $\{X_i\}$, we have

$$\mathcal{T}^i_{jk} = \Gamma^i_{jk} - \Gamma^i_{kj}, \quad (12.63)$$

$$\mathcal{R}^i_{jkl} = \frac{\partial \Gamma^i_{kl}}{\partial X_j} - \frac{\partial \Gamma^i_{jl}}{\partial X_k} + \Gamma^i_{jm} \Gamma^m_{kl} - \Gamma^i_{km} \Gamma^m_{jl}. \quad (12.64)$$

Note that these two tensors should not be confused with the Frenet torsion and curvature of a curve as defined in Part II, even though the curvature tensor does contain information about the Frenet curvature when reduced to a one-dimensional manifold.

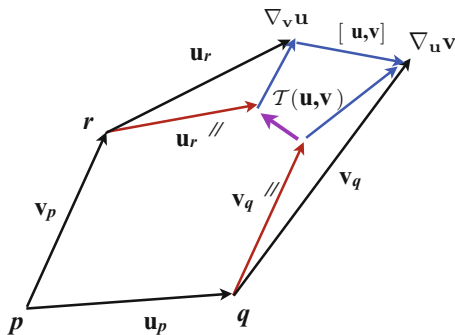


Figure 12.13 The torsion tensor can be interpreted as a failure of closure under parallel transport. Consider two vector fields $\mathbf{u}$ and $\mathbf{v}$, and compute the difference between the parallel transports of each vector field along the other one. If this difference does not vanish, the manifold has non-zero torsion. Note that q and r are assumed to be infinitesimally near p so that their tangent spaces can be identified (adapted from [558]).

There are two important special cases of Riemann–Cartan manifolds when either the torsion or the curvature vanishes as shown in Figure 12.14.

Riemannian manifolds. Given a metric $\mathbf{M}$ on a manifold $\mathcal{V}$, there is a unique linear connection $\overset{\circ}{\nabla}$ that is compatible with $\mathbf{G}$ and is torsion-free, that is,

$$\overset{\circ}{\nabla}_{\mathbf{u}}\mathbf{v} - \overset{\circ}{\nabla}_{\mathbf{v}}\mathbf{u} = [\mathbf{u}, \mathbf{v}]. \quad (12.65)$$

This connection is the *Levi-Civita connection* defined by the following Christoffel symbols

$$\overset{\circ}{\Gamma}_{ij}^k = \frac{M^{kl}}{2} (\partial_j M_{ik} + \partial_i M_{jk} - \partial_k M_{ij}). \quad (12.66)$$

This connection is identical to the one defined by (12.27). In this special case where the connection is induced by the metric, the curvature tensor is the *Riemannian curvature tensor associated with the metric $\mathbf{M}$* given by (12.29).

It is important to make the distinction between the Riemannian curvature tensor defined on a Riemannian manifold by the metric and the curvature tensor defined on a general Riemann–Cartan manifold through the connection. These two objects only coincide when the torsion vanishes.

The existence of a connection induced by the metric and leading to a torsion-free manifold is a fundamental result of differential geometry and the starting point for the theory of general relativity [383].

Weitzenböck manifolds. If the curvature tensor vanishes identically, the Riemann–Cartan manifold is called a *Weitzenböck manifold*. Whereas the Levi-Civita

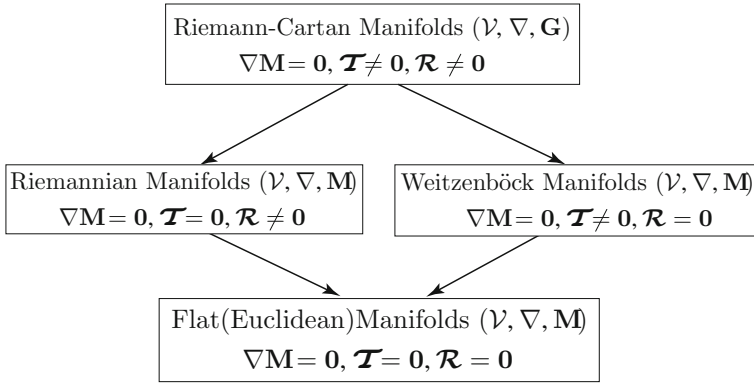


Figure 12.14 Special cases of Riemann–Cartan manifolds. The case of vanishing torsion leads to a Riemannian manifold whereas the case of a vanishing curvature leads to a Weitzenböck manifold. These two cases further reduce to a Euclidean manifold where both curvature or torsion vanish.

connection gives us a direct construction of a torsion-free manifold, it is not clear how to create a curvature-free manifold. However, the particular choice of a connection defined through a deformation tensor $\mathbf{G}$ provides such a construction. Indeed, consider an invertible second-order tensor $\mathbf{G}$ of class C^2 and its associated metric $\mathbf{M} = \mathbf{G}^T \mathbf{G}$. In a given coordinate chart $\{X_i\}$, we define the Weitzenböck connection by

$$\Gamma^i_{jk} = (\mathbf{G}^{-1})^i_l \partial_j (G)^l_k. \quad (12.67)$$

With respect to this connection, it can be checked that the curvature tensor (12.64) vanishes identically. The torsion tensor associated with the growth tensor $\mathbf{G}$ is defined in an orthonormal basis as the third-order tensor [3, 1352]

$$\mathcal{T} = \mathbf{G}^{-1} \text{Skw}(\text{Grad } \mathbf{G}), \quad (12.68)$$

where $\text{Skw}(\cdot)$ is the skew-symmetric part of a tensor, defined by $\text{Skw}(T)_{kij} = T_{kij} - T_{kji}$.

12.5.1.5 Example: The Torsion of a Growing Ring

We consider again a growing cylinder with growth tensor $[\mathbf{G}(R_0)] = \text{diag}(\gamma_r, \gamma_\theta, \gamma_z)$ in cylindrical coordinates as defined by (12.18). A direct computation of the torsion tensor gives (denoting by $[\mathcal{T}_{k..}]$ the matrix components of the second-order tensor for a given k)

$$[\mathcal{T}_{1..}] = \mathbf{0}, [\mathcal{T}_{2..}] = \begin{bmatrix} 0 & \frac{\gamma_\theta - \gamma_r}{\gamma_\theta R_0} - \frac{\gamma'_\theta}{\gamma_\theta} & 0 \\ \frac{\gamma_r - \gamma_\theta}{\gamma_\theta R_0} + \frac{\gamma'_\theta}{\gamma_\theta} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, [\mathcal{T}_{3..}] = \begin{bmatrix} 0 & 0 & \frac{\gamma'_z}{\gamma_z} \\ 0 & 0 & 0 \\ -\frac{\gamma'_z}{\gamma_z} & 0 & 0 \end{bmatrix}. \quad (12.69)$$

and the vanishing of the torsion tensor leads to

$$\gamma'_z = 0 \quad \text{and} \quad \frac{\gamma_\theta - \gamma_r}{R_0} = \gamma'_\theta. \quad (12.70)$$

Comparing these conditions with Equations (12.47–12.49), we see that the condition for the compatibility of the growth tensor are stricter ($C = 0$ and γ_z constant) than for the compatibility of the metric, as expected.

12.5.1.6 Summary on Geometry and Incompatibility

From a practical point of view, we can use the information provided by the geometry of the growth deformation to establish important properties of the deformation with respect to local compatibility.

We recall that a deformation tensor is *locally compatible* if there exists a smooth mapping $\mathbf{X} = \varphi(\mathbf{X}_0)$ such that $\mathbf{G} = \text{Grad}_0 \varphi$. The strain tensor $\mathbf{M} = \mathbf{G}^T \mathbf{G}$ is said to be *locally compatible* if there exists a compatible deformation tensor $\tilde{\mathbf{F}}$ such that $\mathbf{M} = \tilde{\mathbf{F}}^T \tilde{\mathbf{F}}$.

Given the growth tensor $\mathbf{G}$, by construction the curvature tensor $\mathcal{R}$ vanishes identically. We compute the two fundamental objects for compatibility: the Riemannian curvature tensor $\overset{\circ}{\mathcal{R}}(\mathbf{G})$ and the torsion tensor $\mathcal{T}(\mathbf{G})$. We then have the following cases:

- **Case 1: Local compatibility.** If $\mathcal{T}(\mathbf{G}) = \mathbf{0}$, then $\overset{\circ}{\mathcal{R}}(\mathbf{G}) = \mathbf{0}$ and both the strain tensor $\mathbf{M}$ and the growth tensors $\mathbf{G}$ are locally compatible. From a mechanical perspective, if a body is residually stressed due to a growth characterized by such a tensor $\mathbf{G}$, then these stresses are only created by global incompatibility and they can be completely relieved by a finite number of cuts. This situation arises, for instance, for a growing ring with constant γ_r and γ_θ . If $\gamma_\theta > \gamma_r$, then the deformation would create an overlap in the circumferential direction that would result in compressive stress. A finite number of cuts in the radial direction will completely relieve the stress. Note, however, that the ring is not simply connected but that a nongrowing inner disk can be added to the ring to restore connectedness without changing its local compatibility.
- **Case 2: Contorted aleotropy.** If $\overset{\circ}{\mathcal{R}}(\mathbf{G}) = \mathbf{0}$ but $\mathcal{T}(\mathbf{G}) \neq \mathbf{0}$, then the strain tensor $\mathbf{M}$ is locally compatible but $\mathbf{G}$ is not. However, there exists a rotation tensor $\mathbf{R}$ such that $\mathbf{R}\mathbf{G}$ is compatible. The difficulty in this case is that the rotation $\mathbf{R}$ can vary from point to point. Note that despite the fact that the growth tensor is not compatible, there is no stress created through the growth process (apart from the

possibility of global incompatibility).

An example of contorted aleotropy is provided by the growth of a small enough sector of a growing ring of initial radius and such that $R_0\gamma'_\theta = C\gamma_r - \gamma_\theta$ with $C \neq 1$ and $C \neq 0$. From a modeling perspective, this situation is somewhat artificial and points to the fact that the growth tensor has not been properly defined. Indeed for isotropic material, there is a freedom in the decomposition of the deformation gradient as

$$\mathbf{F} = \mathbf{A}\mathbf{G} = \mathbf{A}\mathbf{R}^\top\mathbf{R}\mathbf{G}, \quad \forall \mathbf{R} \in SO(3). \quad (12.71)$$

Therefore, replacing the growth deformation $\mathbf{G}$ by $\mathbf{R}\mathbf{G}$ where $\mathbf{R}$ is chosen to restore compatibility does not change the description of mass addition or the residual stress field for isotropic materials, but may change the computation of residual stress for anisotropic materials.

- **Case 3: Local incompatibility.** If $\overset{\circ}{\mathcal{R}} \neq \mathbf{0}$ then $\mathcal{T}(\mathbf{G}) \neq \mathbf{0}$. In this case, both strain and deformation tensors are locally incompatible. Mechanically, it implies that, in the regions of the body where the Riemannian curvature tensor does not vanish, an infinite number of cuts would be necessary to relieve all stresses. A simple example of this situation is provided by a sector of a growing ring with $\gamma_\theta = 1$ and $\gamma_r = R_0$.

12.5.2 An Analytic Perspective

Incompatibility can also be understood from a purely analytic perspective based on Stokes' theorem [3]. Recall that in a simply-connected domain a differentiable vector field is the gradient of a differentiable function if and only if its curl vanishes identically. It is therefore appropriate to introduce a similar notion for tensor fields [180, 524]. The *curl* of a differentiable second-order tensor $\mathbf{T}$ is the second-order tensor defined by [526]

$$(\text{curl } \mathbf{T})\mathbf{c} = (\text{curl } \mathbf{T}^\top)\mathbf{c} \quad \text{for all constant vectors } \mathbf{c}. \quad (12.72)$$

In a Cartesian basis, the curl can be expressed as

$$(\text{curl } \mathbf{T})_{ij} = \epsilon^{ikl} \frac{\partial T_{jl}}{\partial x_k}, \quad (12.73)$$

where ϵ^{ikl} is the Levi-Civita permutation symbol. Note the particular choice of the transpose of the tensor in (12.72) that guarantees the following identity for all twice continuously differentiable vector fields $\mathbf{v}$:

$$\text{curl}(\text{grad } \mathbf{v}) = \mathbf{0}. \quad (12.74)$$

The Stokes' theorem naturally generalizes to

$$\int_{\partial S} \mathbf{T} \, d\mathbf{x} = \int_S (\text{curl } \mathbf{T})^\top \mathbf{n} \, d\mathbf{x}, \quad (12.75)$$

where S is an oriented surface in a simply-connected region of $\mathbb{R}^3$ with unit normal $\mathbf{n}$ and boundary ∂S . Similarly if $\text{curl}(\mathbf{T}) = \mathbf{0}$ in a simply-connected region $\Omega \subset \mathcal{B}_t$ then by using the Stokes' theorem the integral of $\mathbf{T}$ vanishes on all arbitrary paths in Ω and we conclude that [32]: *In a simply-connected domain for a continuously differentiable tensor $\mathbf{T}$, $\text{curl}(\mathbf{T}) = \mathbf{0}$ if and only if there exists a twice continuously differentiable vector field $\boldsymbol{\varphi}$ such that $\mathbf{T} = \text{grad } \boldsymbol{\varphi}$.*

We apply these ideas to the growth tensor. We define $\text{Curl}_0(\mathbf{G})$ to be the curl of the tensor $\mathbf{G}$, where the derivatives are taken with respect to the initial coordinates. It follows from our discussion that if $\mathbf{G}$ is the gradient of a vector field, then $\text{Curl}_0(\mathbf{G})$ vanishes identically. We can therefore use $\text{Curl}_0(\mathbf{G})$ or $\text{curl}(\mathbf{A}^{-1})$ to quantify incompatibility. Different functions of $\text{Curl}_0(\mathbf{G})$ and $\mathbf{G}$ have been proposed for this purpose in the theory of dislocations. The original proposal is *Nye's dislocation tensor* [969]:

$$\boldsymbol{\alpha} = (\text{curl } \mathbf{A}^{-1})^\top. \quad (12.76)$$

This tensor can be directly related to the *cumulative Burger's vector* $\mathbf{b}$, that measures the presence of dislocations on a loop as the closed path integral around a surface S in $\mathcal{B}$:

$$\mathbf{b} = \int_{\partial S} \mathbf{A}^{-1} \, d\mathbf{x}. \quad (12.77)$$

By using Stokes' theorem, we have

$$\mathbf{b} = \int_S \boldsymbol{\alpha} \mathbf{n} \, d\mathbf{x}, \quad (12.78)$$

where $\mathbf{n}$ is a unit vector normal to S . The traditional geometric interpretation of the cumulative Burger's vector is that its magnitude and direction quantifies the failure of the closure of the image of the path integral around a point. However, particular care must be taken when considering path integral in the virtual state as discussed by Ozakin and Yavari [1003].

Another interesting quantifier of incompatibility is the *true incompatibility tensor* proposed in [180, 1224] and defined as

$$\mathbf{K}(\mathbf{G}) = J_{\mathbf{G}}^{-1} \mathbf{G} \text{Curl}_0 \mathbf{G}, \quad (12.79)$$

where $J_{\mathbf{G}} = \det(\mathbf{G})$. This tensorial function $\mathbf{K}$ has the remarkable property that it is invariant under arbitrary differentiable variations of the configuration: If $\mathbf{Q}$ is the gradient of a deformation, then

$$\mathbf{K}(\mathbf{GQ}) = \mathbf{K}(\mathbf{G}). \quad (12.80)$$

Since $\mathbf{G} = \mathbf{A}^{-1}\mathbf{F}$ and $\mathbf{F}$ is, by definition, a deformation gradient, it naturally follows that $\mathbf{K}(\mathbf{G}) = \mathbf{K}(\mathbf{A}^{-1})$, that is

$$\mathbf{K}(\mathbf{G}) = J_{\mathbf{G}}^{-1} \mathbf{G} \text{Curl}_0 \mathbf{G} = J_{\mathbf{A}} \mathbf{A}^{-1} \text{curl } \mathbf{A}^{-1} = \mathbf{K}(\mathbf{A}^{-1}). \quad (12.81)$$

Further, it was shown in [180] that $\mathbf{K}$ is closely related to the density of Burger's vectors in the theory of dislocations and that all functions that are invariant under a compatible change of configuration are necessarily functions of $\mathbf{K}$, which places the true incompatibility tensor as a central measure of incompatibility.

Finally, we note that the tensor $\mathbf{K}$ is closely related to the torsion tensor associated with the growth tensor $\mathbf{G}$. In components, $K_{ij} = [\mathbf{K}(\mathbf{G})]_{ij}$, the two tensors are related by

$$K_{ij} = \frac{1}{2} J_{\mathbf{G}} G_{ik} \epsilon^{klm} (\mathbf{G}T)_{jlm}. \quad (12.82)$$

12.5.2.1 The True Incompatibility Tensor for a Growing Cylinder

We consider again our example of a growing cylinder with growth tensor $[\mathbf{G}(R_0)] = \text{diag}(\gamma_r, \gamma_\theta, \gamma_z)$ in cylindrical coordinates. The true incompatibility tensor can be readily evaluated as

$$[\mathbf{K}_{\mathbf{G}}] = \frac{1}{\gamma_r \gamma_\theta \gamma_z} \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & -\gamma_\theta \gamma'_z \\ 0 & \gamma_z \left(\frac{\gamma_\theta - \gamma_r}{R_0} - \gamma'_\theta \right) & 0 \end{bmatrix}, \quad (12.83)$$

and we conclude that $\mathbf{G}$ is locally compatible if and only if

$$\gamma'_z = 0 \quad \text{and} \quad \frac{\gamma_\theta - \gamma_r}{R_0} = \gamma'_\theta. \quad (12.84)$$

As expected, we recover the conditions (12.70) obtained from the geometric argument.

Chapter 13

Balance Laws



We adopt the view that growth is modeled by a multiplicative decomposition of the deformation gradient from an unstressed configuration to the reference configuration through a virtual state suitable to describe the stress at each material point. To summarize the previous chapter, we start from a known initial stress-free configuration $\mathcal{B}_0$ of a body $B \subset \mathbb{E}^3$ and consider a growth deformation $\mathbf{G}$ at each material point, mapping locally the tangent space $T_p\mathcal{B}_0$ at a point p in the initial configuration to a linear space $T_p\mathcal{V}$ in the virtual state $\mathcal{V}$ as shown in Figure 12.7. The study of stresses is done by considering an elastic deformation $\mathbf{A}$ mapping $T_p\mathcal{V}$ to $T_p\mathcal{B}$. The composition of $\mathbf{A}$ and $\mathbf{G}$ defines a map from the initial to the current configuration with deformation gradient $\mathbf{F}$ at all material points:

$$\mathbf{F} = \mathbf{A}\mathbf{G}, \quad (13.1)$$

where both $\mathbf{A}$ and $\mathbf{G}$ have strictly positive determinants. The elastic tensor $\mathbf{A}$ restores the integrity of the body under the constraint that the physical balance laws in the current configuration $\mathcal{B}$ are respected. We now discuss balance laws for a growing continuum. We start with the discussion of a crucial assumption based on time scales in growing media.

13.1 The Slow-Growth Assumption

The decomposition (13.1) is instantaneous. It applies continuously with respect to time, but in general, elastic and growth processes do not operate on the same time scales. In typical biological growth processes or in the swelling of soft materials, we can identify five important time scales:

- **Elastic time scales.** These time scales, denoted τ_{elas} , are associated with inertial effects such as vibration or the propagation of waves in a tissue. Since most tissues and organs have a typical size of 10 cm and typical waves propagate with velocities in the order of 10–100 m/s, we choose $\tau_{\text{elas}} \approx 10^{-2}$ s.
- **Viscous time scales.** Inertial effects are damped in elastic tissues due to internal friction. Depending on the softness of the tissue and its viscosity, a typical viscous time scale is $\tau_{\text{vis}} \approx 1$ s.
- **Stress relaxation time scales.** In some systems, the residual stresses built up during growth are relaxed due to internal rearrangement. In a morphogenetic process, this rearrangement can act on the same scale as growth itself. An example of this relaxation is the evolution of the intrinsic shape found in loaded plants and discussed in Section 6.3. In physiological regimes, however, residual stresses develop in order to carry specific functions and are therefore associated with a plastic-like relaxation of stresses due to internal rearrangement with a typical time scale τ_{rel} .
- **Loading time scales.** These time scales, τ_{load} are associated with typical strain rates due to loading such as the cell cycle, blood flow, the forces applied on muscles during exercise, or the circadian rhythm which may vary from seconds to days.
- **Growth time scales.** Typically, growth acts on time scales τ_{growth} longer than most of the above processes. Even when we consider the fastest growth process found in nature, they are typically orders of magnitude slower than other effects acting on the system. For instance, the fastest doubling time found in bacteria is of the order of 10 minutes for some thermophilic anaerobic bacteria found in the hot hydrothermal vent of Lake Tanganyika [330]. It has been argued that a doubling time found in *Escherichia coli* of about 20 min to 1 hour is close to the thermodynamic limit [332]. Estimates of doubling times for cancer cell *in vivo* are typically of the order of 24–60 hours [1186], but the doubling times for tumors varies between 100 days for fast growing tumors to years for slow ones [36]. For terrestrial vertebrates, Case gives an extensive list of postnatal growth rates with typical doubling times in the range of years during early growth years [174]. In plants, maximum growth rates vary with doubling times ranging from 3 hours in unicellular algae to 4–7 years in some trees [950]. Moso bamboos are often cited as the fastest growing plants with linear growth of more than 100 cm in 24 hour [396].

These various considerations lead to the following ordering of time scales for typical growth processes in biological systems:

$$\tau_{\text{elas}} \ll \tau_{\text{visc}} < \tau_{\text{load}} \ll \tau_{\text{growth}}. \quad (13.2)$$

The relaxation time scales is absent from this list as it defines different types of growth. Therefore, an explicit time scale will enter the evolution laws for the tensor $\mathbf{G}$. If growth is mostly elastic as found in mature organs, there is little or no relaxation of the internal stresses and $\tau_{\text{growth}} > \tau_{\text{rel}}$ so that relaxation effects can be safely ignored. However, in development there is a quick rearrangement of cells within the tissue that dissipates rapidly the mechanical effect of mass addition. The system then behaves more in a fluid-like manner and τ_{rel} is comparable to τ_{growth} . Yet, in other systems, such as in the growth of stems discussed in Section 6.3, there is a balance between relaxation and stresses so that as growth proceeds the system maintains a given level of stresses while still adding mass.

In the rest of this chapter, we focus on the physical balance laws in a growing continuum. We consider a body in the current configuration subject to loads, and generalize the balance laws obtained in Section 11.2 to include the possibility of mass addition, change in density, as well as fluxes of linear and angular momenta due to new material entering the body. These new fluxes are associated with the time scale of growth. Based on the ordering of time scales, we will use the *slow-growth assumption of morphoelasticity*, that is, we will assume that the time scales of growth processes are much larger than any other time scales and respect (13.2). Therefore, the time scale of growth and elastic response are widely separated and it is reasonable to assume that for growth processes, the elastic dynamics of the material is dependent on the growth only through the change of geometry and not through the dynamics of the fluxes associated with growth processes. That is, at any given time and on short-time scales, we assume that the material is hyperelastic. The generalization to a theory with possible viscoelastic components follows naturally, but it will not be discussed here. In order to see how the slow-growth assumption affects the balance equations, we will first include these terms formally before neglecting them. This process allows for generalizing the theory if necessary. Further discussion and details on the derivation of balance laws in anelasticity can be found in several articles and books [339–341, 809, 811].

13.2 Balance of Mass

We follow the evolution of a subset $\Omega \subseteq \mathcal{B}_t$ of a body B . Assuming that growth can occur either through volumetric growth or through material flux across the boundary, the rate of local increase by volumetric growth is captured by the growth rate function $\rho\gamma(\mathbf{x})$, and the flux of material through the boundary $\partial\Omega$ is described by the vector $\mathbf{\Pi}(\mathbf{x})$. We note that the body B is fixed, i.e., we do not have surface growth on the boundary of the body. The flux $\mathbf{\Pi}(\mathbf{x})$ describes a possible effect of diffusion of matter

into itself [340]. The balance of mass, applied to an arbitrary volume element Ω with outward normal boundary vector $\mathbf{n}$, reads now

$$\frac{d}{dt} \int_{\Omega} \rho \, dv = \int_{\Omega} \rho \gamma \, dv + \int_{\partial\Omega} \mathbf{\Pi} \mathbf{n} \, da. \quad (13.3)$$

We follow the Maxwell transport and localization procedure given in Section 11.2.1. That is, we apply the divergence theorem and the transport formula (11.96). Then assuming that the integrands are all continuous and using the fact that Ω is arbitrary, we use the localization procedure to obtain the local version of the *mass balance equation* for a growing continuum:

$$\dot{\rho} + \rho \operatorname{div} \mathbf{v} = \rho \gamma + \operatorname{div} \mathbf{\Pi}. \quad (13.4)$$

Using the slow-growth assumption, we neglect fluxes through the boundary and their associated momenta, that is, we set $\mathbf{\Pi} = \mathbf{0}$ so that

$$\dot{\rho} + \rho \operatorname{div} \mathbf{v} = \rho \gamma. \quad (13.5)$$

We can relate the growth tensor $\mathbf{G}$ to the growth rate function $\gamma(\mathbf{x})$ appearing in the mass balance equation (13.5). To do this, we first note that expressed in the initial configuration, the mass equation is

$$\frac{d}{dt}(J\rho) = J\rho\gamma. \quad (13.6)$$

Next, we write $J = J_A J_G$, where $J_A = \det(\mathbf{A})$ and $J_G = \det(\mathbf{G})$ measure the change in volume due to the elastic deformation and growth deformation, respectively. Let ρ_G be the density with respect to the virtual state, and consider an element of mass in the virtual state, $dM = \rho_G \, dV$. Since mass is not added in the elastic deformation, the mass in the current state is

$$dm = \rho \, dv = dM = \rho_G \, dV, \quad (13.7)$$

and since $dv = J_A dV$, we have $\rho J_A = \rho_G$. Using this relationship along with Jacobi's identity (11.86) for $\mathbf{G}$:

$$\frac{\partial}{\partial t}(\det \mathbf{G}) = (\det \mathbf{G}) \operatorname{tr} \left(\mathbf{G}^{-1} \frac{\partial \mathbf{G}}{\partial t} \right), \quad (13.8)$$

Equation (13.6) can be written

$$\dot{\rho}_G + \rho_G \operatorname{tr}(\mathbf{G}^{-1} \dot{\mathbf{G}}) = \rho_G \gamma. \quad (13.9)$$

There are two important limits when either the density or the volume does not change with growth.

- **Constant density.** In this case, $\dot{\rho} = 0$, and the relation between the growth tensor $\mathbf{G}$ and the rate of growth is simply

$$\text{tr}(\mathbf{G}^{-1}\dot{\mathbf{G}}) = \gamma. \quad (13.10)$$

- **Constant volume.** If there is no change in volume, then $J_G = 1$, and the evolution of the density can be written

$$\dot{\rho}_G = \rho_G \gamma. \quad (13.11)$$

That is, γ is a rate of densification, adding mass to the system without changing its volume.

We can also relate the growth tensor and growth rate to the experimental kinematics of growth presented in Section 1.4. Assuming that there is no elastic deformation, that is, $\mathbf{A} = \mathbf{1}$, we have $\mathbf{G} = \text{Grad } \chi$ and we define the *growth velocity* as

$$\mathbf{v}_G(\mathbf{x}, t) = \dot{\mathbf{x}} = \frac{\partial \chi}{\partial t}. \quad (13.12)$$

The *growth velocity gradient tensor* is then

$$\mathbf{L}_G = \text{grad } \mathbf{v}_G. \quad (13.13)$$

Using the chain rule, we have $\text{Grad } \mathbf{v}_G = (\text{grad } \mathbf{v}_G) \mathbf{G} = \mathbf{L}_G \mathbf{G}$, but since $\text{Grad } \dot{\mathbf{x}} = \partial_t \text{Grad } \mathbf{x}$, it follows that

$$\dot{\mathbf{G}} = \mathbf{L}_G \mathbf{G}. \quad (13.14)$$

Using again identity (13.8) and $\text{tr } \mathbf{L}_G = \text{div } \mathbf{v}_G$, we have

$$\dot{J}_G = J_G \text{div } \mathbf{v}_G, \quad (13.15)$$

which in the case of constant density specializes to Equation (1.15). We note that if $\mathbf{G}$ is not a multiple of the identity (isotropic growth), there is much more information in $\mathbf{G}$ than in γ , so that in general for the description of anisotropic growth, all components of the tensor $\mathbf{G}$ may be needed.

13.3 Balance of Linear and Angular Momenta

The balance of linear momentum is modified to take into account the possible contributions coming from the addition of mass through the boundary. We have two types of contributions. First, newly added material may have the same properties as the material at the same point. We call these types of sources *compliant*, using the terminology of [339]. Typically, these contributions balance out and do not appear in the local statement of the balance laws. Second, the new material may have sources that are different from the pre-grown material, having for instance locally a higher energy density than the surrounding tissue, or due to microscopic organization, a lower entropy. We call these sources *non-compliant* and we denote them with an overbar. They appear as extra contributions in the local statements. For instance, in the case of the balance of linear momentum for a grown material, we have

$$\frac{d}{dt} \int_{\Omega} \rho \mathbf{v} dv = \underbrace{\int_{\partial\Omega} \mathbf{T} \mathbf{n} da}_{\text{body and traction forces}} + \underbrace{\int_{\Omega} \rho \mathbf{b} dv}_{\text{compliant}} + \underbrace{\int_{\Omega} \rho \gamma \mathbf{v} dv}_{\text{compliant}} + \underbrace{\int_{\Omega} \bar{\mathbf{p}} dv}_{\text{non-compliant}}. \quad (13.16)$$

The compliant source is a direct result of the mass uptake. As the mass is added to the material, it carries a momentum that needs to be included in the overall balance of linear momentum. The non-compliant source $\bar{\mathbf{p}}$ is more delicate. It corresponds to other possible sources of linear momenta acting on the system due to growth. It can be used to model internal microscopic processes that would add momenta in the open system.

The use of the divergence theorem on the terms integrated over $\partial\Omega$ as well as the transport formula (11.97) lead to

$$\int_{\Omega} (\rho \dot{\mathbf{v}} + \dot{\rho} \mathbf{v} + \rho (\operatorname{div} \mathbf{v}) \mathbf{v}) dv = \int_{\Omega} (\operatorname{div} \mathbf{T} + \rho \mathbf{b} + \gamma \mathbf{v} + \bar{\mathbf{p}}) dv. \quad (13.17)$$

Inserting the expression for $\dot{\rho}$ from (13.4), applying the transport formula (11.97), and using the arbitrary nature of Ω , (13.17) simplifies to

$$\rho \dot{\mathbf{v}} = \operatorname{div}(\mathbf{T}^T) + \rho \mathbf{b} + \bar{\mathbf{p}}. \quad (13.18)$$

Again, using the slow-growth assumption, we set $\bar{\mathbf{p}} = \mathbf{0}$ and recover the usual balance of linear momentum

$$\rho \dot{\mathbf{v}} = \operatorname{div}(\mathbf{T}^T) + \rho \mathbf{b}. \quad (13.19)$$

The balance between change in angular momentum and applied torques with respect to the origin can be stated as

$$\begin{aligned}
\frac{d}{dt} \int_{\Omega} \rho \mathbf{x} \times \mathbf{v} \, dv = & \underbrace{\int_{\partial\Omega} \mathbf{x} \times (\mathbf{T} \cdot \mathbf{n}) \, da}_{\text{torques due to body and traction forces}} + \int_{\Omega} \rho \mathbf{x} \times \mathbf{b} \, dv \\
& + \underbrace{\int_{\Omega} \rho \gamma \mathbf{x} \times \mathbf{v} \, dv}_{\text{compliant}} + \underbrace{\int_{\Omega} \mathbf{x} \times \bar{\mathbf{p}} \, dv}_{\text{non-compliant}}. \quad (13.20)
\end{aligned}$$

Since the non-compliant linear momentum source $\bar{\mathbf{p}}$ enters the angular momentum balance, we require no additional non-compliant angular momentum source. We assume again that the material is non-polar and that there are no sources of internal torques acting on the system, compliant or otherwise. The transport and localization procedure leads to the standard condition that, even in the presence of growth fluxes, the Cauchy stress tensor $\mathbf{T}$ is symmetric:

$$\mathbf{T}^T = \mathbf{T}. \quad (13.21)$$

13.4 Energy Balance

The energy balance is the first law of thermodynamics. It relates the change in the total energy of the body and contributions from mechanical power, heat, and extra sources of energy due to new material entering the system that can be either compliant or non-compliant:

$$\frac{d}{dt} (\mathcal{E} + \mathcal{K}) = \mathcal{P} + \mathcal{Q} + \mathcal{S} + \bar{\mathcal{S}}, \quad (13.22)$$

where the total energy has been decomposed into an internal energy $\mathcal{E}$ (i.e., elastic and chemical energy) and a kinetic energy $\mathcal{K}$. The mechanical power $\mathcal{P}$ is the work per unit time that the body is exposed to through volumetric forces $\mathbf{b}$ and surface tractions $\mathbf{t}$. The heating $\mathcal{Q}$ is composed of a volumetric heat source r (for radiation) and a surface flux $\mathbf{q}$ called the Fourier heat flux. In addition, we have the compliant energy contribution $\mathcal{S}$ and the non-compliant contribution $\bar{\mathcal{S}}$ due to non-compliant energy source density $\bar{\varepsilon}$ and the power associated with the non-compliant source of linear momentum $\bar{\mathbf{p}}$. The energy balance on an arbitrary domain Ω reads

$$\begin{aligned}
\frac{d}{dt} \underbrace{\int_{\Omega} \rho \left(\varepsilon + \frac{1}{2} |\mathbf{v}|^2 \right) \, dv}_{\mathcal{E}(\Omega) + \mathcal{K}(\Omega)} = & \underbrace{\int_{\Omega} \rho \mathbf{b} \cdot \mathbf{v} \, dv + \int_{\partial\Omega} \mathbf{n} \cdot \mathbf{T} \mathbf{v} \, da}_{\mathcal{P}(\Omega)} \\
& + \underbrace{\int_{\Omega} \rho r \, dv + \int_{\partial\Omega} \mathbf{q} \cdot \mathbf{n} \, da}_{\mathcal{Q}(\Omega)}
\end{aligned}$$

$$+ \underbrace{\int_{\Omega} \gamma \left(\varepsilon + \frac{1}{2} |\mathbf{v}|^2 \right) dv}_{\mathcal{S}: \text{compliant}} + \underbrace{\int_{\Omega} (\bar{\varepsilon} + \bar{\mathbf{p}} \cdot \mathbf{v}) dv}_{\bar{\mathcal{S}}: \text{non-compliant}}. \quad (13.23)$$

A tedious, but otherwise uneventful, process of transport and localization using the other balance laws leads to the local statement of energy balance

$$\rho \dot{\varepsilon} = \text{tr}(\mathbf{TL}) + \rho r - \text{grad } \mathbf{q} \cdot \bar{\varepsilon}, \quad (13.24)$$

where $\mathbf{L}$ is the velocity gradient tensor introduced in Section 11.1.8. We observe again that apart from possible non-compliant sources of energy, this balance is the one that we would expect for a non-growing material.

13.5 Imbalance of Entropy

For a non-growing medium, entropy typically measures the disorder induced by microscopic fluctuations, and entropy increases with disorder [390]. The second law of thermodynamics states that the rate of change of internal entropy of a system is larger than or equal to the flow of entropy transferred to that system. Locally, it implies that the change in entropy density (per unit mass), η , measuring the system's disorder is greater than the local entropy transfer given by the heat supply $\mathcal{Q}$, defined in the previous section, divided by the temperature $\theta > 0$. In the case of a growing material, we also need to include the non-compliant energy source $\bar{\varepsilon}$ and new possible *non-compliant entropy* contribution $-\bar{h}$ which takes into account both non-compliant entropy fluxes and sources [737]. This law, known as the *Clausius–Duhem inequality* takes the form

$$\frac{d}{dt} \int_{\Omega} \rho \eta dv \geq \underbrace{\int_{\Omega} \frac{\rho r}{\theta} dv - \int_{\partial\Omega} \frac{\mathbf{q} \cdot \mathbf{n}}{\theta} da}_{\text{entropy due to heat supply}} + \underbrace{\int_{\Omega} \gamma \eta dv}_{\text{compliant}} + \underbrace{\int_{\Omega} \frac{\bar{\varepsilon} - \bar{h}}{\theta} dv}_{\text{non-compliant}}. \quad (13.25)$$

The local version of the Clausius–Duhem inequality in the current configuration, assuming all fields are smooth [526, p. 186], is given by

$$\rho \dot{\eta} \geq \frac{\rho r}{\theta} - \text{div} \left(\frac{\mathbf{q}}{\theta} \right) + \frac{\bar{\varepsilon} - \bar{h}}{\theta}. \quad (13.26)$$

The entropy balance together with the energy balance can be used to derive another inequality by applying a Legendre transform to the specific free-energy density function

$$\psi = \varepsilon - \theta \eta. \quad (13.27)$$

In the current configuration, this inequality reads

$$\rho \dot{\psi} \leq \text{tr}(\mathbf{T}\mathbf{L}) - \rho \eta \dot{\theta} - \frac{1}{\theta} \mathbf{q} \cdot \text{grad}(\theta) + \bar{h}, \quad (13.28)$$

where $\mathbf{L} = \dot{\mathbf{F}}\mathbf{F}^{-1}$ is the velocity gradient tensor. We can rewrite this inequality by introducing an important quantity, the *dissipation* Γ as

$$-\theta \Gamma = \rho(\dot{\psi} + \eta \dot{\theta}) \leq \text{tr}(\mathbf{T}\mathbf{L}) - \frac{1}{\theta} \mathbf{q} \cdot \text{grad}(\theta) + \bar{h} \leq 0. \quad (13.29)$$

The term $\theta \Gamma$ represents the energy dissipation per unit volume. In the present context, a re-statement of the second law of thermodynamics, is the *dissipation inequality*, that states that the dissipation in the system is positive, that is, $\Gamma \geq 0$.

13.6 Elastic Constitutive Laws

The imbalance of entropy can be used in a general context to derive constitutive laws between stresses and strains. This can be done systematically by using the *Coleman–Noll procedure* [222] of rational thermodynamics. We will use this procedure in the next chapter to extract information on both the growth laws and the elastic constitutive laws.

Here, we simply assume that the material is hyperelastic and isothermal when considered on elastic time scales defined in Section 11.3. Therefore, using both the hyperelastic and the slow-growth assumptions, there exists an internal energy density that depends only on the elastic deformation tensor $\mathbf{A}$, so that

$$\epsilon = \frac{1}{J_A \rho} W, \quad (13.30)$$

where, as before, $W = W(\mathbf{A})$ is the internal strain-energy density per unit volume (of the virtual state). That is, the material is hyperelastic *with respect to* the virtual state viewed as an unstressed configuration. The stresses are then given by

$$\mathbf{T} = J_A^{-1} \mathbf{A} \frac{\partial W}{\partial \mathbf{A}} - p \mathbf{1}. \quad (13.31)$$

If the material is elastically incompressible, $J_A = 1$ and p is the hydrostatic pressure; for an elastically compressible material $p = 0$. All kinematic quantities associated with $\mathbf{F}$ such as the invariants, the principal stretches, and the elastic strain tensors, needed to obtain different explicit forms of this constitutive law, can now be written in terms of the elastic deformation tensors $\mathbf{A}$ instead of $\mathbf{F}$.

13.7 Summary of Volumetric Morphoelasticity

In our approach to growth, we start with an *initial* unstressed configuration $\mathcal{B}_0$. We assume that a volume element at any material point is free to grow. Locally, this growth process transforms an infinitesimal sphere into an infinitesimal ellipsoid. The size and orientation of this ellipsoid is fully specified by the growth deformation tensor $\mathbf{G}$. The application of $\mathbf{G}$ transforms the initial configuration into a *virtual state* $\mathcal{V}$. This state is also unstressed and is used to compute the elastic strains that ensure both the integrity of the continuum body and the elastic stresses that balance the applied body loads and the boundary conditions. These strains are defined through an elastic deformation tensor $\mathbf{A}$ that maps the virtual state to the *current configuration* $\mathcal{B}$. The deformation gradient tensor $\mathbf{F}$ that defines the local deformation between $\mathcal{B}_0$ and $\mathcal{B}$ is therefore decomposed as $\mathbf{F} = \mathbf{A}\mathbf{G}$.

In the current configuration $\mathcal{B}$, the balances of mass, linear and angular momenta lead to the usual Cauchy equations for the Cauchy stress tensor $\mathbf{T}$ and mass density ρ . The stresses are related to the elastic strains for a hyperelastic material from a strain-energy function W . Altogether, we have

$$\mathbf{F} = \mathbf{A}\mathbf{G} \quad (13.32)$$

$$\dot{\rho} + \rho \operatorname{div} \mathbf{v} = \rho \gamma, \quad (13.33)$$

$$\rho \dot{\mathbf{v}} = \operatorname{div}(\mathbf{T}) + \rho \mathbf{b}, \quad (13.34)$$

$$\mathbf{T}^\top = \mathbf{T}, \quad (13.35)$$

$$\mathbf{T} = J_A^{-1} \mathbf{A} \frac{\partial W}{\partial \mathbf{A}} - p \mathbf{1}, \quad (13.36)$$

where $\mathbf{b}$ is the body force density, ρ the density, $\mathbf{v}$ the velocity, and $J_A = \det(\mathbf{A})$. As before, $J_A = \det(\mathbf{A}) = 1$ for an incompressible material and $p = 0$ for a compressible material.

The key difference with the classic theory of elasticity is that geometry and elasticity are divorced. That is, the stresses are computed with respect to the elastic deformation tensors $\mathbf{A}$ and not the entire deformation tensor $\mathbf{F}$. The constitutive equations give $\mathbf{T}$ as a function of $\mathbf{A}$ which can be rewritten as a function of $\mathbf{F}\mathbf{G}^{-1}$ and Equation (13.34) can be solved as usual with respect to the initial or current coordinates.

Note that we still need to specify $\mathbf{G}$ constitutively. Before doing so, we consider a couple of examples where $\mathbf{G}$ is specified.

13.8 Simple Examples

13.8.1 A Growing Cuboid

To understand the steps involved in solving a problem of elastic growth, we first consider the simple problem of an isotropic incompressible cuboid constrained between two blocks and allowed to grow along its axis as shown in Figure 13.1. That is, the growth deformation transforms a cuboid initially of length L_0 into a longer one of length L and the boundaries along this axis prevent this expansion so that its length remains $l = L_0$. This growth process is compatible and does not generate residual stress. Therefore, it could easily be solved by the methods of nonlinear elasticity following the steps of Section 11.8.1 by considering the equivalent problem of compressing a block of length L to a block of length l . The purpose here is to understand the steps involved in the multiplicative decomposition.

Using the same Cartesian basis $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$ for the three configurations and assuming uniform growth in the $\mathbf{e}_3$ -direction, the three deformation tensors are

$$[\mathbf{F}] = \text{diag}(\lambda_1, \lambda_2, \lambda_3), \quad [\mathbf{A}] = \text{diag}(\alpha_1, \alpha_2, \alpha_3), \quad [\mathbf{G}] = \text{diag}(1, 1, \gamma^2), \quad (13.37)$$

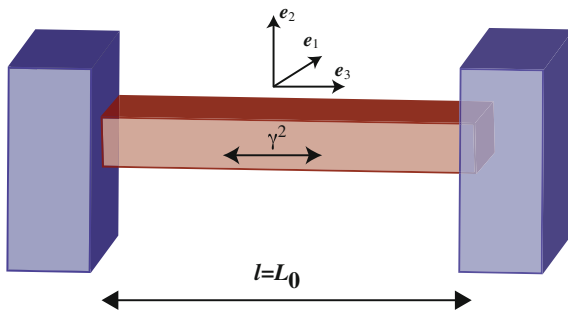
where $\gamma^2 = L/L_0$. The multiplicative decomposition implies that $\lambda_{1,2} = \alpha_{1,2}$ and $\lambda_3 = \alpha_3 \gamma^2$. Since the block is isotropic and there is no load applied in the directions normal to growth, we have $\alpha_1 = \alpha_2 = \alpha$ which together with the incompressibility condition, $\det(\mathbf{A}) = 1$, implies $\alpha_3 = 1/\alpha^2$. The rigid boundary condition along the $\mathbf{e}_3$ -axis gives $\lambda_3 = 1$, that is, $\alpha = \gamma$.

The Cauchy equations for the Cauchy tensor $[\mathbf{T}] = \text{diag}(t_1, t_2, t_3)$ are identically satisfied since the deformation is homogeneous. The constitutive equations simplify to

$$t_1 = \alpha W_1(\alpha, \alpha, 1/\alpha^2) - p, \quad (13.38)$$

$$t_2 = \alpha W_2(\alpha, \alpha, 1/\alpha^2) - p, \quad (13.39)$$

Figure 13.1 Growth of a block constrained between two plates. Stress will develop in the growth process.



$$t_3 = \frac{1}{\alpha^2} W_3(\alpha, \alpha, 1/\alpha^2) - p, \quad (13.40)$$

where $W_i = \partial_{\alpha_i} W$. Since t_1 and t_2 are constant and vanish at the boundary, we have $p = \alpha W_2(\alpha, \alpha, 1/\alpha^2)$ and the stress generated during growth is

$$t_3 = \frac{1}{\gamma^2} W_3(\gamma, \gamma, 1/\gamma^2) - \gamma W_2(\gamma, \gamma, 1/\gamma^2). \quad (13.41)$$

If we introduce the auxiliary function $\widehat{W}(\gamma) = W(\gamma, \gamma, 1/\gamma^2)$, we obtain

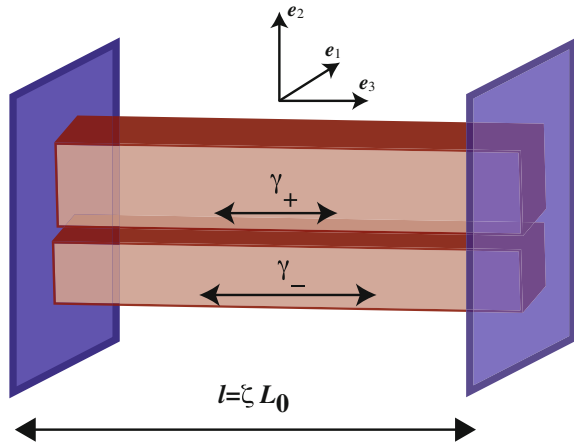
$$t_3 = -\frac{\gamma}{2} \partial_\gamma \widehat{W}. \quad (13.42)$$

13.8.2 Two Growing Cuboids

Next, consider a block made out of two layers characterized by a strain-energy function $W_\pm$ and growing independently with $\gamma_{3,\pm} = \gamma_\pm$ as sketched in Figure 13.2. A similar example has been considered in [423]. Initially, the layers have the same width, height, and length and they can slide along each other apart in the $\mathbf{e}_3$ -direction where they are constrained by two lubricated platens that can move with the deformation. The problem is then to find the stretch $\zeta = \lambda_3$ of this sandwich structure. Following the same steps as above but without the restriction $\zeta = 1$, we find that the axial stress in each layer is

$$t_{3,\pm} = -\left(\frac{\alpha}{2} \partial_\alpha \widehat{W}_\pm\right)\Big|_{\alpha=\sqrt{\gamma_\pm/\zeta}}. \quad (13.43)$$

Figure 13.2 Growth of a two-layer block. Each block has different growth and is attached to the other one so that their lengths remain equal in the current configuration.



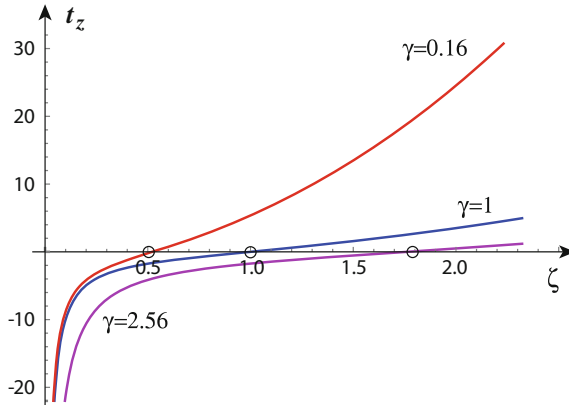


Figure 13.3 Stress-strain curves for the growing structure shown in Figure 13.2. Here, both strain-energy functions are neo-Hookean with $\mu_{\pm} = 1$ and $\gamma = \gamma_+$, $\gamma_- = 1$.

The total stress exerted on the platens is given by

$$t_z = \frac{\alpha_+^2 t_{3,+} + \alpha_-^2 t_{3,-}}{\alpha_+^2 + \alpha_-^2}. \quad (13.44)$$

Examples of the total stress t_z as a function of ζ are shown in Figure 13.3 where it is observed that a residual stress is obtained for $t_z = 0$. The extension of the structure in the absence of stress $t_z = 0$ leads to the condition

$$\gamma_+ t_{3,+} + \gamma_- t_{3,-} = 0, \quad (13.45)$$

that can be solved for ζ for a given strain-energy function. In this deformation the cuboids are residually stressed due to their connection with the platens, one is in compression and the other one is in tension.

We can generalize this problem to a block with a continuous growth distribution $\gamma = \gamma(Z_0)$ in the $\mathbf{e}_3$ -direction and such that stresses are transmitted only through the interaction of the platens, that is, by neglecting all possible shear stresses in the block. In this case, the same steps lead to the following equation for ζ

$$0 = \int dZ_0 \gamma^3 (\partial_\alpha \widehat{W})|_{\alpha=\gamma/\sqrt{\zeta}}. \quad (13.46)$$

13.8.3 A Growing Ring

A detailed analysis of the growth of a cylindrical shell is given in Chapter 16. Here, we consider the simpler case of the incompressible isotropic growing ring. The growing ring is a section of a cylindrical shell (a tube) that is only allowed to deform in a plane perpendicular to its axis. We assume that it can only grow in the radial and hoop directions, as depicted in Figure 12.8. In this simple case, assuming that there is no deformation in the axial direction, the deformation from the initial configuration $\mathcal{B}_0$ to the current configuration $\mathcal{B}$ is given by the specialization of (11.196) with $\zeta = 1$. This deformation defines, in cylindrical coordinates, the deformation gradient

$$[\mathbf{F}] = \text{diag}(r'(R_0), r/R_0, 1). \quad (13.47)$$

The elastic strain and the growth tensors are assumed to be diagonal:

$$[\mathbf{A}] = \text{diag}(\alpha_r, \alpha_\theta, 1), \quad [\mathbf{G}] = \text{diag}(\gamma_r(R_0), \gamma_\theta(R_0), 1). \quad (13.48)$$

As described in Section 12.4, γ_r corresponds to radial growth, and γ_θ to hoop growth. Since $\mathbf{F} = \mathbf{AG}$, we have

$$\alpha_r = \frac{r'}{\gamma_r}, \quad \alpha_\theta = \frac{r}{R_0 \gamma_\theta}. \quad (13.49)$$

Material incompressibility implies $\det \mathbf{A} = 1$, that is, $\alpha_r \alpha_\theta = 1$ which implies $r dr = R_0 g(R_0) dR_0$, that is,

$$r^2 = a^2 + 2 \int_{A_0}^{R_0} g(\rho) \rho d\rho, \quad (13.50)$$

where $g(R_0) = \det \mathbf{G} = \gamma_r \gamma_\theta$.

In the reference configuration, the equilibrium conditions have not been modified from those derived in Section 11.8.3. They are still given by the only non-vanishing Cauchy equation

$$\frac{dt_r}{dr} + \frac{1}{r}(t_r - t_\theta) = 0, \quad (13.51)$$

and the applications of the boundary condition

$$\int_a^b \frac{t_\theta - t_r}{r} dr = P, \quad (13.52)$$

where P is the internal pressure. The difficulty here is that the bounds of the integrals a and b are functions of the growth terms γ_i . It is therefore simpler to reformulate these integrals in the initial configuration. We first define

$$\tau(A_0, R_0; a) \equiv \int_{A_0}^{R_0} \frac{t_\theta - t_r}{r^2(R_0)} g(R_0) R_0 dR_0, \quad (13.53)$$

where $r(R_0)$ is given by (13.50). The inner radius a can then be found to find as a function of P by solving

$$\tau(A_0, B_0; a) = P. \quad (13.54)$$

We use the constitutive law

$$t_r = \alpha_r \frac{\partial W}{\partial \alpha_r} - p, \quad t_\theta = \alpha_\theta \frac{\partial W}{\partial \alpha_\theta} - p, \quad (13.55)$$

and the relationship

$$\alpha_r = \frac{R_0 \gamma_\theta}{r(R_0)}, \quad \alpha_\theta = \frac{r(R_0)}{R_0 \gamma_\theta}, \quad (13.56)$$

so that after using (13.55–13.56), Equation (13.54) is a definite integral on R_0 only, with a single unknown constant a that can be obtained for a given pressure P . Once a is known, the radial and hoop stresses are obtained as

$$t_r(R_0) = -P + \tau(A_0, R_0; a), \quad (13.57)$$

$$t_\theta(R_0) = t_r(R_0) + \alpha_\theta \frac{\partial W}{\partial \alpha_\theta} - \alpha_r \frac{\partial W}{\partial \alpha_r}. \quad (13.58)$$

13.8.3.1 Homogeneous but Anisotropic Growth

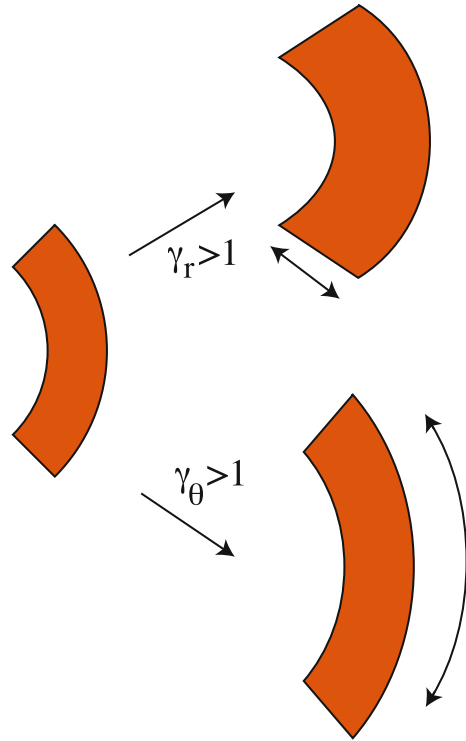
We consider first the case where γ_r and γ_θ are both constant as described in Section 12.4 and illustrated again in Figure 13.4. For illustration purposes, we assume that the material is neo-Hookean: It is characterized by the strain-energy function

$$W = \frac{\mu}{2}(\alpha_r^2 + \alpha_\theta^2 - 2), \quad (13.59)$$

with $\mu > 0$. The first problem is to compute the stress profile in the absence of load. This is done by explicitly integrating (13.57) and solving $t_r(A_0) = 0$ for the unknown a when $P = 0$ (Figure 13.4).

If growth is chosen to be transversely isotropic ($\gamma_r = \gamma_\theta$), no residual stress is created and the new ring is a dilation of the original one, that is, $r = \gamma_r R_0$. If, however, we consider anisotropic homogeneous growth ($\gamma_r \neq \gamma_\theta$), then residual stress is created as shown in Figure 13.5A where excess of radial growth with respect to hoop growth induces a compressive residual radial stress in the material. In terms of the hoop stress, the inner radius is in compression while the outer radius is in tension. Circumferential growth, or equivalently radial resorption, creates a tensile radial stress (not shown).

Figure 13.4 Growth of ring elements. A ring sector remains a ring sector when either grown through hoop and/or radial growth.



Next, we consider hoop stress in the material when $P < 0$ (internal pressure) as shown in Figure 13.5B. In the absence of growth, one observes a steep profile as a function of R_0 , whereas with suitable growth this profile flattens.

It was this simple, but crucial, observation that provided the first indication that residual stress could play an important role in physiology. Indeed, in arteries, the residual stress acts in the same way suggesting that differential growth in arteries might take place in order to reduce gradients of hoop stress preventing material failure associated with tissue separation [22, 208, 406].

The residual stress created through this homogeneous growth process can be visualized by cutting the ring, creating either an overlap (in the case of compressive hoop stress) or an opening (in the case of tensile hoop stress) as shown in Figure 12.9. Both cases lead to locally compatible strain tensors as discussed in Section 12.5.1.2. Therefore, these stress fields could have been computed by considering a sector of a ring, and by computing the stresses developed in the deformation necessary to close it into a ring. Nevertheless, the decomposition of the deformation into a growth process and an elastic process allows to obtain systematically the stresses and deformations generated through growth, within a single modeling framework.

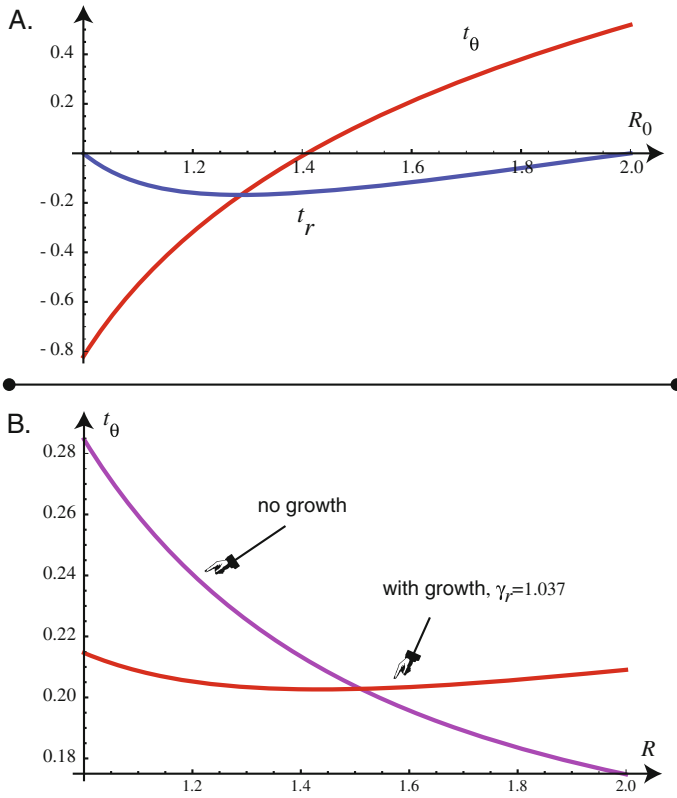


Figure 13.5 Residual stress due to growth. A. In the absence of loads ($P = 0$, $\gamma_r = 3$, $\gamma_\theta = 2$), radial and hoop growth result in a compressive radial stress and non-vanishing hoop stress. B. Under pressure ($P = 1/10$) and in the absence of residual stress ($\gamma_r = \gamma_\theta = 1$), large hoop stress gradients are observed. With appropriate growth ($\gamma_r = 1.037$, $\gamma_\theta = 1$), the hoop stress profile flattens out. In both cases $\mu = 1$ is chosen without loss of generality.

13.8.3.2 Non-homogeneous but Isotropic Growth

We now consider the possibility that the growth deformation is locally incompatible by choosing an isotropic but homogeneous growth profile: $\gamma_\theta = \gamma_r = \gamma$ with

$$\gamma = \frac{\gamma_b - \gamma_a}{B_0 - A_0}(R_0 - A) + \gamma_b, \quad \gamma_{a,b} > 0. \quad (13.60)$$

This choice corresponds to a simple model for the growth of a tissue where growth of a material element decays (or increases) linearly with respect to the initial radius. In this case, condition (12.47) is not satisfied and the residual stresses generated by the growth process could not be removed by a finite number of cuts. The computation

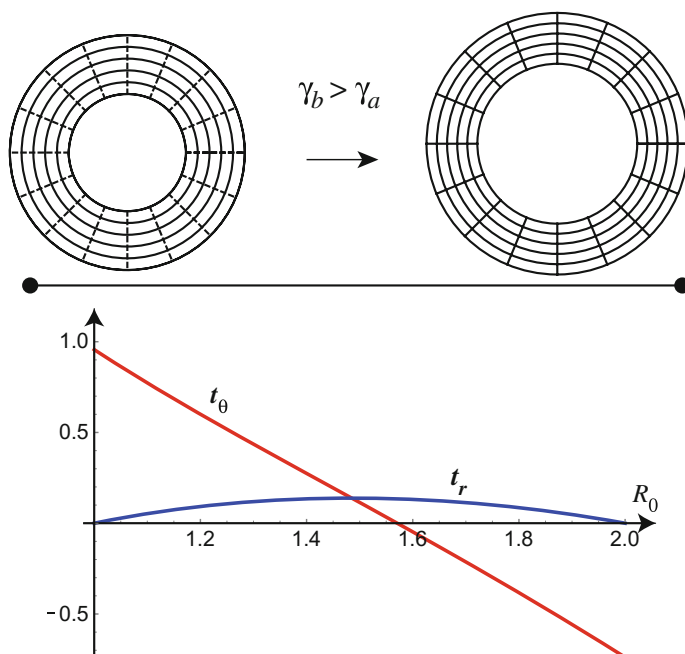


Figure 13.6 Homogeneous, non-uniform growth in a ring of radii $A_0 = 1$, $B_0 = 2$. Here, growth is larger on the outer surface $\gamma_a = 1$, $\gamma_b = 1.2$.

proceeds as before by solving $\tau(A_0, B_0; a) = 0$ for a and computing the stresses. As expected, this growth process for $\gamma_b \neq \gamma_a$ creates non-vanishing residual stresses as shown in Figures 13.6 and 13.7.

13.9 Mixture Models

Most of the emphasis in this monograph is on the growth and remodeling of a continuum composed of a single constituent. An example of an additional constituent is the fiber contribution, included as a single anisotropic contribution in the theory of morphoelastic materials. However, biological tissues and organs are much more complicated structures. The load-bearing components are composed of multiple proteins bathed in biological fluids subject to multiple diffusing fields such as small ions, oxygen, and glucose. Growth and remodeling is caused by the production and removal of constituents and are the direct consequences of biochemical reactions [409]. Therefore, if we wish to understand the relative effect of different constituents in the growth and remodeling of tissues, we need to take into account the contribution of all these constituents. We briefly review some mixture models.

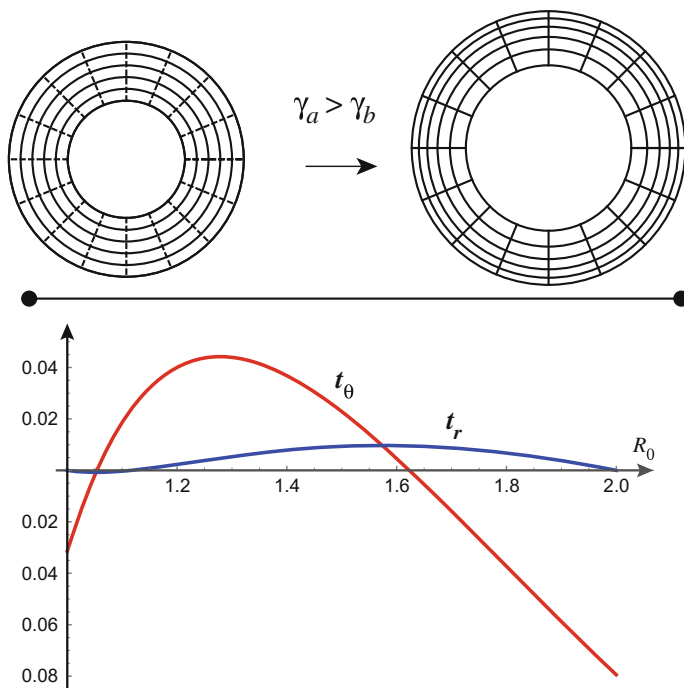


Figure 13.7 Homogeneous, non-uniform growth in a ring of radii $A_0 = 1$, $B_0 = 2$. Here, growth is larger on the inner surface $\gamma_a = 1.2$, $\gamma_b = 1$. Note the complex stress profile created by the incompatible growth.

13.9.1 Classical Mixture Theory

At the continuum level, a material composed of different constituents can be modeled by the *theory of mixtures*. This theory finds its origin in classical work of poroelasticity and multiple diffusion by Fick and Darcy and has been formalized by Truesdell [1250, 1252]. A mixture is seen as the weighted superposition of different constituents, all defined at each point of the domain. To build a theory, Truesdell uses three basic principles [538]:

1. All properties of the mixture must be mathematical consequences of the properties of the constituents;
2. So as to describe the motion of a constituent, we may virtually isolate it from the rest of the mixture, provided we allow properly for the actions of other constituents upon it;
3. The motion of the mixture is governed by the same equations as a single body.

This last assumption is important as it states that, even though the structure is heterogeneous at the microscale, it should be considered as a homogeneous material at the continuum level. In particular the mixture respects the traditional balance equations

for mass, linear and angular momenta, and energy. Therefore under a body force $\mathbf{b}$, it must obey

$$\frac{\partial \rho}{\partial t} + \operatorname{div}(\rho \mathbf{v}) = \rho \gamma, \quad (13.61)$$

$$\operatorname{div} \mathbf{T} + \rho \mathbf{b} = \dot{\mathbf{v}}, \quad (13.62)$$

where, as before, ρ is the mass density of the homogenized mixture, $\mathbf{v}$ its velocity, and $\mathbf{T}$ the Cauchy stress tensor. If we consider an open system, we allow for the possibility of an overall mass increase or decrease through γ as described in Section 13.2. Similarly, the N constituents of the mixture obey the same balance laws individually. Using a Greek superscript to denote each component, we have [638]:

$$\frac{\partial \rho^\alpha}{\partial t} + \operatorname{div}(\rho^\alpha \mathbf{v}^\alpha) = \rho^\alpha \gamma^\alpha, \quad \alpha = 1, \dots, N, \quad (13.63)$$

$$\operatorname{div} \mathbf{T}^\alpha + \rho^\alpha (\mathbf{b}^\alpha - \dot{\mathbf{v}}^\alpha) = \mathbf{p}^\alpha, \quad \alpha = 1, \dots, N, \quad (13.64)$$

where for each constituent, ρ^α is the density, $\mathbf{v}^\alpha$ denotes the velocity, and $\mathbf{b}^\alpha$ the body force acting on the constituents.

The exchange of mass and linear momentum between the different constituents is contained in the term γ^α and $\mathbf{p}^\alpha$, respectively. These terms must be specified constitutively. Note here that the upper dot denotes the material derivative taken with respect to time as measured by an observer moving with constituent α [636],

$$\rho = \sum_{\alpha} \rho^\alpha, \quad \rho \mathbf{v} = \sum_{\alpha} \rho^\alpha \mathbf{v}^\alpha, \quad \mathbf{T} = \sum_{\alpha} \mathbf{T}^\alpha. \quad (13.65)$$

Despite great advances in the thermodynamics and mechanics of mixtures [118, 346, 503], a number of difficult fundamental and computational problems remain. For instance, it is still not clear that the total stress can be simply decomposed into the sum of stresses or, rather, weighted by the volume fraction [340]. Similarly, there is no definite way to split the boundary tractions between the different constituents: Without detailed knowledge of the constituents, how should the external load be distributed among constituents? Another key issue is to specify the relative contribution of each constituent to mass and linear momentum exchanges. Without a model for the microstructure, there is no systematic way to derive constitutive laws for the interaction between constituents. While a general theory is still lacking, there have been a number of successful applications of the theory to soft tissues and other biological problems.

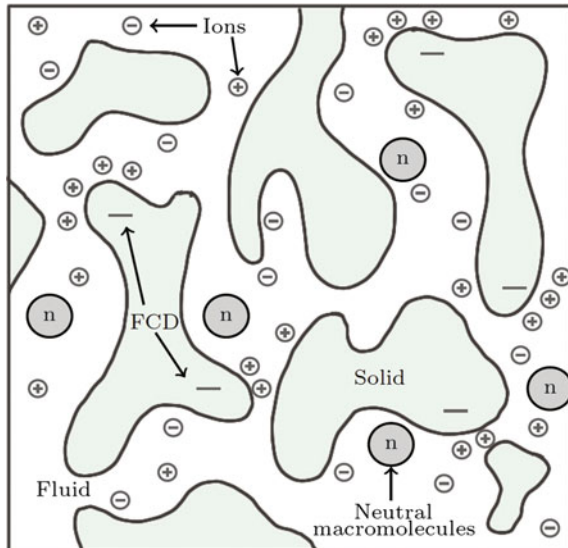
The simplest two-constituent models for soft tissue incorporate just solid and fluid constituents: a porous, elastic solid matrix (representing the extracellular matrix and cells), and an interpenetrating fluid phase (representing interstitial fluid). When the solid constituent is elastic, there are two formulations of these models: poroelastic and mixture-based. Poroelastic models were first developed in the field of soil mechanics and in particular by Biot and Terzaghi [101]. These poroelastic models

were originally derived from constitutive assumptions about the coupling between applied stress, pore pressure, and volume changes for a fluid filled, porous, elastic medium, but can be obtained either through homogenization theory [151, 1027], or from mixture theory by assuming that the mixture is saturated and both solid and fluid constituents are intrinsically incompressible [1165].

Two-constituent models were developed to model the behavior of articular cartilage [245, 596, 821, 919] and gel-like tissues [595]. An important generalization of these models takes into account the contribution of charged electrolytes in dilute concentrations, leading to three or more constituents [519, 650, 749, 841, 1201]. Such models are referred to as *triphasic* or *quadriphasic* models. They typically include an extra net charge attached to the solid phase, a *fixed charge density*, which may be relevant to biological tissues when the extracellular matrix can block the motion of large negatively charged biomolecules as sketched in Figure 13.8. These models allow for the coupling between tissue deformation, fluid flux, and solute movement due to both osmotic and hydrostatic pressure gradients. The case of a mixture with a single growing solid phase with application to cartilages has been considered by Klisch and co-workers [707, 708, 710, 711].

The original triphasic model [749] considered a mixture of a linear elastic solid, a saturating fluid and species of positive and negative ions. To close the model, constitutive laws must be chosen for the drag between constituents; typically solid-fluid drag is assumed to follow Darcy's law and fluid-solute drag satisfies Fickian diffusion while other interactions are neglected. Apart from cartilages, biphasic, triphasic, and quadriphasic models have also been used to investigate the swelling of brain tissues [297, 327, 762, 763, 931].

Figure 13.8 A quadriphasic model is composed of a solid phase, fluid phase, and solutes (positive (+) and negative (−) ion species, and non-permeating solutes (n)). Some components of the solid phase have a net negative charge (fixed charge density), that induces ion concentrations to satisfy charge neutralization (adapted from [762]).



In tissue engineering, a typical method to grow new tissue is to use a porous scaffold seeded with cells and continuously fed with nutrients. Assuming that the stresses generated by the solid constituents are sufficiently small, the theory of mixtures (usually referred to as *multiphase modeling*) can be used to model the overall growth of the composite by coupling a fluid and cells constituents [971]. These reduced models naturally lend themselves to analytic studies and computational simulations [972, 1279]. The same approach has been used to model tumor [157, 1099] and bone growth [781].

13.9.2 *Constrained Mixture Theory*

The previous applications mostly focus on the fluid and solute constituents flowing and diffusing through a solid matrix. In many soft tissues the solid, load-bearing, structure is itself composed of different constituents. For instance, it is known that the response of arteries under loads is due to muscle cells, elastin proteins, and different collagen molecules. If we want to know how residual stress arises through the interaction, production, and removal of these different components, they must be followed individually. For solid constituents, an additional problem arises: Each new constituent may have a different reference configuration. As new fibers are added to the system, they may be added either without stresses or with a certain level of stress to match the existing stress in the system. Therefore, the reference configuration of a certain fraction of a constituent added at a certain time must be tracked through the evolution of the system, as sketched in Figure 13.9. Essentially, a multiplicative decomposition of the deformation gradient for each constituent and for each time must be performed. However, since the focus is now mostly on the solid phase, the theory of mixture can be simplified by assuming that all solid phases have the same velocity. This *constrained mixture theory*, put forward by Humphrey, Rajagopal and co-workers [638–641, 1271], is particularly relevant to explore growth and remodeling in collagen-rich tissues in which there is a continual turnover of collagen, such as arteries, ligaments, and tendons [447, 448]. One of the difficulties of this approach is that it becomes rapidly analytically intractable as even the simplest one-dimensional examples require a full numerical approach and dedicated finite-element methods must be developed [255].

From a mathematical point of view, the constrained mixture theory can be seen as the generalization of the multiplicative decomposition to a case where the solid is composed of a finite number of constituents each described by a different decomposition at each point in the domain and at each time in the evolution of the system. The overall stress at any given point is therefore not only a sum over all constituents but also an integral over the entire history of each constituent weighted by a kernel that describes the removal and addition of material with a given state of stress [1055, 1056]. Therefore, mixture theory is not an alternative to multiplicative decomposition but a generalization to multiple evolving constituents, each of which must be described by a different reference configuration for each time. If the rules of pro-

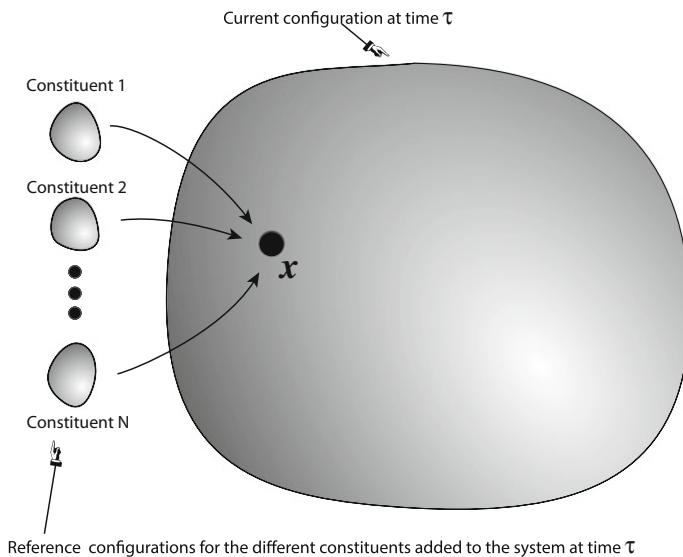


Figure 13.9 In a constrained mixture theory, each solid constituent has a different reference configuration at each time τ at which they are added to the system. For growth and remodeling, constrained mixture theory accounts for different properties of the different constituents.

duction and removal of each constituents, their interactions, and the level of stress at which they are produced can be fully elucidated through dedicated experiments, constrained mixture theory holds the promise to characterize fully the intricate relationships between constituents that leads to homeostasis and pathology. The development of such a theory represents a formidable challenge as these rules are typically not known even for a single constituent.

Chapter 14

Evolution Laws and Stability



The growth tensor adds a kinematic descriptor to the theory of elasticity. Therefore, it requires a corresponding set of constitutive laws. Since, we think of growth as a dynamical process, we refer to these laws as *evolution laws*. The prescription of evolution laws for growth, in particular in their interaction with the physical environment, is a fundamental problem of biology and, mostly an open field of research. Within our framework, the question is to specify the dynamics of the growth tensor $\mathbf{G}$ in terms of other biological or physical quantities.

These laws could be dictated by the system's ability to provide new material, be a function of the available nutrient, or be mediated by stresses acting on the system. Formally, we can write an equation for the relative growth rate:

$$\dot{\mathbf{G}}\mathbf{G}^{-1} = \mathcal{G}(\mathbf{T}, \mathbf{F}, \mathbf{G}, \boldsymbol{\mu}; t, \mathbf{x}, \mathbf{X}_0), \quad (14.1)$$

where the function $\mathcal{G}$ is a function of the stress tensor, the geometric deformation $\mathbf{F}$, the growth tensor $\mathbf{G}$ itself, the initial or current position, or any other chemical, biochemical, or physical fields $\boldsymbol{\mu}$.

Before we study the properties of the growth tensor and discuss simple growth laws, it is of interest to review the various proposals for the functional form of the relative growth rate.

- **Constant growth.** The simplest choice for the tensorial function $\mathcal{G}$ is to take it as a constant in time. If we further assume that it is constant in space in a given coordinate system, analytical results can be obtained [80, 196, 709] and the residual stress can be computed. In the theory of material defects, the choice of a constant tensor $\mathbf{G}$ is equivalent to the problem of specifying constant *eigenstrains* [925, 1356, 1357]. These *pre-strains* are also known in the literature as *initial strains* [722], *inherent strains* [1266], and *transformation strains* [348].
- **Position dependent growth.** Many growth processes depend on the location in the material. This effect is sometimes referred to as *differential growth* to indicate that some parts of a tissue grow faster than others. In morphoelasticity, it implies that $\mathbf{G}$ is a function of either $\mathbf{X}_0$ or $\mathbf{x}$ [463, 464]. Both situations are of interest. In the first case, growth is a function of the material position $\mathbf{X}_0$ in the initial configuration and this dependence assumes that the material is made out of points that grow at different rates and keep growing differentially as time goes by. In the second case, the ability of a group of cells to grow depends on its location $\mathbf{x}$ in space at any given time. This is the case, for instance, when cell reproduction depends on the availability of nutrients that diffuse through the boundary. At any given time, the amount of nutrients may be described by the distance to the boundary as in the case in the spheroid growth studied in Section 4.3.2.
- **Stress-dependence.** As discussed in the main Introduction, it has been recognized experimentally and theoretically in many systems, such as aorta, muscles and bones, that one of the main biomechanical regulators of growth is stress [409, 627, 1054, 1091, 1206, 1208, 1212]. It has even been suggested that stresses on cell walls play the role of a pacemaker for the collective regulation of tissue growth [1154]. Accordingly, in these systems, the growth rate tensor should be a function of the Cauchy stress tensor, which could also vary according to the position of tissue elements in the reference configuration. The study of the coupling between stress and growth remains largely unexplored and only simple functional forms have been proposed [409].

Before proposing possible forms for the evolution laws, we discuss first the basic properties of the growth tensor.

14.1 Symmetry of the Growth Tensor

In many problems, it is useful to restrict the form of the growth tensor. Similar to the decomposition used to describe material symmetries, we can use different tensorial forms to describe growth processes occurring with a prescribed symmetry. We first restrict our attention to the case of isotropic materials with a strain-energy function $W = W(\mathbf{A})$. There is an ambiguity in the multiplicative decomposition: If $\mathbf{F}$ is known, the elastic and growth tensors $\mathbf{A}$ and $\mathbf{G}$ are not uniquely prescribed. Indeed, if $\mathbf{A}$ and $\mathbf{G}$ are such that $\mathbf{F} = \mathbf{A}\mathbf{G}$ then the tensors

$$\tilde{\mathbf{A}} = \mathbf{A}\mathbf{R}, \quad \text{and} \quad \tilde{\mathbf{G}} = \mathbf{R}^T \mathbf{G}, \quad \mathbf{R} \in O(3) \quad (14.2)$$

also provide a possible decomposition since $\mathbf{F} = \tilde{\mathbf{A}}\tilde{\mathbf{G}}$.

Using the polar decomposition theorem discussed in Section 11.1.7, we can decompose $\mathbf{G} = \mathbf{R}_G \mathbf{U}_G$ where $\mathbf{U}_G$ is a symmetric tensor and $\mathbf{R}_G$ is a proper orthogonal tensor. For isotropic materials, the energy density satisfies $W(\mathbf{A}) = W(\mathbf{A}\mathbf{R})$ for any proper orthogonal tensor $\mathbf{R}$, and we have

$$\begin{aligned} W(\mathbf{A}) &= W(\mathbf{F}\mathbf{G}^{-1}) \\ &= W(\mathbf{F}\mathbf{U}_G^{-1}\mathbf{R}_G^T) \\ &= W(\mathbf{F}\mathbf{U}_G). \end{aligned} \quad (14.3)$$

Therefore, we conclude that $W(\mathbf{F}\mathbf{G}^{-1}) = W(\mathbf{F}\mathbf{U}_G)$. That is, the elastic energy of a growing isotropic material only depends on the symmetric part of the growth tensor. Note that this property does not hold for anisotropic materials. In that case, even if the deformation gradient can be decomposed into an elastic deformation tensor and a symmetric growth tensor, the elastic energy will depend on the particular choice of the rotation matrix.

The non-uniqueness of the multiplicative decomposition has been discussed at length in the context of finite strain plasticity [176, 933] and is often cited as an argument against using this approach for the modeling of physical phenomena. Instead, we view this ambiguity as a possible gauge that allows us to restrict the form of the growth tensor by choosing it to be symmetric [585]. Within this class, we further characterize different types of growth laws [733, 811, 873], following similar descriptions in elasto-plasticity [120].

- **Orthotropic growth.** A rather useful and general way to describe growth is to identify two directions in which growth can take place differentially. That is, in the initial configuration, we identify two unit vectors γ_1 and γ_2 and introduce the particular, but rather large, class of growth tensors

$$\mathbf{G} = g_0 \mathbf{1} + (g_1 - 1)\gamma_1 \otimes \gamma_1 + (g_2 - 1)\gamma_2 \otimes \gamma_2, \quad (14.4)$$

where g_0 represents the isotropic contribution to the growth process and g_1, g_2 its anisotropic contributions. Note that, in this description, we are using the same vectors γ_i in both the initial and virtual states. The advantage of such a representation is that it reduces the number of growth descriptors to three functions for the increase in volume and two unit vectors for the directions in which growth takes place anisotropically. For semi-inverse problems with a diagonal deformation gradient in a given set of coordinates, this particular form is suitable for analytic treatment. Indeed, a diagonal growth tensor in the same set of coordinates leads to an anelastic system that can be solved explicitly for all isotropic strain-energy functions.

- **Transversely isotropic growth.** In transverse isotropic growth, we assume that, locally, growth takes place isotropically in the directions normal to a unit vector

γ so that

$$\mathbf{G} = g_0 \mathbf{1} + (g_1 - 1) \gamma \otimes \gamma. \quad (14.5)$$

The growth stretch in the direction γ is obtained by applying the growth tensor on γ , that is,

$$\mathbf{G}\gamma = (g_0 + g_1 - 1)\gamma. \quad (14.6)$$

This growth stretch shows explicitly the contribution of both isotropic and anisotropic expansions in that direction, while the growth stretch in a direction normal to γ is just g_0 . This description of growth is particularly useful for fiber-reinforced systems with growth along the fibers. In this case, γ can be chosen to coincide with the fiber direction. The determinant of $\mathbf{G}$ is

$$J_G = g_0^2(g_1 + g_0 - 1), \quad (14.7)$$

and, with the prescription $J_G \neq 0$, its inverse can be directly computed from the Sherman–Morrison formula [1146]:

$$\mathbf{G}^{-1} = g_0^{-1} \mathbf{1} - \frac{(g_1 - 1)}{g_0(g_1 + g_0 - 1)} \gamma \otimes \gamma. \quad (14.8)$$

- **Pure fiber growth.** If we further restrict growth along a single fiber we obtain

$$\mathbf{G} = \mathbf{1} + (g - 1) \gamma \otimes \gamma, \quad (14.9)$$

and following the previous argument we can identify γ with the growth stretch in the γ -direction. This description of growth is particularly useful for describe the growth of cardiac and skeletal muscle fibers [449, 450].

- **Area growth.** The particular case of in-plane growth obtained as a reduction of (14.5) is interesting as it provides a simple characterization for problems of growing plates and membranes [591, 1014] and is given by

$$\mathbf{G} = \sqrt{g} \mathbf{1} + (1 - \sqrt{g}) \gamma \otimes \gamma. \quad (14.10)$$

By taking g different from the identity only in a small layer near the boundary and γ as the normal vector to the boundary, this particular form for the growth tensor is a suitable model for growing boundaries.

- **Isotropic growth.** The simplest nontrivial form for the growth tensor is to take it as a multiple of the identity, that is,

$$\mathbf{G} = g \mathbf{1}, \quad (14.11)$$

and we have $J_G = g^3$ representing the isotropic change of a volume element. In this case, the growth function g can be related directly to the growth rate γ through (13.9), which for constant density reads simply

$$\dot{g} = \frac{\gamma}{3}g. \quad (14.12)$$

We further study this special case in connection to gel swelling in the next section.

14.2 Isotropic Growth and Gel Swelling

The simplest growing materials are polymeric gels. Polymeric hydrogels are cross-linked, hydrophilic polymer networks. When mixed with water, they can exhibit large volumetric swelling in response to different chemical and physical stimuli. These gels can be used as microfluidic actuators as well as scaffolds for engineered tissues [325, 581, 999]. They have also been used to study pattern formation in growing and shrinking materials as they display a variety of interesting shapes following buckling-type instabilities [115, 116, 839, 1220, 1221]. Most gels are isotropic due to the random nature of the network and, as a material, they behave elastically before rupture. They are also mostly incompressible due to their high water content. Despite the fact that they exhibit unusual properties compared to elastomers, such as a negative Poynting effect [663], they can be modeled as incompressible hyperelastic materials when viscous effects are neglected [888].

Upon addition of water, gels can swell and a theory of growth is appropriate for their description. However, since both growth and materials can be modeled as isotropic, the kinematics of swelling can be further simplified as first proposed by Flory [369]. Indeed, the machinery of the multiplicative decomposition becomes superfluous in the sense that the effect of growth can be completely taken into account through a proper definition of the determinant of $\mathbf{F}$ and a rescaling of the strain-energy function [288, 610, 1023, 1024, 1343]. The key is to realize that since $\mathbf{G} = g\mathbf{1}$, the deformation gradient $\mathbf{F}$ can be written as $\mathbf{F} = g\mathbf{A}$. Assuming that the gel is hyperelastic and incompressible, a suitable choice for W is then

$$W_S(\mathbf{A}, g) = m(g)W_1(\mathbf{A}), \quad (14.13)$$

with $m(g) > 0$ and $m(1) = 1$ so that $W_S(\mathbf{A}, 1) = W_1(\mathbf{A})$ represents the strain-energy function of a gel before swelling. The function $m(g)$ takes into account the remodeling of the gel during swelling. If the same material is added during swelling then $m(g) = 1$. However, if swelling is due to the addition of water, the elastic energy density, per unit unstressed volume, decreases as water cannot store elastic energy and we have $m(g) < 1$. A simple modeling choice for this effect is

$$m(g) = g^q, \quad (14.14)$$

where $q < 0$ is chosen to model softening during swelling. Therefore, the constitutive law (13.31) for this material can now be written

$$\begin{aligned}
\mathbf{T} &= m(g)\mathbf{A} \frac{\partial W_1(\mathbf{A})}{\partial \mathbf{A}} - p\mathbf{1} \\
&= m(g)(g^{-1}\mathbf{F}) \frac{\partial}{\partial \mathbf{F}} W_1(\mathbf{A}(\mathbf{F})) \frac{\partial \mathbf{F}}{\partial \mathbf{A}} - p\mathbf{1} \\
&= m(g)\mathbf{F} \frac{\partial}{\partial \mathbf{F}} W_1(g^{-1}\mathbf{F}) - p\mathbf{1} \\
&= \mathbf{F} \frac{\partial}{\partial \mathbf{F}} W_S(g^{-1}\mathbf{F}, g) - p\mathbf{1}.
\end{aligned} \tag{14.15}$$

This last expression is now only a function of $\mathbf{F}$ and g . No further reference to the virtual state is needed.

For example, if the strain-energy function of the material before swelling is given in terms of its invariant $W_1 = W(I_1, I_2)$, then we have

$$W_S(g^{-1}\mathbf{F}, g) = m(g)W(g^{-2}I_1, g^{-4}I_2), \tag{14.16}$$

and the explicit expression for the Cauchy stress (11.156) in terms of the derivatives of W with respect to the invariants is still valid (with $J = 1$). Note that in our case, the unstressed state is the free isotropic swollen state given by $\mathbf{F} = g\mathbf{1}$. With this new constitutive law, all standard equations given in Section 11.4 still apply and can be solved for any given geometry and strain-energy functions.

14.3 Discrete Growth Steps

The decomposition $\mathbf{F} = \mathbf{A}\mathbf{G}$ is clear as a one-step process, but proper care must be taken when looking at the cumulative effect of growth and long-time evolution [706]. 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 tensor $\mathbf{G}(\mathbf{X}_0, t)$ depends continuously on the configuration $\mathcal{B}_t$ at time t . Moreover the growth tensor is defined from an unstressed configuration $\mathcal{B}_0$, but it takes values that depend on the stressed configuration $\mathcal{B}_t$. The virtual state also depends on time and evolves with the current configuration according to Equation (14.1). Following the original proposal of Rodriguez et al. [1091], the evolution of growth can be understood by discretizing the evolution law forward in time to obtain a sequence of growth increments

$$\mathbf{G}(t + \delta t) = \mathbf{G}(t) + \delta t \mathcal{G}(\mathbf{T}, \mathbf{F}, \mathbf{G}, \mu; t, \mathbf{x}, \mathbf{X}_0), \tag{14.17}$$

where all arguments in the left hand side of this relation are evaluated at time t . That is, initially, the growth tensor depends on the configuration $\mathcal{B}_0$, and we define $\mathbf{G}_1 = \mathbf{G}(\delta t)$, corresponding to a small time increment δt . Given $\mathbf{G}_1$, we compute the residual stress field and elastic deformations due to external loading to obtain 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 define a new growth tensor

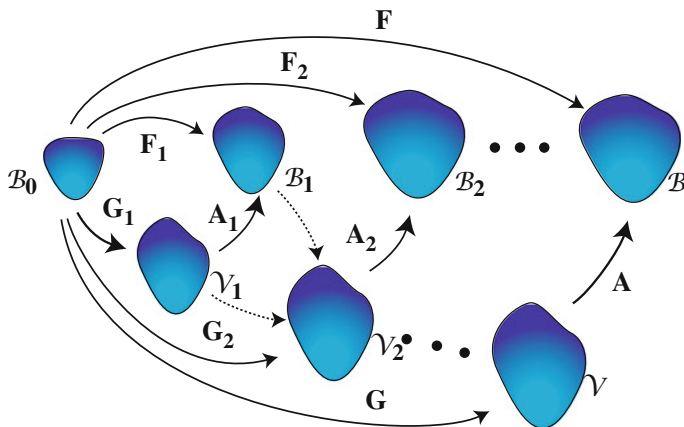


Figure 14.1 Evolution of the virtual grown state. The reference configuration evolves incrementally with time. To compute $\mathbf{G}_2$, we need the information contained in the state $\mathcal{V}_2$ and $\mathcal{B}_2$ as indicated by the dashed lines.

$$\mathbf{G}_2 = \mathbf{G}(2\delta t) = \mathbf{G}_1 + \delta t \mathcal{G}. \quad (14.18)$$

Once the virtual state $\mathcal{V}_2$ is obtained, a new elastic deformation tensor $\mathbf{A}_2$ can be computed. The process is iterated as shown in Figure 14.1. The cumulative effect of all 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. Through this process, the continuous limit is well defined. Note that at each incremental time, a nontrivial boundary-value problem needs to be solved. Then, the geometric deformation tensor is known and the reference configuration 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 directly the differential equation to obtain a continuous description of growth.

14.4 The Thermodynamics Perspective

The problem of determining a suitable form for the growth law remains. The general approach in rational thermodynamics to find restrictions on evolution laws is to use the Clausius–Duhem inequality to constrain the functional form of those laws. The standard procedure, known as the *Coleman–Noll procedure* [222], has been used efficiently to derive constitutive laws for systems with coupled fields such as the theory of thermoelasticity [526]. Nevertheless, as is the case with most fundamental ther-

modynamics concepts, the use and interpretation of the Clausius–Duhem inequality remain topics of debate in the rational mechanics literature [774, 842].

We first recall the form of the Clausius–Duhem inequality (13.28), derived in Section 13.5, for the free-energy density

$$\rho\dot{\psi} \leq \mathbf{T} : \mathbf{L} - \rho\eta\dot{\theta} - \frac{1}{\theta} \mathbf{q} \cdot \boldsymbol{\kappa} + \bar{h}, \quad (14.19)$$

where $\mathbf{L} = \dot{\mathbf{F}}\mathbf{F}^{-1}$ is the velocity gradient tensor, $\boldsymbol{\kappa} = \text{grad } \theta$, and $-\bar{h}$ is the non-compliant entropy contribution to the process. We now view the free-energy density $\psi = \psi(\mathbf{A}, \theta, \boldsymbol{\kappa})$, the entropy density $\eta = \eta(\mathbf{A}, \theta, \boldsymbol{\kappa})$, the Cauchy stress tensor $\mathbf{T} = \mathbf{T}(\mathbf{A}, \theta, \boldsymbol{\kappa})$ and the heat flux $\mathbf{q} = \mathbf{q}(\mathbf{A}, \theta, \boldsymbol{\kappa})$ as functions of the elastic tensors $\mathbf{A}$ as well as the temperature θ and temperature gradient $\boldsymbol{\kappa}$.

The basic assumption in the Coleman–Noll procedure is that the inequality (14.19) is expected to hold for all admissible thermodynamic processes, which means that it must hold for arbitrary deformation gradients and temperature fields. This condition puts restrictions on the possible functional forms for the fields $\mathbf{T}$ and $\mathbf{q}$.

We first expand $\dot{\psi}$ and $(\mathbf{T} : \mathbf{L})$ by using the chain rule and the substitution $\mathbf{F} = \mathbf{A}\mathbf{G}$ to obtain

$$\dot{\psi}(\mathbf{A}, \theta, \boldsymbol{\kappa}) = \frac{\partial \psi}{\partial \mathbf{A}} : \dot{\mathbf{A}} + \frac{\partial \psi}{\partial \theta} \dot{\theta} + \frac{\partial \psi}{\partial \boldsymbol{\kappa}} \cdot \dot{\boldsymbol{\kappa}}, \quad (14.20)$$

$$\mathbf{T} : \mathbf{L} = \mathbf{T} : \dot{\mathbf{F}}\mathbf{F}^{-1} = (\mathbf{T}\mathbf{A}^{-\text{T}}) : \dot{\mathbf{A}} + (\mathbf{A}^{\text{T}}\mathbf{T}\mathbf{A}^{-\text{T}}) : (\dot{\mathbf{G}}\mathbf{G}^{-1}). \quad (14.21)$$

We substitute these two expressions in (14.19) to obtain

$$\begin{aligned} & \left(\rho \frac{\partial \psi}{\partial \mathbf{A}} - \mathbf{T}\mathbf{A}^{-\text{T}} \right) : \dot{\mathbf{A}} + \rho \left(\frac{\partial \psi}{\partial \theta} + \eta \right) \dot{\theta} + \rho \frac{\partial \psi}{\partial \boldsymbol{\kappa}} \cdot \dot{\boldsymbol{\kappa}} \\ & \leq \mathbf{A}^{\text{T}} (\mathbf{T}\mathbf{A}^{-\text{T}}) : \dot{\mathbf{G}}\mathbf{G}^{-1} - \frac{1}{\theta} \mathbf{q} \cdot \boldsymbol{\kappa} + \bar{h}. \end{aligned} \quad (14.22)$$

Since the rate of change $\dot{\mathbf{A}}$, $\dot{\theta}$ and $\dot{\boldsymbol{\kappa}}$ can vary independently, this inequality must hold for each term independently, that is,

$$\mathbf{T} = \mathbf{A} \frac{\partial \psi}{\partial \mathbf{A}}, \quad \eta = -\frac{\partial \psi}{\partial \theta}, \quad \frac{\partial \psi}{\partial \boldsymbol{\kappa}} = \mathbf{0}. \quad (14.23)$$

We recover from this procedure, the thermodynamic connection between entropy and the free-energy function as well as the independence of the free-energy density from temperature gradients.

If we introduce $W = J_A \psi$, the internal energy density per unit reference volume, the first relationship gives the traditional form of the constitutive law

$$\mathbf{T} = J_A^{-1} \mathbf{A} \frac{\partial W}{\partial \mathbf{A}}. \quad (14.24)$$

Taking into account (14.23), (14.22) simplifies to

$$0 \leq (\mathbf{A}^T \mathbf{T} \mathbf{A}^{-T}) : (\dot{\mathbf{G}} \mathbf{G}^{-1}) - \frac{1}{\theta} \mathbf{q} \cdot \boldsymbol{\kappa} + \bar{h}. \quad (14.25)$$

We define from this relationship the stress tensor

$$\mathbf{M} = J_A^{-1} \mathbf{A}^T \mathbf{T} \mathbf{A}^{-T}. \quad (14.26)$$

This stress tensor, known as the *Mandel stress tensor*, maps vectors in the virtual state to vectors in the same state. It is therefore a natural descriptor for growth laws as noted by different authors [22–24, 654]. Note that if $\mathbf{A}$ and $\mathbf{T}$ are *coaxial* (that is, $\mathbf{A} \mathbf{T} = \mathbf{T} \mathbf{A}$) then $\mathbf{M} = J_A^{-1} \mathbf{T}$.

If we further neglect temperature gradient by considering those processes with spatially homogeneous temperature fields, then $\boldsymbol{\kappa} = \mathbf{0}$ and

$$\mathbf{M} : \mathcal{G} + J_A \bar{h} \geq 0, \quad (14.27)$$

where $\mathcal{G}$ is the growth law (14.1).

Many authors have emphasized that growth laws should be consistent with the laws of thermodynamics [22, 516, 654], an indisputable fact since, tautologically, all physical processes must obey the laws of physics. However, this last relationship does not provide much information since, within the confines of a macroscopic theory of open systems, the entropy sink $-\bar{h}$ is unknown and, *a priori*, the form of evolution laws cannot be constrained.

This issue is best illustrated on a simple example. We consider the case of a growing incompressible cuboid deformed along its axes and only allowed to grow along a single axis, say $\mathbf{e}_3$, as detailed in Section 13.8.1. Since the Cauchy stress tensor and the deformation gradients are diagonal, the Mandel stress is equal to the Cauchy stress tensor. We assume a simple model where growth takes place to maintain a state of homeostatic tension $t_3^* > 0$. For tension t_3 close to t_3^* , a plausible model is given by

$$[\dot{\mathbf{G}}][\mathbf{G}^{-1}] = \text{diag}(0, 0, g_3(t_3 - t_3^*)), \quad (14.28)$$

where $g_3 > 0$ to ensure that the homeostatic stress is stable in time as shown explicitly in Section 14.6.1.1. The dissipation inequality (14.27), in this case, reads

$$g_3(t_3 - t_3^*)t_3 + \bar{h} \geq 0. \quad (14.29)$$

If initially, $t_3 > t_3^*$, then this inequality is satisfied for $\bar{h} = 0$. This process is analogous to the physical plastic extension of a bar under tension given in Section 4.4.5. However, if we start with $t_3^* > t_3 > 0$, then the inequality requires a sink of entropy $\bar{h}$. Does it mean that we should rule out this process? Does it imply that no biological system could follow this evolution law? The requirement of the existence of a non-vanishing entropy sink only implies that a closed physical system could not be

described by such a law. Starting, for instance with fixed end-to-end displacement, the shortening of a cuboid from its homeostatic state would result in a shrinking of the cuboid along its axis, a process that would need reorganization of matter at the microscopic level.

We conclude that the rational thermodynamics approach, apart from recovering the usual constitutive laws for stress and entropy, cannot restrict the form of evolution laws for general growth processes. Nevertheless, it allows us to identify the Mandel stress as a key quantity (or equivalently, the closely related Eshelby stress tensor [22, 1231]) in the formulation of growth laws. It also allows us to describe two types of growth processes:

- **Passive growth processes.** During these processes, the dissipation inequality is satisfied even in the absence of entropy sinks. This situation is typical for physical systems. It arises, for instance, in plasticity, thermoelasticity, or gel swelling, where a non-compliant entropy contribution is not required for the process to take place [1076]. The observed macroscopic response is then slaved to the overall dissipation mechanism. There could be some active processes involved at the microscopic level but, in principle, this type of growth is not incompatible with physical processes.
- **Active growth processes.** In this case, an additional sink of entropy must be included to satisfy the dissipation inequality. This situation arises in many biological systems where the cell, through its genetic information and internal energy contribution, can alter the entropy of a system by forcing a preprogrammed response to external stimuli, against the physical increase of entropy. Therefore, active processes at the microscopic level must be at work, and indeed, are fundamental for the formation of highly organized structures in a dissipative environment.

Detailed analyses of the Clausius–Duhem inequality involving multiple species, chemical potentials, and higher-order gradients have been proposed by different authors [22, 341, 422, 424, 804]. It provides a comprehensive thermodynamic picture of growth and remodeling processes by identifying the different contributions to energy and entropy and the key players involved in the formulation of constitutive laws. Unfortunately, despite many claims, the thermodynamic approach fails to restrict universally the functional form of evolution laws for growth.

14.5 Phenomenological Laws and Homeostatic Stress

In the absence of fundamental physical principles guiding the formulation of suitable functional forms for a growth law, we consider plausible phenomenological models based on general physiological or biological principles. It is important to make the distinction between developmental and physiological growth processes. During development, the role of growth is to rapidly expand the mass, mostly by cellular division, and to shape tissues and organs. During regular physiological functions, growth is used to maintain the proper mechanical environment within a tissue or an organ so that it functions adequately in response to external loads.

The *homeostatic stress assumption* states that there exists a particular preferred value of the stress field that is regulated through growth and remodeling during regular physiological conditions. *Homeostasis*, a concept first developed by Walter Bradford Cannon in 1926 [165, 227], is the ability of a living organism to regulate its internal state to maintain constancy, such as the ability of mammals to maintain a stable internal temperature. Within mechanobiology, the concept of a homeostatic stress has its origin in the early work of Woods, Thoma, Davis, and Wolf on the heart, arteries, soft tissues, and bones as discussed in Section 2.1. This idea was only formulated as a generic concept following the study of Fung and Liu on residual stress in arteries [411, 795].

In our framework, the homeostatic stress assumption implies the existence of a function of the Cauchy stress tensor $\mathcal{T}^*(\mathbf{T})$ at which no growth takes place. This function could be a scalar (the overall pressure for instance), a vector (e.g., a traction at the boundary), or a tensorial field.

In the simplest case, the homeostatic stress is a tensor $\mathbf{T}^*$ such that, excluding other stimuli for growth, we have

$$\mathcal{G}(\mathbf{T}^*, \mathbf{F}^*, \mathbf{G}^*, \mu; t, \mathbf{x}, \mathbf{X}_0) = \mathbf{0}, \quad (14.30)$$

where $\mathbf{G}^*$ and $\mathbf{F}^*$ are the growth and deformation tensors that brought an initial configuration to its current state of stress $\mathbf{T}^*$. We further require that the homeostatic state must be stable so that under small perturbations growth takes place to recover the preferred state of stress, that is, for $\mathbf{T}$ close enough to $\mathbf{T}^*$, we have

$$(\mathbf{T} - \mathbf{T}^*) \xrightarrow{t \rightarrow \infty} \mathbf{0}. \quad (14.31)$$

This condition cannot be easily formulated in terms of a growth law $\mathcal{G}$ due to the complexity of the dynamics. However, close to a state of homeostasis, it is reasonable to assume that the dynamics can be linearized so that we obtain the *linear homeostasis growth law*:

$$\dot{\mathbf{G}}\mathbf{G}^{-1} = \mathcal{K} : (\mathbf{M} - \mathbf{M}^*), \quad (14.32)$$

where $\mathcal{K}$ is a fourth-order tensor and $\mathbf{M}^*$ represents the homeostatic value of the Mandel stress tensor. Following our discussion on thermodynamics, we have expressed this law in terms of the Mandel stress tensor $\mathbf{M} = J_A^{-1} \mathbf{A}^\top \mathbf{T} \mathbf{A}^{-\top}$ so that all relevant quantities are expressed in the virtual state. Various forms of this linear growth law have been used to model growth in tumors [26], arteries [18, 1054, 1212], muscles [1208], and the heart [1206, 1211].

The concept of homeostasis is central to many aspects of mechanobiology. Yet, it is not clear that it holds as a general principle. While it seems reasonable and well-documented in a normal physiological state, the concept may not apply directly in pathological processes such as tumor growth or wound healing, or in morphogenesis where the mechanical environment and material properties of the tissues change

rapidly. To this end, it has been proposed that homeostatic stress itself should evolve in these processes [1057, 1209, 1210, 1344] following some early experimental work and the theory of *hyper-restoration* of Belousov in embryogenesis [76, 77, 79].

14.6 Dynamics of Homogeneous Deformations

It is particularly useful to consider homogeneous elastic and growth deformations to understand the overall dynamics of growth. We first collect here all relevant equations describing the dynamics of the morphoelastic 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 are looking for solutions $\mathbf{x} = \chi(\mathbf{X}, t)$ for the system

$$\mathbf{F} = \text{Grad } \chi, \quad (14.33)$$

$$\mathbf{F} = \mathbf{A}\mathbf{G}, \quad (14.34)$$

$$\dot{\mathbf{G}}\mathbf{G}^{-1} = \mathcal{G}(\mathbf{T}, \mathbf{A}, \mathbf{G}), \quad (14.35)$$

$$\mathbf{T} = \mathcal{H}(\mathbf{A}), \quad (14.36)$$

$$\text{div } \mathbf{T} = \mathbf{0}. \quad (14.37)$$

These equations are complemented by the initial conditions

$$\chi(t = 0) = \mathbf{0}, \quad (14.38)$$

$$\mathbf{F}(t = 0) = \mathbf{A}(t = 0) = \mathbf{G}(t = 0) = \mathbf{1}, \quad (14.39)$$

$$\mathbf{T}(t = 0) = \mathbf{0}, \quad (14.40)$$

and the boundary conditions

$$\mathcal{F}(\mathbf{F}|_{\partial B}, \mathbf{T}|_{\partial B}) = \mathbf{0}. \quad (14.41)$$

Equations (14.33) to (14.37) form a system of 36 partial algebraic-differential equations to solve for the three components of the vector χ and the nine components of each of the tensors $\mathbf{F}$, $\mathbf{A}$, $\mathbf{G}$, and the six components of $\mathbf{T}$ (due to the symmetry $\mathbf{T}^T = \mathbf{T}$). No obvious analytical progress can be made without further assumptions.

We consider the simple, but informative, case where the deformation gradients are homogeneous. Then, the Cauchy equations (14.37) are trivially satisfied and the boundary conditions provide a global relationship between the fields. By using Equations (14.34) and (14.36), all dependence on $\mathbf{F}$ and $\mathbf{T}$ is removed and the system can be written as a set of 18 equations for $\mathbf{A}$ and $\mathbf{G}$, that is,

$$\dot{\mathbf{G}} = \widehat{\mathcal{G}}(\mathbf{A}, \mathbf{G}), \quad (14.42)$$

$$\mathbf{0} = \widehat{\mathcal{H}}(\mathbf{A}, \mathbf{G}), \quad (14.43)$$

where

$$\widehat{\mathcal{G}}(\mathbf{A}, \mathbf{G}) = \mathcal{G}(\mathcal{H}(\mathbf{A}), \mathbf{A}, \mathbf{G})\mathbf{G}, \quad (14.44)$$

$$\widehat{\mathcal{F}}(\mathbf{A}, \mathbf{G}) = \mathcal{F}(\mathbf{A}\mathbf{G}, \mathcal{H}(\mathbf{A})). \quad (14.45)$$

Therefore, the problem is to solve, for given growth and constitutive laws a set of algebraic-differential equations.

For an incompressible system, we introduce the extra variable p , so that the system reads now

$$\dot{\mathbf{G}} = \widehat{\mathcal{G}}(\mathbf{A}, \mathbf{G}, p), \quad (14.46)$$

$$\mathbf{0} = \widehat{\mathcal{F}}(\mathbf{A}, \mathbf{G}, p), \quad (14.47)$$

$$0 = \det \mathbf{A} - 1, \quad (14.48)$$

where

$$\widehat{\mathcal{G}}(\mathbf{A}, \mathbf{G}, p) = \mathcal{G}(\mathcal{H}(\mathbf{A}, p), \mathbf{A}, \mathbf{G}, p)\mathbf{G}, \quad (14.49)$$

$$\widehat{\mathcal{F}}(\mathbf{A}, \mathbf{G}, p) = \mathcal{F}(\mathbf{A}\mathbf{G}, \mathcal{H}(\mathbf{A}), p). \quad (14.50)$$

14.6.1 Diagonal Deformations

We further focus on the case where the material is incompressible and the deformation is diagonal so that, in the Cartesian basis $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$, we have

$$[\mathbf{F}] = \text{diag}(\lambda_1, \lambda_2, \lambda_3), \quad [\mathbf{A}] = \text{diag}(\alpha_1, \alpha_2, \alpha_3), \quad [\mathbf{G}] = \text{diag}(\gamma_1, \gamma_2, \gamma_3). \quad (14.51)$$

Note that the Cauchy stress tensor is also diagonal in the same basis

$$[\mathbf{T}] = \text{diag}(t_1, t_2, t_3), \quad (14.52)$$

and therefore equal to the Mandel stress.

Viewed as a dynamical system, the system (14.46–14.48) can be reduced to a system for two sets of variables, the vector $\boldsymbol{\gamma} = (\gamma_1, \gamma_2, \gamma_3)$ and $\boldsymbol{\alpha} = (\alpha_1, \alpha_2, \alpha_3, \alpha_4)$, where $\alpha_4 = p$. Then the algebraic-differential system of seven variable simply reads

$$\dot{\boldsymbol{\gamma}} = \mathbf{g}(\boldsymbol{\gamma}, \boldsymbol{\alpha}), \quad (14.53)$$

$$\mathbf{0} = \mathbf{f}(\boldsymbol{\gamma}, \boldsymbol{\alpha}). \quad (14.54)$$

We assume the existence of a homeostatic state of elastic strain $(\boldsymbol{\alpha}^*, \boldsymbol{\gamma}^*)$ associated with a state of elastic stress $\mathbf{t}^*$ and such that

$$\mathbf{g}(\gamma^*, \alpha^*) = \mathbf{0}, \quad \mathbf{f}(\gamma^*, \alpha^*) = \mathbf{0}. \quad (14.55)$$

In the simplest case, the stability of this state is obtained by linearizing the equations around the equilibrium. That is, we write

$$\gamma = \gamma^* + \varepsilon \bar{\gamma}, \quad \alpha = \alpha^* + \varepsilon \bar{\alpha}, \quad (14.56)$$

and expand all equations to first order in ε to obtain

$$\dot{\bar{\gamma}} = D_\gamma \mathbf{g} \bar{\gamma} + D_\alpha \mathbf{g} \bar{\alpha}, \quad (14.57)$$

$$\mathbf{0} = D_\gamma \mathbf{f} \bar{\gamma} + D_\alpha \mathbf{f} \bar{\alpha}, \quad (14.58)$$

where the notation

$$D_\gamma \mathbf{g} \equiv \left. \frac{\partial \mathbf{g}}{\partial \gamma} \right|_{(\alpha^*, \gamma^*)}, \quad (14.59)$$

stands for the Jacobian matrix of $\mathbf{g}$ with respect to γ evaluated at the equilibrium point (α^*, γ^*) . Assuming that $D_\alpha \mathbf{f}$ is invertible, we have

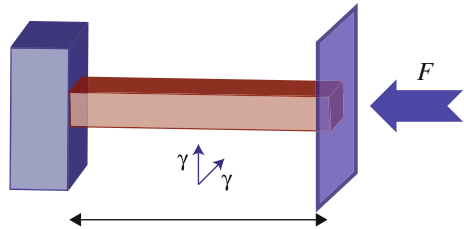
$$\begin{aligned} \dot{\bar{\gamma}} &= [D_\gamma \mathbf{g} + (D_\alpha \mathbf{g}) (D_\alpha \mathbf{f})^{-1} (D_\gamma \mathbf{f})] \bar{\gamma} \\ &\equiv \mathbf{K} \bar{\gamma}. \end{aligned} \quad (14.60)$$

Therefore, it follows from the linear stability theorem [520] that the stability of the equilibrium (α^*, γ^*) state depends on the eigenvalues of the matrix $\mathbf{K}$ as long as none of them have zero real part. However, due to underlying symmetries in the system, typically, some eigenvalues vanish identically and no information can be obtained from the linear stability theorem. In this case, a reduction of the system to a smaller dimensional system can often be obtained as we show in the following examples.

14.6.1.1 A One-Dimensional Example

We first revisit the case of a growing rectangular cuboid subject to constant compression along one of its axes and allowed to grow in the two other directions as originally studied in [1091] and depicted in Figure 14.2. The growth evolution is a

Figure 14.2 Growth of a block constrained between a wall and a plate on which a constant compressive force is applied. The block grows in response to stress in the two directions normal to the force.



function of the stress and we assume the existence of a homeostatic stress t_3^* along the compression $\mathbf{e}_3$ -axis. Therefore, the material will grow or resorb along the $\mathbf{e}_1$ and $\mathbf{e}_2$ directions until equilibrium is restored. We assume that the growth and elastic deformation tensors are both diagonal and that the material is hyperelastic, incompressible, and under uniaxial loading, so that in the Cartesian basis $\{\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3\}$, we have

$$[\mathbf{F}] = \text{diag}(\lambda, \lambda, \frac{1}{\alpha^2}), [\mathbf{A}] = \text{diag}(\alpha, \alpha, \frac{1}{\alpha^2}), [\mathbf{G}] = \text{diag}(\gamma, \gamma, 1), \quad (14.61)$$

In components, the Cauchy stress tensor is given by

$$t_1 = \alpha W_1(\alpha, \alpha, 1/\alpha^2) - p, \quad (14.62)$$

$$t_2 = \alpha W_2(\alpha, \alpha, 1/\alpha^2) - p, \quad (14.63)$$

$$t_3 = \frac{1}{\alpha^2} W_3(\alpha, \alpha, 1/\alpha^2) - p, \quad (14.64)$$

where $W_i = \partial_{\alpha_i} W$. We adopt here the evolution law

$$\dot{\gamma} = k\gamma(t_3 - t_3^*), \quad (14.65)$$

where t_3^* is a given homeostatic stress. We impose as boundary conditions a compressive force on the faces normal to the $\mathbf{e}_3$ direction and no traction on the other four faces. Since the deformation is homogeneous, we have

$$t_1(t) = t_2(t) = 0, \quad (14.66)$$

$$F = A(t)t_3 = A(0)\lambda_1\lambda_2t_3 = \alpha^2\gamma^2t_3, \quad (14.67)$$

where $A(t)$ is the surface area at time t of the face normal to $\mathbf{e}_3$ and $A(0) = 1$ is chosen without loss of generality. Note that since $t_1(t) = t_2(t) = 0$, we have $p(t) = \alpha W_1$ which implies

$$t_3 = h(\alpha) = -\frac{\alpha}{2} \widehat{W}'(\alpha), \quad (14.68)$$

where $\widehat{W}(\alpha) = W(\alpha, \alpha, 1/\alpha^2)$. By using the constitutive relationships the equations for (α, γ) are

$$\dot{\gamma} = k\gamma(h(\alpha) - t_3^*), \quad (14.69)$$

$$0 = F - \gamma^2 g(\alpha), \quad (14.70)$$

where $g(\alpha) = \alpha^2 h(\alpha)$. These last equations are a particularly simple example of a reduction of the general relationships (14.53–14.54). Following the same steps, we obtain a single linearized equation for $\bar{\gamma}$

$$\dot{\bar{\gamma}} = \mu \bar{\gamma}, \quad \mu = -2k(\alpha^*)^2 h'(\alpha^*) \frac{g(\alpha^*)}{g'(\alpha^*)}. \quad (14.71)$$

The local dynamics near the fixed state can be directly inferred from this equation. Assume that F^* is chosen so that the equation $h(\alpha^*) = t_3^*$ has at least one solution. This fixed point α^* is an equilibrium solution that corresponds to a growth

$$\gamma^* = \frac{1}{\alpha^*} \sqrt{\frac{F^*}{t_3^*}}. \quad (14.72)$$

The stability of this fixed point is determined by the sign of the linear stability exponent μ . We know from the Baker-Ericksen and the ordered-force inequalities that an increase in compressive force or stress reduces the length of the bar. These inequalities therefore imply that $h(\alpha) > 0$ and both $h'(\alpha) < 0$ and $g'(\alpha) < 0$. Therefore, we conclude that $\mu < 0$ for $k > 0$ and the equilibrium point is asymptotically stable.

14.6.1.2 Two Growing Beams in Parallel

Next, we revisit the example shown in Figure 13.2 where two beams grow in parallel and are connected by a platen through which forces balance. We assume that both beams have a homeostatic stress $t_{\pm}^*$ with a growth law

$$\dot{\gamma}_{\pm} = k_{\pm} \gamma_{\pm} (t_{3,\pm} - t_{\pm}^*), \quad (14.73)$$

where $k_{\pm} > 0$ and

$$t_{3,\pm} = h_{\pm}(\alpha_{\pm}) = - \left(\frac{\alpha}{2} \partial_{\alpha} \widehat{W}_{\pm} \right) \Big|_{\alpha=\alpha_{\pm}}, \quad (14.74)$$

similar to Equation (13.44). In the absence of external force applied on the platen, we have

$$0 = \alpha_+^2 t_{3,+} + \alpha_-^2 t_{3,-}, \quad (14.75)$$

$$\gamma_+ \alpha_-^2 = \gamma_- \alpha_+^2. \quad (14.76)$$

Depending on the values of $t_{\pm}^*$, we have different dynamics. Let $\alpha_{\pm}^*$ be the stretches associated with the homeostatic stress so that $h_{\pm}(\alpha_{\pm}^*) = t_{\pm}^*$. In the phase plane (α_+, α_-) , the dynamics is constrained to lie at all time on a curve given by the force balance

$$0 = \alpha_+^2 t_{3,+} + \alpha_-^2 t_{3,-}. \quad (14.77)$$

We start the dynamics at $\alpha_{\pm} = 1$ and consider different cases depending on the homeostatic stress:

- **Case I.** First, we assume that the homeostatic stresses are compatible with the force balance, that is,

$$(\alpha_+^*)^2 t_+^* + (\alpha_-^*)^2 t_-^* = 0, \quad (14.78)$$

as shown, for instance, by the circle I in Figure 14.3. Then, one of the homeostatic stresses must be compressive and the other one must be tensile. Starting from the initial state $\alpha_{\pm}(t=0) = 1$, the system evolves monotonically (see arrow): One beam grows while the other shrinks until the system reaches the equilibrium state.

- **Case II.** Assume now, that

$$(\alpha_+^*)^2 t_+^* + (\alpha_-^*)^2 t_-^* \neq 0, \quad (14.79)$$

and $t_+ t_- < 0$ as illustrated by the circle II in Figure 14.3. Taking without loss of generality $t_-^* > 0$, we have initially $t_{3,-} - t_-^* < 0$, that is, $\dot{\gamma}_- < 0$, and $t_{3,+} - t_+^* > 0$, that is, $\dot{\gamma}_+ > 0$ as indicated by the segment IIa in the figure. The minus beam shrinks until the minus stretch α_- crosses α_-^* after which point, both beams grow (IIb) until the stretch of the plus beam crosses α_+^* . After this point the minus beam grows and the plus beam shrinks without bounds (IIc) as the homeostatic balance can never be established.

- **Case III.** Assume now, that $(\alpha_+^*)^2 t_+^* + (\alpha_-^*)^2 t_-^* \neq 0$ but $t_+ t_- > 0$. Assume that both homeostatic stresses are tensile. Then initially one beam shrinks while the other grows (IIIa) until the growing beam reaches its homeostatic stretch after which both beams will shrink indefinitely (IIIb), unable to achieve a state of homeostatic stress. If both homeostatic stresses are compressive, both beams will grow indefinitely.

This simple example already demonstrates the possible complexity of growth dynamics which includes non-monotonic behavior and unstable dynamics. Clearly, as growth proceeds without bounds, both the elastic model and the evolution laws loose their validity and other mechanisms must be at work to prevent infinite growth, compression, or extension.

A simple evolution law, linear in the stress difference with respect to the homeostatic stress may only be valid close to that state. Such a law assumes, implicitly, that the homeostatic stress can be reached. However, mechanical or geometric constraint may prevent this state to be reached leading to unstable dynamics.

14.6.2 A Two-Dimensional Example

We consider again a growing cuboid constrained to grow and deform along its axes, such that the deformation and Cauchy stress tensors are diagonal and subject to the applied compressive forces

$$F_i = A_i(t)t_i = \lambda_j \lambda_k t_i, \quad i, j, k = 1, 2, 3, \quad i \neq j < k \neq i, \quad (14.80)$$

where $A_i(t)$ is the area of the face perpendicular to the $\mathbf{e}_i$ -axis and chosen to be equal to one at time $t = 0$, that is, $A_i(0) = 1$, $i = 1, 2, 3$. We consider here the particular case where $\alpha_3 = \alpha_2 \equiv \alpha$. From the incompressibility condition, we have $\alpha_1 = \alpha^{-2}$. We assume that $\gamma_3 = \gamma_2$ and a growth law for γ_1 and γ_2 of the form

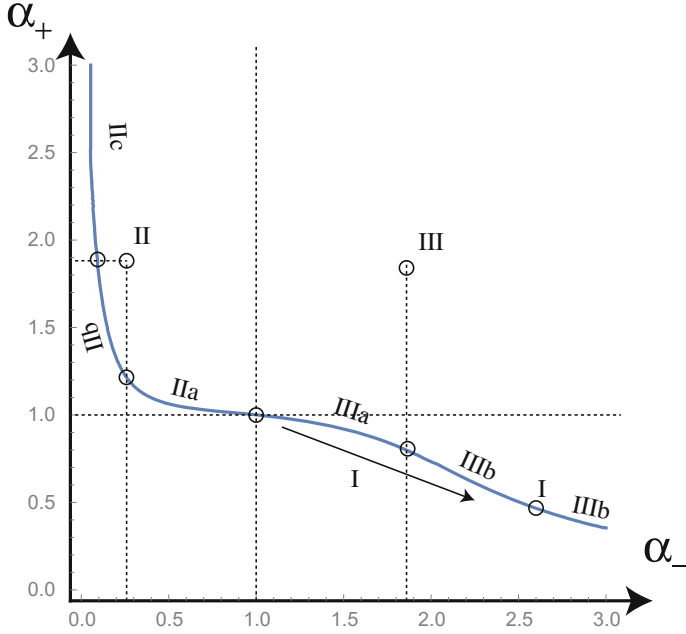


Figure 14.3 Dynamics of growing parallel beams shown in Figure 13.2. The curve represents the force balance that constrains the growth process. At any given time, the system evolves along this curve. Here, both strain-energy functions are neo-Hookean with $\mu_-/\mu_+ = 10$.

$$\dot{\gamma}_i = \gamma_i \sum_{j=1}^2 K_{ij}(t_j - t_j^*), \quad i = 1, 2, \quad (14.81)$$

where $\mathbf{K}$ is a constant matrix and t_1^*, t_2^* are prescribed homeostatic stresses. The constitutive relationships can be written

$$t_1 = -p + \alpha^{-2}(\partial_{\alpha_1} W), \quad (14.82)$$

$$t_2 = -p + \alpha(\partial_{\alpha_2} W), \quad (14.83)$$

so that the two remaining boundary conditions can be written as a single equation after eliminating p , that is,

$$\gamma_1 F_1 - \alpha^3 \gamma_2 F_2 = \gamma_1 \gamma_2^2 \alpha^2 h, \quad h(\alpha) \equiv -\frac{\alpha}{2} \partial_{\alpha} \widehat{W}, \quad (14.84)$$

where $\widehat{W} = W(\alpha^{-2}, \alpha, \alpha)$. Assuming that $\det(\mathbf{K}) \neq 0$, the equilibrium solution is given by

$$h(\alpha^*) = t_1^* - t_2^*, \quad \gamma_1^* = (\alpha^*)^2 \frac{F_2}{t_2^*} \sqrt{\frac{t_1^*}{F_1}}, \quad \gamma_2^* = \frac{1}{\alpha^*} \sqrt{\frac{F_1}{t_1^*}}. \quad (14.85)$$

Close to such an equilibrium point, the dynamics for $\bar{\gamma}_i = \gamma_i - \gamma_i^*$ reduces to

$$\dot{\bar{\gamma}}_i = \bar{\gamma}_i \sum_{j=1}^2 M_{ij} \bar{\gamma}_j. \quad (14.86)$$

The determinant and trace of the matrix $\mathbf{M}$ are given by

$$\det(\mathbf{M}) = -2 \det(\mathbf{K}) \frac{\alpha^* h'(\alpha^*) t_1^* t_2^*}{\alpha^* h'(\alpha^* + 2t_1^* + t_2^*)}, \quad (14.87)$$

$$\begin{aligned} \text{tr}(\mathbf{M}) = & \\ & - \frac{\alpha^* h'(\alpha^*) (K_{12} + 2K_{21} + K_{22}) + 2t_1^* t_2^* (K_{11} + K_{12} + 2K_{21} + 2K_{22})}{\alpha^* h'(\alpha^*) + 2t_1^* + t_2^*}. \end{aligned} \quad (14.88)$$

Interestingly, the position of the equilibrium point depends on the applied force, but its stability does not. Since we are interested in compressive homeostatic stresses, we have $t_i^* < 0$ and $h'(\alpha^*) < 0$. Therefore, a necessary condition for stability is $\det(\mathbf{K}) < 0$.

To illustrate the possible dynamics in this system, we further restrict our attention to the case $t_1^* = t_2^* = -1$ which implies $\alpha^* = 1$. We take $h'(1) = -6$ and the particular dynamics

$$[\mathbf{K}] = \begin{bmatrix} 1 & \beta \\ 0 & -1 \end{bmatrix}, \quad (14.89)$$

where β is a control parameter. Independently of the form of the strain-energy function and the applied forces, the stability of the equilibrium state (γ_1^*, γ_2^*) is fully determined by the parameter β :

$$\begin{aligned} \text{For } \beta &\leq \frac{1}{2}(2 - 3\sqrt{3}) & (\gamma_1^*, \gamma_2^*) \text{ is a stable node;} \\ \text{For } \frac{1}{2}(2 - 3\sqrt{3}) &< \beta < 1 & (\gamma_1^*, \gamma_2^*) \text{ is a stable spiral;} \\ \text{For } \beta &> 1 & (\gamma_1^*, \gamma_2^*) \text{ is an unstable equilibrium.} \end{aligned}$$

The dynamics has a bifurcation point at $\beta_{\text{crit}} = \frac{1}{2}(2 - 3\sqrt{3})$ as shown in Figure 14.4.

This simple example demonstrates the complexity of possible dynamics. The coupling between growth and the nonlinear response of the material implies that growth dynamics is highly nonlinear.

However, with a particularly simple choice for the evolution laws in terms of the stresses, this dynamics is simple as it only allows for a single equilibrium point (when the matrix $\mathbf{K}$ is not singular). The stability of such a fixed point and the behavior of the

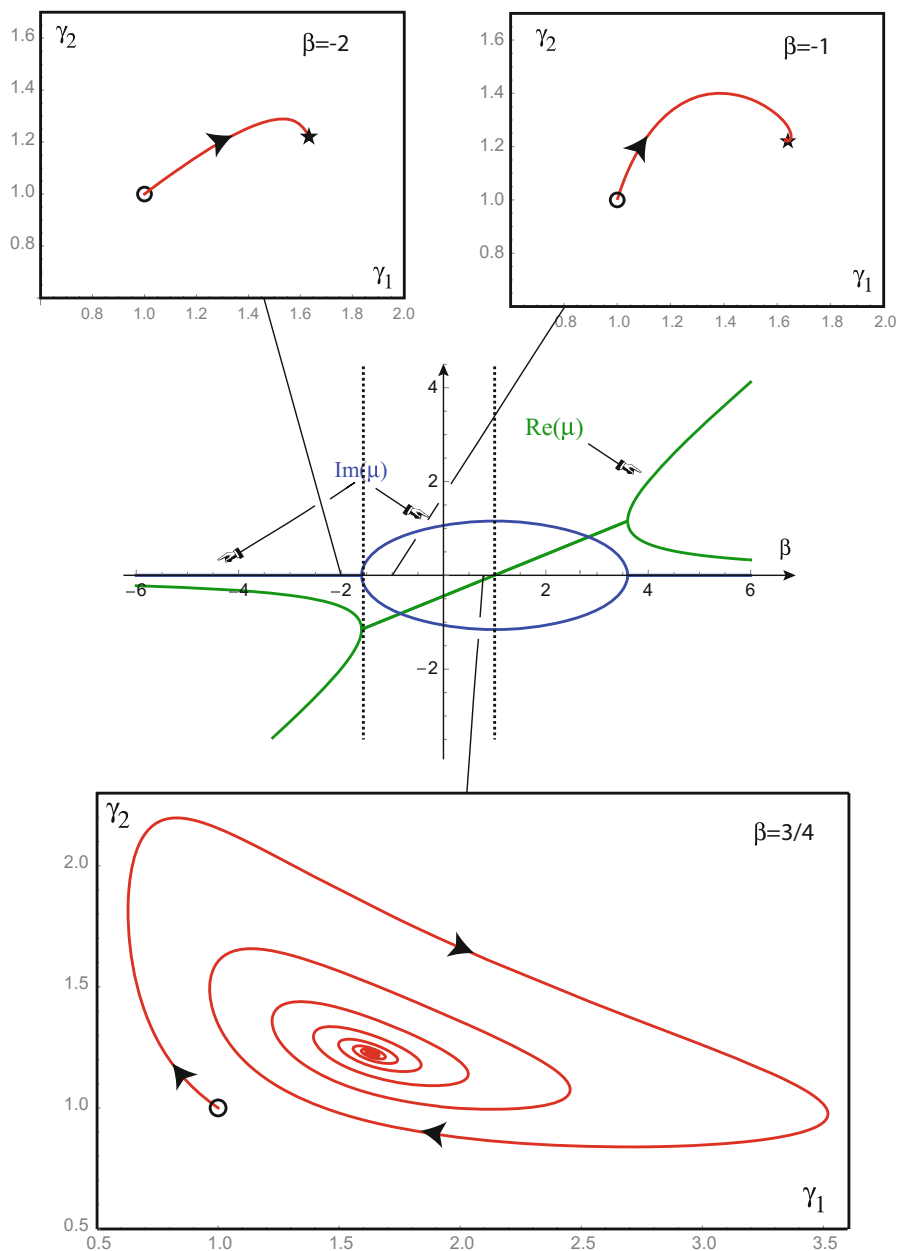


Figure 14.4 Real and imaginary parts of the eigenvalues $\mathbf{M}$ as a function of β . A bifurcation appears at $\beta_{\text{crit}} = \frac{1}{2}(2 - 3\sqrt{3})$ and stable oscillations are present for values of $\beta_{\text{crit}} < \beta < 1$, indicated by vertical dashed lines.

solutions close to this point depends nontrivially on the parameters of the system and, in particular, allows for oscillating dynamics. Oscillations during growth are found in many biological systems [78, 123, 354, 728, 799]. However, a proper modeling of the phenomenon of growth oscillation requires the coupling with other important fields, such as calcium concentration for pollen tubes [188, 360, 590]. The goal of this example is merely to show the possibility of interesting dynamics related to the structure of the equations for elastic growth.

14.7 Remodeling

Apart for the addition of mass, an important feature of evolving tissues is their capacity for remodeling. Remodeling is defined as a change in a tissue or organ that takes place without addition of mass. An evolution of material stiffness as it ages is an example of a remodeling process. In this case, the different parameters appearing in the strain-energy function are allowed to vary over the slow growth time. The anisotropic response of a material can also evolve in time. For instance, in many fiber-reinforced tissues, there is a constant renewal of fibers based on the mechanical environment and the fibers strength and alignment can evolve according to external stimuli in order to change the effective properties of the material. These changes include growth, deposition, cleavage of fibers, changes in fiber diameter and orientation, and cross-linking of fibers [872, 873]. In mammalian tissues, these processes take place during both development and adulthood, when they either help maintain proper tissue function or lead to pathologies.

Since remodeling in biological tissues occur in response to mechanical stimuli, it is believed to be closely related to the optimization of mechanical properties. For instance, as discussed in Section 2.1.5, Wolff's law states that bones adapt to external loads by reinforcement in order to resist these loads [883]. This process can be modeled by a local change in density depending on the stress. This example of density growth is accompanied by a local change of volume (hence growth), but it can also be seen a remodeling process for the entire structure as it affects its anisotropic response as seen in Figure 14.5. Similarly, it has been suggested that growth in the arterial wall optimizes its load-bearing functions [1213].

In the particular case of collagen-reinforced tissues, it has been observed *in vitro* that fibroblast respond to mechanical loading by changing the orientation of collagen fibers [320]. This reorientation may arise from either realignment of existing fibers or collagen turnover as cells are able to synthesize highly aligned collagen [1293]. Mechanically-induced fiber reorientation is believed to play an important role in the proper function of aortic valves [302–304] and arterial walls [305, 540, 736].

Within our framework, remodeling can take place at two different levels. First, it can appear kinematically by considering growth processes whose deformation tensor $\mathbf{G}$ does not change volume, that is $\det(\mathbf{G}) = 1$. It corresponds locally to a reorganization of mass in some preferred directions. This remodeling process is a particular case of the evolution laws discussed in this chapter and is described by

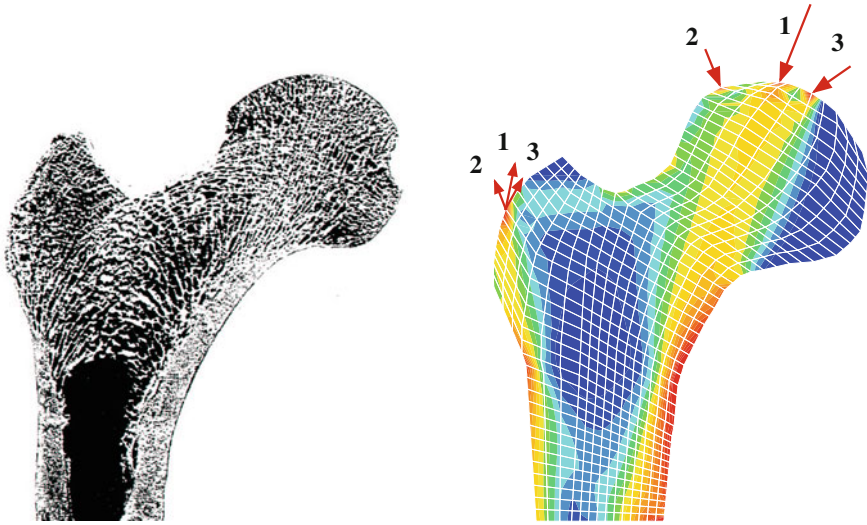


Figure 14.5 Illustration of remodeling in bone through density growth. Left: Illustration from Wolff (1892). Right: Computation of bone evolution [734] (picture courtesy of Ellen Kuhl).

either the evolution of the tensors $\mathbf{G}$ as given by Equation (14.1) or, equivalently, by an equation for the evolution of the growth directions γ_i appearing in the description of the growth tensors given in Section 14.1. Since a growth direction γ is prescribed by a unit vector, its evolution in time is fully determined by a spin vector φ such that

$$\frac{\partial \gamma}{\partial t} = \varphi \times \gamma. \quad (14.90)$$

Second, in an anisotropic material, remodeling can take place to change the directions of anisotropy. For instance, in a fiber-reinforced material, the reference fiber direction $\mathbf{M}$ can evolve in time as a function of the applied loads or strains. Again, since $\mathbf{M}$ is a unit vector, its evolution is fully specified by a spin vector ω such that

$$\frac{\partial \mathbf{M}}{\partial t} = \omega \times \mathbf{M}. \quad (14.91)$$

In both instances of remodeling, the central problem is to find a suitable law for the rotation vectors φ and ω as a function of stresses or strains. A standard approach is to assume that fiber reorientation follows either the directions of positive principal strains [302], maximum principal stretch, maximum principal stress [577, 735, 870], or a direction that depends on the stretch or stress [304, 305, 540, 736]. In the case of a system with fiber dispersion, the evolution of the probability density function for fiber alignment also needs to be specified [303, 304].

A simple evolution law [870] that is consistent with the realignment of a fiber in the direction $\mathbf{M}$ in a given direction $\mathbf{N}$ is

$$\frac{\partial \mathbf{M}}{\partial t} = \frac{1}{\tau} (\mathbf{N} - (\mathbf{N} \cdot \mathbf{M})\mathbf{M}), \quad (14.92)$$

where both $\mathbf{M}$ and $\mathbf{N}$ are taken in the reference configuration and τ is the typical relaxation time. Since $\mathbf{M}$ is initially a unit vector, we verify that $\mathbf{M} \cdot \partial_t \mathbf{M} = 0$, that is, $\mathbf{M}$ remains a unit vector during the dynamics. This formulation is equivalent to (14.91) with

$$\boldsymbol{\omega} = \frac{1}{\tau} \mathbf{M} \times \mathbf{N}. \quad (14.93)$$

In a theory of *maximum stretch remodeling*, we choose $\mathbf{N}$ to be the direction of largest stretch, then (14.92) implies that the fibers reinforce the most stretched direction by reorienting toward it and that $\mathbf{M} \rightarrow \mathbf{N}$ as $t \rightarrow +\infty$. In that limit, the stress and strain tensors are coaxial, which is a necessary condition for the strain-energy to reach an extremum [577, 1280]. Note that, if the maximum principal stretch is not unique, it is assumed that $\partial_t \mathbf{M} = \mathbf{0}$. An example of a similar strain-driven fiber reorientation embedded in a three-dimensional model is shown in Figure 14.6.

14.7.1 Fiber Remodeling of a Cuboid in Tension

To gain insight into the dynamics of remodeling, we consider a fiber-reinforced cuboid under fixed tensional loading as depicted in Figure 11.28. We assume that the assumptions on material properties, geometry, and boundary conditions, given in Section 11.11.3, hold with the added assumption that the fiber angle θ is not fixed in time, but that it evolves on a slow time scale according to the strain-driven remodeling assumption.

Following [865], we assume that the fibers are initially oriented in the $X_1 - X_2$ plane and remain equal and symmetric in the same plane during reorientation. Then, the reorientation law (14.92) can be expressed as an evolution law for the fiber orientation angle Θ

$$\frac{d\Theta}{dt} = \begin{cases} -\frac{1}{\tau} \sin \Theta, & \lambda_1 > \lambda_2, \\ 0, & \lambda_1 = \lambda_2, \\ \frac{1}{\tau} \cos \Theta, & \lambda_1 < \lambda_2. \end{cases} \quad (14.94)$$

Therefore, the problem can now be cast as the evolution of three dynamical variables $\{\lambda_1(t), \lambda_2(t), \Theta(t)\}$ for the dynamical system consisting of Equation (14.94) together with the equilibrium conditions (11.303)–(11.304) that we repeat here for convenience

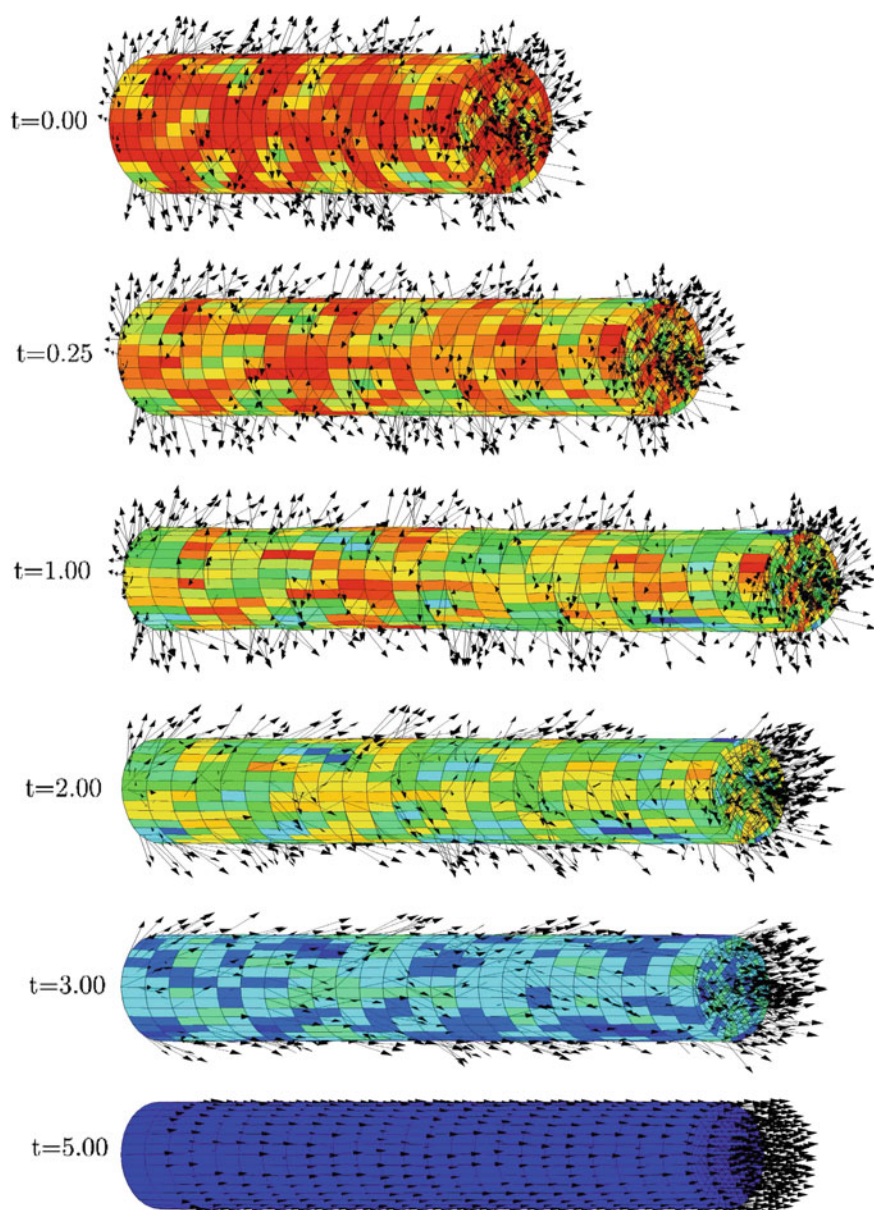


Figure 14.6 Remodeling of an anisotropic cylindrical tendon based on strain. Initially, fibers have random orientation and the tendon is in tension. As time evolves, the fibers align with the strain [735]. Picture courtesy of Ellen Kuhl.

$$A = \frac{\lambda_1^2 - \lambda_2^2}{4\gamma} + (\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)(\lambda_1^2 \cos^2 \Theta - \lambda_2^2 \sin^2 \Theta), \quad (14.95)$$

$$B = \frac{-1}{2\gamma\lambda_1^2\lambda_2^2} + \frac{\lambda_1^2 + \lambda_2^2}{4\gamma} + (\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta - 1)(\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta), \quad (14.96)$$

where $A = (t_1 - t_2)/4\gamma$, $B = (t_1 + t_2 - 2t_3)/4\gamma$, and we have set, without loss of generality, $\mu = 1$.

The initial conditions for the system (14.94–14.96) are given by a choice of $\Theta(0) = \Theta_0$ and $\lambda_i(0) = \lambda_{i0}$, where λ_{i0} , Θ_0 must satisfy (14.95–14.96).

In phase space the trajectories lie at the intersection of the level set $A(\lambda_1, \lambda_2, \Theta) = A_1$ and $B(\lambda_1, \lambda_2, \Theta) = B_1$. On this curve the dynamics is controlled by (14.94) as shown in Figure 14.7. Since we assume that fibers do not support compression, the dynamics of the system is further restricted by requiring that the systems remains in the *fiber-tensile region*, defined by

$$\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta \geq 1, \quad \Theta \in [0, \pi/2]. \quad (14.97)$$

Fibers are unstrained on the boundary of region (14.97), and the material behaves as a regular isotropic neo-Hookean material when $\lambda_1^2 \cos^2 \Theta + \lambda_2^2 \sin^2 \Theta < 1$.

The key question is to understand the asymptotic dynamics of the system. Starting with given boundary tensions, specified through A and B , what is the asymptotic state of the system?

We start from the observation that System (14.94–14.96) has only three possible steady states:

- $\Theta = 0$, $\lambda_1 \geq \lambda_2$ (Θ achieves its minimum and λ_1 is the dominant stretch);
- $\Theta = \frac{\pi}{2}$, $\lambda_1 \leq \lambda_2$ (Θ achieves its maximum and λ_2 is the dominant stretch);
- $\Theta = \Theta^* \in (0; \frac{\pi}{2})$, $\lambda_1 = \lambda_2 = \lambda$ (there is no dominant stretch in $X_1 - X_2$ plane).

Equilibria of the first and second type are called *extreme equilibria*, whereas the third type are *intermediate equilibria*.

The system is symmetric with respect to the change of variables: $\lambda_1 \mapsto \lambda_2$, $\lambda_2 \mapsto \lambda_1$, $\Theta \mapsto \frac{\pi}{2} - \Theta$, $A \mapsto -A$. Thus, we only consider extreme equilibria with $\lambda_1 > \lambda_2$ and intermediate equilibria with $A \geq 0$, the other cases following via this symmetry.

The existence and stability of the different equilibria depend on the geometry of the level sets and their intersections in phase space. A detailed analysis [865] reveals that there is always a unique stable equilibrium when the loads place the fibers in tension for some orientations. Moreover, this equilibrium point does not depend on the initial conditions. Rather, it corresponds either to a complete alignment of fibers along the direction of maximum principal stretch, or an intermediate alignment between two principal stretches. In the case of intermediate alignment, the asymptotic fiber orientation depends critically on the applied loads.

As can be seen from Figure 14.8, if the difference between the two loads in the fiber plane is large enough, then the fibers gradually rotate toward the direction of

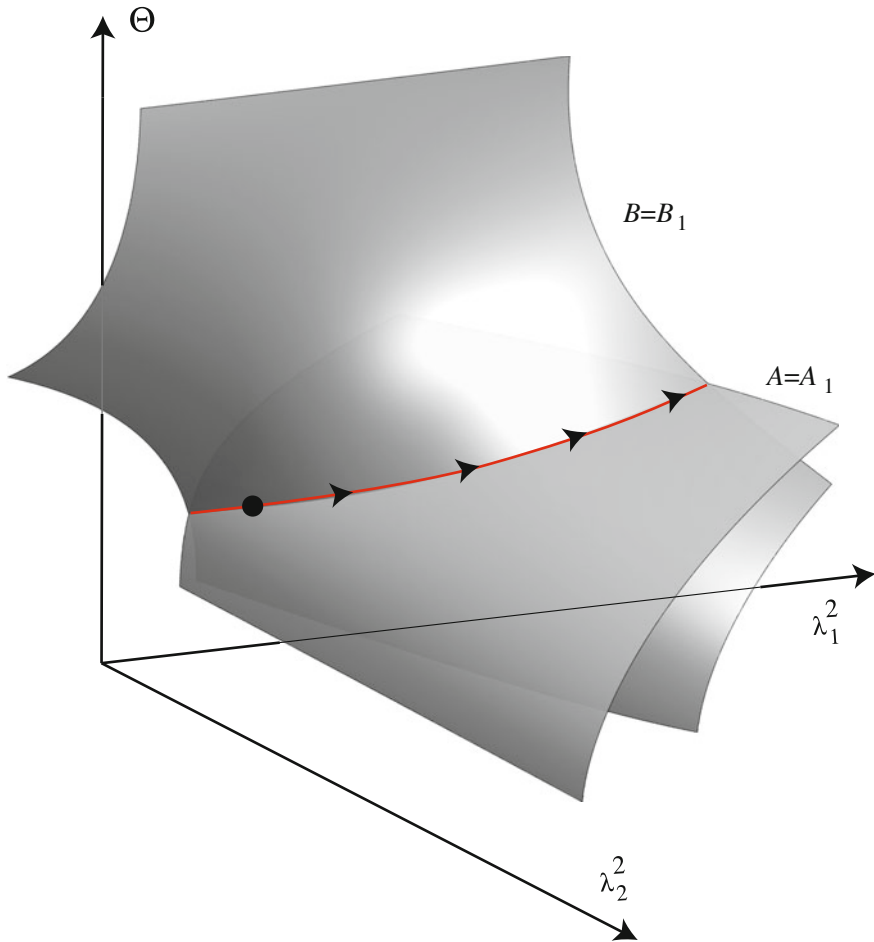


Figure 14.7 The remodeling trajectory in the phase space $(\lambda_1^2, \lambda_2^2, \Theta)$ is an oriented curve in phase space located at the intersection of the level sets of $A(\lambda_1^2, \lambda_2^2, \Theta) = A_1$ and $B(\lambda_1^2, \lambda_2^2, \Theta) = B_1$ (shown: $\gamma = 2$, $\mu = 1$, $A_1 = 1/2$, $B = 1$). The solution shown is within the fiber-tensile region.

the greater load, asymptotically approaching it. As a result of fiber reorientation, the specimen contracts in this direction.

For smaller differences in loads, fibers initially reorient toward the direction of current maximum stretch and reinforce it. Thus, the maximum principal stretch is decreasing, while the remaining stretch in the fiber plane is increasing. Eventually, reorientation stops when the two stretches are equal. For some applied loads, there is no tensile state and therefore no fiber remodeling. This simple remodeling law creates an interesting dynamics of fiber through which the strains, hence the loads, balance each other dynamically.

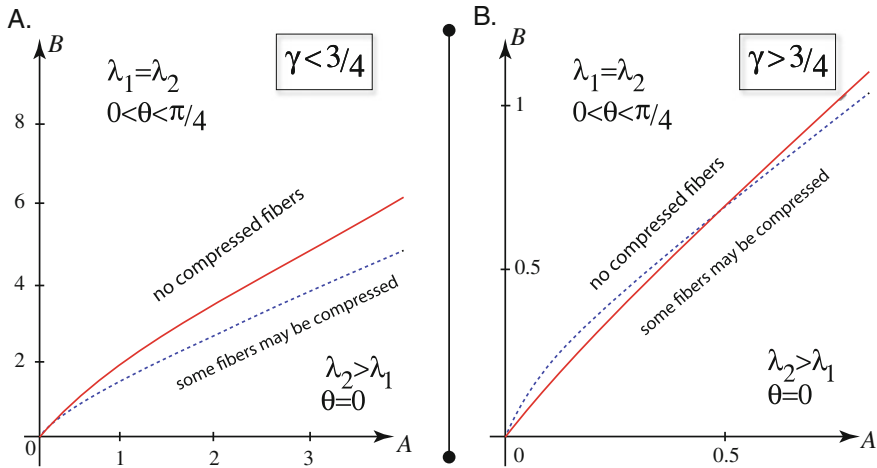


Figure 14.8 Possible asymptotic dynamics for the remodeling of a fiber-reinforced cuboid for $A > 0$ and $B > 0$. A. $\gamma < 3/4$. B. $\gamma > 3/4$. For values of A and B above the solid line, the dynamics settles on a stable intermediate equilibrium, whereas for values of A and B below that line, only the extreme equilibrium is reached. (shown: $\gamma = 2$, $\mu = 1$, $A_1 = 1/2$, $B = 1$). The dashed line denotes the possibility of compressed fibers: Above the line, the equilibrium fibers are always in tension whereas below the line, they may be in compression (depending on the angle).

14.8 Growth Induced Instability

In the previous sections, we studied the dynamics and stability of simple configurations. Next, we consider the possibility of buckling induced by growth and expand the bifurcation method developed in Section 11.10 to the case of a growing elastic body.

We restrict our attention to the case where the growth tensor $\mathbf{G}$ is given and does not evolve through the deformation. That is, growth is driven from outside and is not influenced by the state of the system such as stresses or strains. Therefore, the growth tensor can be seen as a control parameter that changes the geometry of the body and its residual stress, but it is not affected by the deformation itself. We are interested in the loads and growth parameters for which a bifurcation occurs. We assume the existence of a base solution and look for the existence of small incremental solutions superimposed on the finite deformation.

As before, we assume that a family of solutions, the *base solution*, for the Cauchy stress $\mathbf{T}^{(0)}$ and deformations $\chi^{(0)}$ are known for given boundary conditions and controlled by several parameters, such as external loading or prescribed growth. We seek solutions close to the base solution by formally linearizing the governing equations around the base state. We assume that there is no body force and that the elastic response of the material is governed by a strain-energy function $W = W(\mathbf{A})$ subjected, possibly, to a single kinematic constraint $C(\mathbf{A}) = 0$. We further focus on

where $\mathbf{A}^{(0)} = \mathbf{F}^{(0)} \mathbf{G}^{-1}$ and $\mathbf{A}^{(1)} = \mathbf{F}^{(1)}$. The peculiar form of the expansions for $\mathbf{F}$ and $\mathbf{A}$ with $\mathbf{F}^{(0)}$ as a factor is chosen so that the incremental deformation is expressed in the current configuration rather than the reference configuration. Figure 14.9 presents a diagram of the decomposition of the different deformation tensors.

The kinematic constraint $C(\mathbf{A}) = 0$ is expanded to first order as

$$\begin{aligned} C(\mathbf{A}) &= C(\mathbf{A}^{(0)} + \epsilon \mathbf{A}^{(1)} \mathbf{A}^{(0)}) \\ &= C(\mathbf{A}^{(0)}) + \epsilon \operatorname{tr} \left(C_{\mathbf{A}}^{(0)} \mathbf{A}^{(1)} \mathbf{A}^{(0)} \right) + \mathcal{O}(\epsilon^2). \end{aligned} \quad (14.101)$$

That is, to first order, we have the condition

$$\operatorname{tr} \left(C_{\mathbf{A}}^{(0)} \mathbf{A}^{(1)} \mathbf{A}^{(0)} \right) = 0, \quad (14.102)$$

where $C_{\mathbf{A}}^{(0)}$ denotes the second-order tensor obtained as the derivative of C with respect to $\mathbf{A}$ evaluated at $\mathbf{A}^{(0)}$. In the particular case of incompressibility, we have

$$C_{\mathbf{A}}^{(0)} = \det(\mathbf{A}^{(0)}) (\mathbf{A}^{(0)})^{-1}, \quad (14.103)$$

so that

$$\operatorname{tr}(\mathbf{A}^{(1)}) = 0. \quad (14.104)$$

Step 2: Linearized equations. Since both the incremental deformation $\mathbf{F}^{(1)}$ and the boundary conditions are expressed in the current configuration we only consider the Cauchy stress tensor and assume that it can be expanded in ϵ :

$$\mathbf{T} = \mathbf{T}^{(0)} + \epsilon \mathbf{T}^{(1)} + \mathcal{O}(\epsilon^2). \quad (14.105)$$

To first order, in the absence of body loads, the Cauchy equation reads

$$\operatorname{div}(\mathbf{T}^{(1)}) = \mathbf{0}. \quad (14.106)$$

Step 3: Linearized constitutive equations. We can now relate the incremental stresses to the incremental strains by the constitutive relationship. For a single scalar constraint, $C(\mathbf{A}) = 0$, the constitutive relationship is given by Equation (11.132). That is,

$$\mathbf{T} = J^{-1} \mathbf{A} \left(\frac{\partial W}{\partial \mathbf{A}} - q \frac{\partial C}{\partial \mathbf{A}} \right). \quad (14.107)$$

To leading and first orders, this constitutive relationship becomes

$$\mathbf{T}^{(0)} = \mathbf{A}^{(0)} \left(W_{\mathbf{A}}^{(0)} - q^{(0)} C_{\mathbf{A}}^{(0)} \right), \quad (14.108)$$

and

$$\mathbf{T}^{(1)} = \mathbf{F}^{(1)} \mathbf{T}^{(0)} - q^{(1)} \mathbf{A}^{(0)} C_{\mathbf{A}}^{(0)} + \mathcal{L} : \mathbf{F}^{(1)} - q^{(0)} \mathcal{C} : \mathbf{F}^{(1)}, \quad (14.109)$$

where $q = q^{(0)} + \epsilon q^{(1)}$, and $\mathcal{L}, \mathcal{C}$ are the fourth-order tensors defined by the operation $(:)$ on a second-order tensor

$$\mathcal{L} : \mathbf{F}^{(1)} = \mathbf{A}^{(0)} \text{tr} \left(W_{\mathbf{A}\mathbf{A}}^{(0)} \mathbf{F}^{(1)} \mathbf{A}^{(0)} \right), \quad (14.110)$$

$$\mathcal{C} : \mathbf{F}^{(1)} = \mathbf{A}^{(0)} \text{tr} \left(C_{\mathbf{A}\mathbf{A}}^{(0)} \mathbf{F}^{(1)} \mathbf{A}^{(0)} \right), \quad (14.111)$$

and $W_{\mathbf{A}}^{(0)}, W_{\mathbf{A}\mathbf{A}}^{(0)}$ are the first and second derivatives of W with respect to $\mathbf{A}$ evaluated on $\mathbf{A}^{(0)}$. The components of the fourth-order tensor $\mathcal{L}$ are the *instantaneous elastic moduli* and their explicit form for isotropic materials is given below.

In the incompressible case, $C = \det(\mathbf{A}) - 1$, so that (14.108) now reads

$$\mathbf{T}^{(0)} = \mathbf{A}^{(0)} W_{\mathbf{A}}^{(0)} - q^{(0)} \mathbf{1}, \quad (14.112)$$

and we can use Equation (11.53) to show that

$$\mathcal{C} : \mathbf{F}^{(1)} = -\mathbf{F}^{(1)}. \quad (14.113)$$

The incremental Cauchy stress tensor then becomes

$$\mathbf{T}^{(1)} = \mathcal{L} : \mathbf{F}^{(1)} + \mathbf{F}^{(1)} \mathbf{A}^{(0)} W_{\mathbf{A}}^{(0)} - p^{(1)} \mathbf{1}. \quad (14.114)$$

Linearized equations for incompressible materials. We substitute (14.114) in (14.106) to obtain

$$\text{div}(\mathcal{L} : \mathbf{F}^{(1)}) + (\mathbf{F}^{(1)})^T \text{grad}(q^{(0)}) - \text{grad}(q^{(1)}) = \mathbf{0}. \quad (14.115)$$

where we have used $(\mathbf{T}^{(i)})^T = \mathbf{T}^{(i)}$, $\text{div}(\mathbf{T}^{(0)}) = \mathbf{0}$ and

$$\text{div}(\mathbf{F}^{(1)}) = \mathbf{0}. \quad (14.116)$$

This last relation comes from the application of Nanson's formula to the transformation of a volume element so that

$$\text{div}(J^{-1} \mathbf{F}) = \mathbf{0}, \quad (14.117)$$

which implies both $\text{div}(J^{-1} \mathbf{F}^{(0)}) = \mathbf{0}$ and (14.116).

Step 4: The boundary-value problem. The boundary conditions are prescribed by fixing $\chi^{(1)}$ on some part of the boundary and $\mathbf{T}^{(1)} \mathbf{n}$ on the remainder of the boundary, where, as before, $\mathbf{n}$ is the unit outward vector normal to the current boundary.

Relation (14.115) is the central equation for the stability analysis of the configuration associated with the deformation $\chi^{(0)}$. For given boundary conditions, the existence of solutions to this system of equations indicates a bifurcation and the possibility of an instability.

Instantaneous elastic moduli. The elastic moduli are similar to those given in Section 11.10 with the main difference that we have now a mixture of elastic strains and geometric first-order deformations. For $W = W(\mathbf{A})$, we define $\mathcal{A} = W_{\mathbf{A}\mathbf{A}}^{(0)}$, the elastic moduli evaluated in the reference configuration. The *instantaneous elastic moduli* are the elements of the fourth-order tensor $\mathcal{L}$ defined by the relation

$$\mathcal{L} : \mathbf{F}^{(1)} = \mathbf{A}^{(0)} \text{tr}(\mathcal{A} \mathbf{F}^{(1)} \mathbf{A}^{(0)}). \quad (14.118)$$

In Cartesian components, the elastic moduli are given by

$$\mathcal{A}_{ijkl} = \frac{\partial W}{\partial A_{ji} \partial A_{lk}}, \quad (14.119)$$

and the instantaneous elastic moduli are

$$\mathcal{L}_{ijkl} = A_{im}^{(0)} \mathcal{A}_{mjkn} A_{nl}^{(0)}. \quad (14.120)$$

Let α_i be the principal values of $\mathbf{A}$, then for an isotropic hyperelastic material the components of $\mathcal{L}$ on the Eulerian principal axes associated with $\mathbf{A}$ are

$$\mathcal{L}_{iijj} = \alpha_i \alpha_j \frac{\partial^2 W}{\partial \alpha_i \partial \alpha_j}, \quad (14.121)$$

$$\mathcal{L}_{ijij} = \left[\alpha_i \frac{\partial W}{\partial \alpha_i} - \alpha_j \frac{\partial W}{\partial \alpha_j} \right] \frac{\alpha_i^2}{(\alpha_i^2 - \alpha_j^2)}, \quad i \neq j, \quad (14.122)$$

$$\mathcal{L}_{ijji} = \mathcal{L}_{jiii} = \mathcal{L}_{ijij} - \alpha_i \frac{\partial W}{\partial \alpha_i}, \quad i \neq j. \quad (14.123)$$

If $\alpha_i = \alpha_j$ for some $i \neq j$, then

$$\mathcal{L}_{ijij} = \frac{1}{2} \left(\mathcal{L}_{iiii} - \mathcal{L}_{iijj} + \alpha_i \frac{\partial W}{\partial \alpha_i} \right), \quad (14.124)$$

$$\mathcal{L}_{iiii} = \mathcal{L}_{jjjj}, \quad \mathcal{L}_{iikk} = \mathcal{L}_{jjkk}, \quad (14.125)$$

$$\mathcal{L}_{ikik} = \mathcal{L}_{jkjk}, \quad \mathcal{L}_{ikki} = \mathcal{L}_{jkkj}. \quad (14.126)$$

In the two following chapters, we will use this general theory to study the possibility of buckling induced by growth.

Chapter 15

Growing Spheres



Sphere-like biological and physical objects appear in many different sizes and contexts. In Figure 15.1, we show examples of spheres either shrinking by evaporation or growing by cell expansion and division. In these processes, stresses develop in the material due to either inhomogeneous or anisotropic addition of mass. In turn, these stresses can lead to buckling or transform the effective properties of the structure. This particular geometry is well adapted to a mathematical treatment as the deformations are sufficiently simple to allow for a full quantitative analysis. In this chapter, we first consider an incompressible hyperelastic spherical shell that preserves its spherical symmetry during the deformation. Second, we compute the stresses generated through different growth processes. We will show how limit-point instabilities, cavitation, and singularity formation can be triggered by growth. Third, we look at the possibility of buckling by considering nonspherical perturbations superimposed on a residually stressed spherical shell.

15.1 The Growing Shell

Throughout this chapter, we use spherical coordinates to describe possible deformations. Briefly, the spherical coordinates in the current configuration (r, θ, ϕ) are

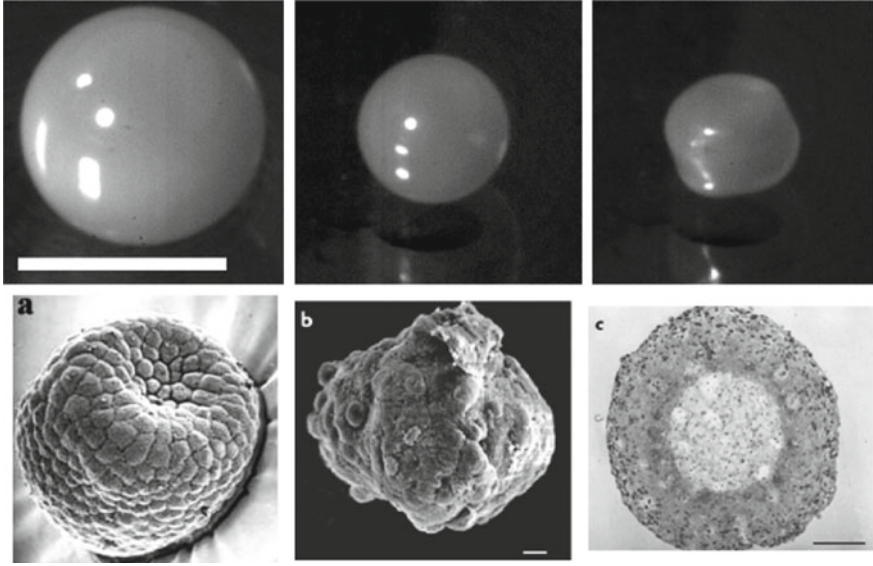


Figure 15.1 Top row: A drying droplet of colloidal suspension on a hot plate. As the drop shrinks, it loses its spherical shape due to the creation of internal stresses [835, 1254] (scale bar 0.5 mm. Picture courtesy of Nicolas Tsapis). Bottom row: a. A scanning electron micrograph of cellular and extracellular patterns during blastulation and gastrulation in the sea urchin, *Lytechinus variegatus* [907]; b. Scanning electron micrograph of a human hepatoma cell (HepG2) (scale bar, is 10 μm). c. Electron microscopy cross-section of a V-79 Chinese hamster lung cell spheroid [1007] (scale bar, is 250 μm).

defined with respect to the Cartesian coordinates (x_1, x_2, x_3) as

$$x_1 = r \cos \theta \sin \phi, \quad (15.1)$$

$$x_2 = r \sin \theta \sin \phi, \quad (15.2)$$

$$x_3 = r \cos \phi, \quad (15.3)$$

where $r \in [0, \infty)$, $\theta \in [0, 2\pi)$, $\phi \in [0, \pi]$ and let $\{\mathbf{e}_r, \mathbf{e}_\theta, \mathbf{e}_\phi\}$ be the associated orthonormal basis. Similarly, we define (R_0, Θ_0, Φ_0) , (R, Θ, Φ) and their associated bases in the initial and virtual configurations.

15.1.1 Kinematics of Growing Spheres

We consider the symmetric growth and deformation of a spherical shell with radii $R_0 = A_0$ and $R_0 = B_0$ in the initial configuration into a spherical shell of radii $r = a$ and $r = b$ in the current configuration. We allow for the possibility where both A_0 and a vanish (a solid growing sphere); the case where $A_0 = 0$ but $a > 0$ (the *cavitation*

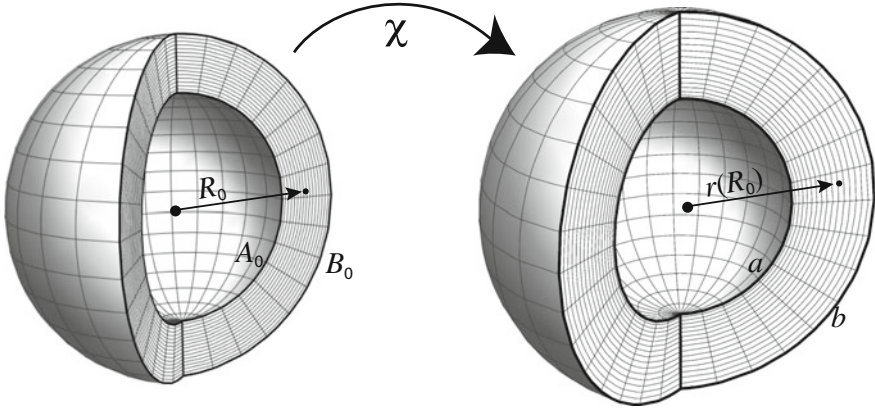


Figure 15.2 Radial deformation of a shell with inner and outer radii A_0 and B_0 to a shell with radii a and b .

of a sphere); as well as the case whereby $A_0 > 0$ and $a = 0$ (the *anti-cavitation* of a spherical shell).

In a spherically symmetric deformation, the shell expands and any point located at (R_0, Θ_0, Φ_0) in the reference configuration is moved to the point $(r(R_0), \Theta_0, \Phi_0)$ in the current configuration, as shown in Figure 15.2. Explicitly, the deformation, $\mathbf{x} = \chi(\mathbf{X}_0)$, reads

$$r = r(R_0), \quad \theta = \Theta_0, \quad \phi = \Phi_0, \quad (15.4)$$

so that the position vectors are, respectively,

$$\mathbf{X}_0 = R_0 \mathbf{E}_{R_0}, \quad \mathbf{x} = r(R_0) \mathbf{e}_r = \frac{r(R_0)}{R} \mathbf{X}_0. \quad (15.5)$$

Due to the symmetry of the deformation, we can identify the basis vectors so that $\mathbf{E}_{R_0} = \mathbf{e}_r$, $\mathbf{E}_{\Theta_0} = \mathbf{e}_\theta$, $\mathbf{E}_{\Phi_0} = \mathbf{e}_\phi$.

To compute the deformation gradient, we use the method described in Section 11.1.5. We have two sets of spherical coordinates $\{q_\alpha\} = \{r, \theta, \phi\}$ and $\{Q_\alpha\} = \{R_0, \Theta_0, \Phi_0\}$. For these coordinates, the scale factors, defined by (11.39), are

$$h_r = 1, \quad H_{R_0} = 1, \quad (15.6)$$

$$h_\theta = r, \quad H_{\Theta_0} = R_0, \quad (15.7)$$

$$h_\phi = r, \quad H_{\Phi_0} = R_0. \quad (15.8)$$

Following Equation (11.60), the deformation gradient is

$$\mathbf{F} = r' \mathbf{e}_r \otimes \mathbf{e}_r + \frac{r}{R_0} \mathbf{e}_\theta \otimes \mathbf{e}_\theta + \frac{r}{R_0} \mathbf{e}_\phi \otimes \mathbf{e}_\phi,$$

which we write

$$[\mathbf{F}] = \text{diag}(r', r/R_0, r/R_0), \quad (15.9)$$

where the primes denote derivatives with respect to R_0 .

Next, we assume that this geometric deformation is the result of both a growth deformation and an elastic deformation. We assume that the growth deformation preserves the spherical symmetry so that in the virtual state $\mathcal{V}$, the growth deformation can be written as

$$\mathbf{G} = \gamma_r \mathbf{e}_r \otimes \mathbf{e}_r + \gamma_\theta \mathbf{e}_\theta \otimes \mathbf{e}_\theta + \gamma_\theta \mathbf{e}_\phi \otimes \mathbf{e}_\phi, \quad (15.10)$$

or

$$[\mathbf{G}] = \text{diag}(\gamma_r, \gamma_\theta, \gamma_\theta), \quad (15.11)$$

where γ_r and γ_θ are functions of R_0 and, again, due to symmetry, we used the current configuration basis, that is, $\mathbf{E}_R = \mathbf{e}_r$, $\mathbf{E}_\Theta = \mathbf{e}_\theta$, $\mathbf{E}_\Phi = \mathbf{e}_\phi$.

We distinguish three types of growth:

- **Isotropic growth.** *Isotropic growth* is achieved when $\gamma_r = \gamma_\theta$. In this case, the grown sphere is a dilation of the original sphere.
- **Area growth.** If $\gamma_r = 1$ and $\gamma_\theta \neq 1$, growth is purely along the two angles, increasing the surface area of any given shell and, is referred to as *area growth*. If $\gamma_\theta > 1$ material is added and removed otherwise.
- **Fiber growth.** If $\gamma_\theta = 1$ and $\gamma_r \neq 1$, *fiber growth* or *radial growth* takes place in the radial direction and each radial material fiber in the shell increases (or decreases) in length [709]. Both area and fiber growth are illustrated in Figure 15.3.

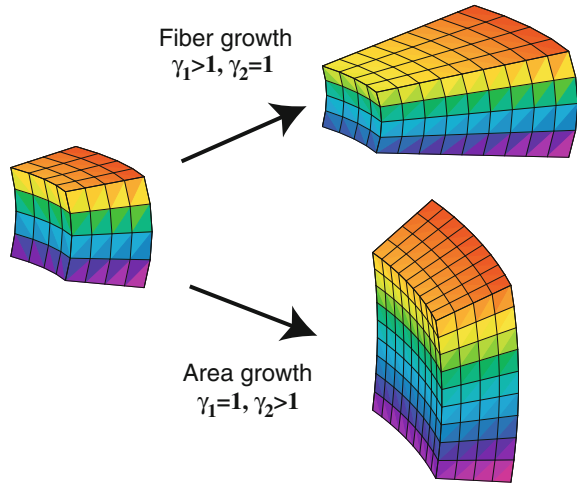
The key parameter in this growth process is the ratio $\gamma = \gamma_r/\gamma_\theta$. Equilibrium solutions with radial growth are equivalent to solutions with hoop resorption ($\gamma > 1$) up to an isotropic growth and a rescaling of an effective applied pressure

$$P_{\text{eff}} = P/\gamma. \quad (15.12)$$

It follows from the multiplicative decomposition, $\mathbf{F} = \mathbf{A}\mathbf{G}$, that the elastic strain tensor can be written in the same spherical basis as

$$[\mathbf{A}] = \text{diag}(\alpha_r, \alpha_\theta, \alpha_\theta). \quad (15.13)$$

Figure 15.3 Transformation of a spherical volume element under radial and hoop growth.



The incompressibility condition, $\det \mathbf{A} = \alpha_r \alpha_\theta^2 = 1$, together with the decomposition, $\mathbf{F} = \mathbf{A}\mathbf{G}$, has two consequences. First, we can define a unique strain $\alpha \equiv \alpha_\theta$, so that $\alpha_r = \alpha^{-2}$ and

$$r' = \frac{\gamma_r}{\alpha^2}, \quad \frac{r}{R_0} = \alpha \gamma_\theta. \quad (15.14)$$

Second, the deformation is completely determined by

$$r' \frac{r^2}{R_0^2} = \gamma_r \gamma_\theta^2, \quad (15.15)$$

that is, after integration

$$r^3 - a^3 = 3 \int_{A_0}^{R_0} \gamma_r(\rho) \gamma_\theta^2(\rho) \rho^2 d\rho. \quad (15.16)$$

where $a = r(A_0)$ and $b = r(B_0)$ denote the inner and outer radii of the deformed shell, respectively. The hoop stretch α is then given by

$$\alpha(R_0) = \frac{\left(a^3 + 3 \int_{A_0}^{R_0} \gamma_r(\rho) \gamma_\theta^2(\rho) \rho^2 d\rho \right)^{1/3}}{R_0 \gamma_\theta(R_0)}. \quad (15.17)$$

15.1.2 Stresses in a Growing Sphere

Next, we compute the static stresses in the absence of body loads in terms of the Cauchy stress tensor. By symmetry, the only nonvanishing spherical components of the stress tensor are its diagonal components, so that

$$[\mathbf{T}] = \text{diag}(t_r, t_\theta, t_\theta), \quad (15.18)$$

where t_r is the *radial stress* and t_θ is the *hoop stress*. Using this particular form for the elastic and stress tensors, the stress–strain relationships (13.37) for a strain-energy function $W = W(\alpha_r, \alpha_\theta, \alpha_\phi)$ read

$$t_r = \alpha_r \frac{\partial W}{\partial \alpha_r} - p, \quad (15.19)$$

$$t_\theta = \alpha_\theta \frac{\partial W}{\partial \alpha_\theta} - p. \quad (15.20)$$

The only nonvanishing Cauchy equation for mechanical equilibrium (13.35) in the current configuration is

$$\frac{\partial t_r}{\partial r} + \frac{2}{r}(t_r - t_\theta) = 0, \quad (15.21)$$

and a closed equation for t_r is obtained:

$$\frac{\partial t_r}{\partial r} = \frac{\alpha}{r} \partial_\alpha \widehat{W}, \quad (15.22)$$

where we have introduced the auxiliary function $\widehat{W}(\alpha) = W(\alpha^{-2}, \alpha, \alpha)$. This last equation can be written as a function of the initial variable R_0 as

$$\frac{\partial t_r}{\partial R_0} = \frac{\gamma}{R_0 \alpha^2} \partial_\alpha \widehat{W}. \quad (15.23)$$

Once the radial stress and the deformation $\alpha = \alpha(R_0)$ are known, the hoop stress is given by

$$t_\theta = t_r + \frac{\alpha}{2} \partial_\alpha \widehat{W}. \quad (15.24)$$

For the case of a shell in the current configuration, the boundary conditions for (15.23) in the case of hydrostatic loading with pressure P are such that $P = t_r(A_0) - t_r(B_0)$. For $A_0 > 0$, we take, without loss of generality,

$$t_r(A_0) = 0, \quad P = -t_r(B_0). \quad (15.25)$$

If $P > 0$, the shell is subject to an external hydrostatic pressure P and if $P < 0$ the shell is inflated with an internal pressure $-P$. A negative radial stress corresponds to a compressive stress and a positive radial stress is tensile. For a given P , the problem is to determine the inner radius a introduced in (15.16). Once a is known, the deformation is fully specified and so are the stresses. In the case of a solid sphere under hydrostatic loading in the current configuration, we have $a = 0$ and $t_r(r(B_0)) = -P$.

15.2 Examples

15.2.1 Anisotropic Growth

We are interested in computing the stresses and the radial deformation that can be created through constant but anisotropic growth (constant γ_r and γ_θ). In this case, (15.17) takes the following form:

$$\alpha^3 = \gamma \left(1 - \frac{A_0^3}{R_0^3} \right) + \frac{a^3}{\gamma_\theta^3 R_0^3}. \quad (15.26)$$

Defining $\alpha_a = \alpha(A_0) = a/(A_0\gamma_\theta)$ and $\alpha_b = \alpha(B) = b/(B_0\gamma_\theta)$, we have

$$\alpha_b^3 = \gamma \left(1 - \frac{A_0^3}{R_0^3} \right) + \alpha_a^3 \left(\frac{A_0}{B_0} \right)^3, \quad (15.27)$$

and using (15.26), Equation (15.23) can be written as a closed equation for $t_r(\alpha)$:

$$\frac{\partial t_r}{\partial \alpha} = \frac{\gamma_r \partial_\alpha \widehat{W}}{\gamma - \alpha^3(\gamma_\theta + R_0 \gamma'_\theta)}. \quad (15.28)$$

Since both γ_r and γ_θ are constant, this last equation can be readily integrated as

$$t_r(\alpha) = \gamma \int_{\alpha_a}^{\alpha} \frac{\partial_\alpha \widehat{W}}{\gamma - \alpha^3} d\alpha. \quad (15.29)$$

The boundary conditions (15.25) lead to

$$-P = \gamma \int_{\alpha_a}^{\alpha_b} \frac{\partial_\alpha \widehat{W}}{\gamma - \alpha^3} d\alpha, \quad (15.30)$$

and since α_b is related to α_a by (15.27), this last relation is an equation for P as a function of α_a . For a given P , one can invert this relation to find the strain at the boundary α_a caused by the traction. Once α_a is known, the position of the inner radius is known and so is the deformation $r = r(R)$ through (15.26).

In Figure 15.4, we show the radial stress as a function of α_a for a neo-Hookean material in the absence of growth ($\gamma_r = \gamma_\theta = 1$). Neo-Hookean materials are characterized by the strain-energy function

$$W = \frac{\mu}{2}(\alpha_r^2 + \alpha_\theta^2 + \alpha_\phi^2 - 3), \quad (15.31)$$

which implies $\widehat{W} = \frac{\mu}{2}(\alpha^{-4} + 2\alpha^2 - 3)$ and

$$t_r(\alpha_b) = \frac{\mu}{2} (4\alpha_b^{-1} + \alpha_b^{-4} - 4\alpha_a^{-1} - \alpha_a^{-4}). \quad (15.32)$$

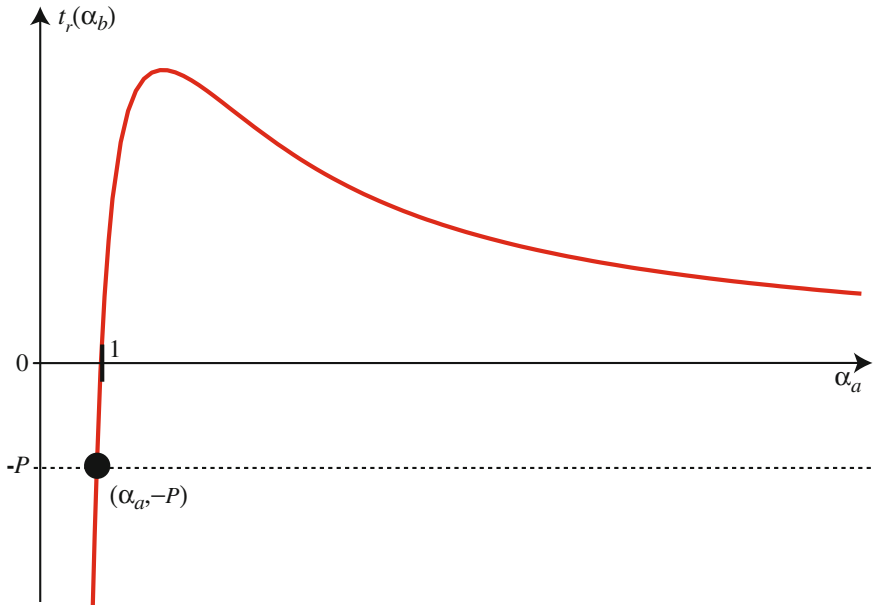


Figure 15.4 The radial stress at the outer boundary for a non-growing neo-Hookean material as a function of the inner boundary strain α_a . For a given P , the strain $\alpha(R)$ and the deformation $r = r(R)$ are specified by finding the value of α_a such that $t_r(\alpha_b) = -P$.

In Figure 15.5, we plot the stresses created by radial and hoop growth for an isotropic neo-Hookean shell with no external loading ($P = 0$). Both radial growth and hoop resorption create a compressive residual stress (i.e., a negative radial stress) in the material, whereas hoop growth and radial resorption create a tensile radial stress (i.e., a positive radial stress). For constant growth, the radial stress vanishes only at the boundaries and its sign depends on whether γ is less than or greater than one. If we consider nonconstant growth, the effect of the γ'_θ term in (15.28) can be sufficiently important so as to create alternating regions of compressive and tensile stresses [196].

15.2.2 Differential Growth

Another possible mechanism to create residual stress is through differential growth. We consider two cases: a shell shrinking differentially and a shell growing inside an infinite elastic medium. We assume that the differential growth process is a function of the current radius and the result of many incremental growth steps as described in Section 14.3 and sketched in Figure 15.6.

We first define an incremental deformation tensor

$$\mathbf{F}_{\text{inc}} = \mathbf{A}_{\text{inc}} \mathbf{G}_{\text{inc}}, \quad (15.33)$$

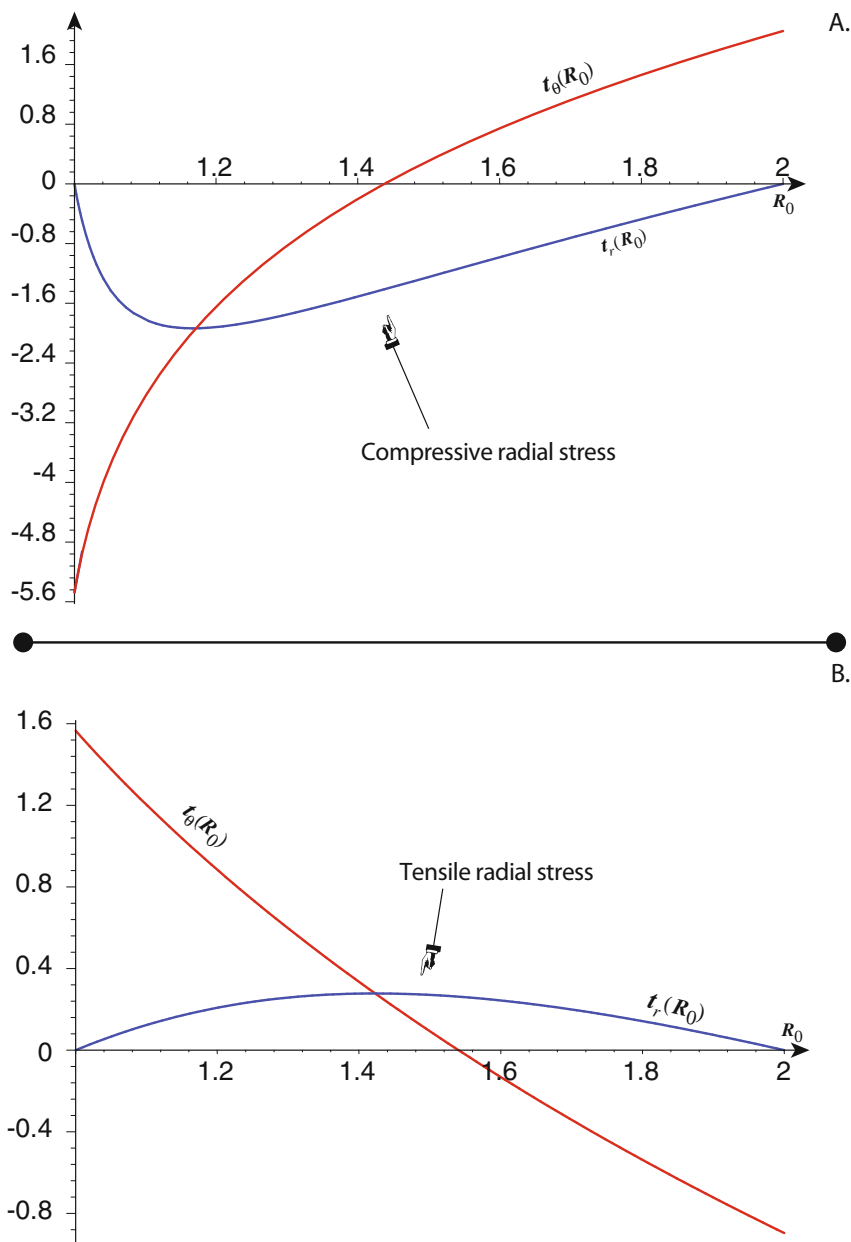


Figure 15.5 Stresses generated by A. fiber growth ($\gamma_r = 2, \gamma_\theta = 1$) and B. area growth ($\gamma_r = 1, \gamma_\theta = \sqrt{2}$) of a neo-Hookean shell $\mu_1 = 1, A = 1, B = 2$. Radial growth creates a compressive radial stress. The hoop stress is tensile on the outer radius and compressive inside. In hoop growth the situation is reversed and similar to fiber resorption.

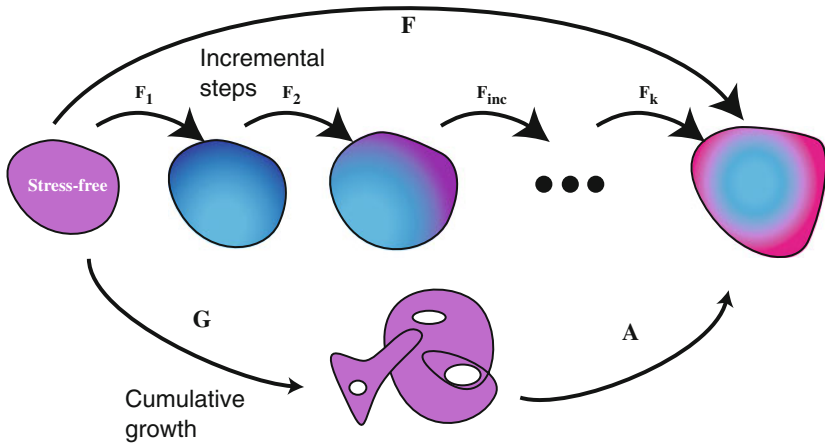


Figure 15.6 The process of incremental and cumulative growth.

where the growth tensor $\mathbf{G}_{\text{inc}}$ is assumed to be isotropic and a function of the radial position r in the current configuration:

$$\mathbf{G}_{\text{inc}} = g_{\text{inc}}(r)\mathbf{1}. \quad (15.34)$$

The decomposition (15.33) represents an incremental deformation step. Once (slow) growth and (fast) elastic response take place, the shell continues its growth, and after successive incremental steps the total cumulative deformation is of the form

$$\mathbf{F} = \mathbf{A}\mathbf{G}, \quad \mathbf{G} = g(r)\mathbf{1}. \quad (15.35)$$

As an example, we choose a simple incremental growth of the form

$$g_{\text{inc}}(r) = 1 + f(r - a), \quad (15.36)$$

with $f(0) = 0$, so that there is no growth at the inner boundary. The problem is then to find a suitable form for the cumulative growth function $g(r)$. Since the solution for a and r as a function of the initial radius R_0 at each step depends on the solution of a boundary-value problem, there is no analytic form for $g(r)$ as a function of $g_{\text{inc}}(r)$. However, a numerical study of the incremental growth process, shown in Figure 15.7, reveals that, for a simple linear incremental law, cumulative growth is also accurately modeled by a linear profile even for large variations of volumes. Therefore, we take

$$g(r) = 1 + \nu(r - a), \quad (15.37)$$

where ν is positive for growth and negative for resorption.

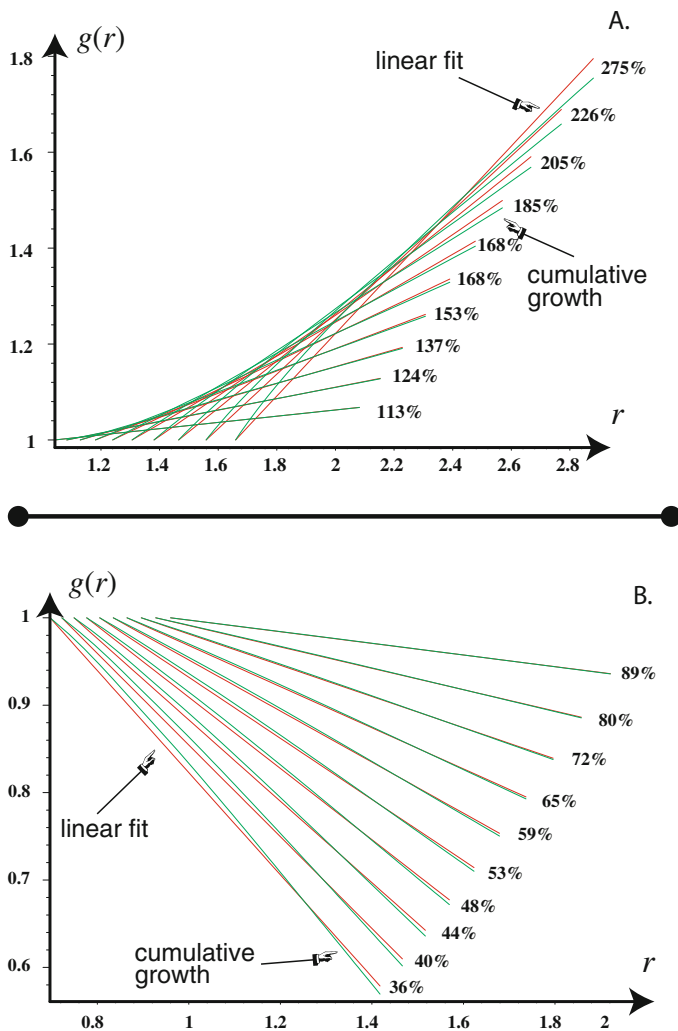


Figure 15.7 The cumulative growth function (solid line) in the current frame $g = g(r)$ together with a linear fit (dashed) for the case of A. growth and B. resorption. The percentage values correspond with the overall volume change of the sphere.

As before, the incompressibility condition determines both the deformation and the strain. However, it is advantageous to formulate the problem in terms of the current radius, for which we have

$$R_0^3 = A_0^3 + 3 \int_a^r \frac{\rho^2}{g^3(\rho)} d\rho, \quad \alpha(r) = \frac{r}{g(r)R_0(r)}, \quad (15.38)$$

from (15.14) and (15.15). As in the previous case, the value of a is obtained from the boundary conditions on the Cauchy stress.

In the absence of an external or internal medium, the radial component of the Cauchy stress for a material characterized by a strain-energy function W_{sh} is given by

$$t_r(r) = \int_a^r \frac{\alpha}{\rho} \partial_\alpha \widehat{W}_{\text{sh}}(\alpha) d\rho, \quad (15.39)$$

with boundary conditions $t_r(b) = -P$, and $t_r(a) = 0$.

When growth occurs inside a medium, the Cauchy stress inside an infinite medium, characterized by a strain-energy function, W_{me} is

$$t_r(r) = \int_b^r \frac{\alpha}{\rho} \partial_\alpha \widehat{W}_{\text{me}}(\alpha) d\rho, \quad (15.40)$$

where it is assumed that $g = 1$ for $r > b$. The boundary condition is now $t_r(\infty) = 0$ and equality of radial stresses at $r = b$.

Once the radial stress is known, the deformation is completely determined and the hoop stress in the shell is given by

$$t_\theta = t_r + \frac{\alpha}{2} \partial_\alpha \widehat{W}_{\text{sh}}(\alpha). \quad (15.41)$$

Typical profiles of radial and hoop stresses for vanishing external pressure are given in Figures 15.8–15.9. The constant ν is fixed by the overall increase in volume

$$\Delta V = \frac{b^3 - a^3}{B_0^3 - A_0^3}. \quad (15.42)$$

Resorption creates a compressive residual stress whereas growth in an elastic medium creates both compressive contact stress (close to the outer boundary) and tensile residual stress (around the inner boundary).

15.3 Limit-point Instability and Inflation Jump

The classic theory of rubber materials predicts that for particular choices of strain-energy functions and parameters, a limit-point instability may occur in spherical shells as the internal pressure is increased [8, 17, 198, 433, 922, 974]. This effect is triggered by the loss of monotonicity of the function $t_r(\alpha_b)$ as a function of α_a , that is, the pressure–stretch curve has a local maximum (see Figure 15.4) and the resulting instability is known as a *limit-point instability*, as discussed in Section 11.8.3.1.

For example, consider the Mooney–Rivlin strain-energy function

$$W = \frac{\mu}{2(1 + \nu)} (\alpha_r^2 + \alpha_\theta^2 + \alpha_\phi^2 - 3) + \frac{\nu}{2(1 + \nu)} (\alpha_r^{-2} + \alpha_\theta^{-2} + \alpha_\phi^{-2} - 3). \quad (15.43)$$

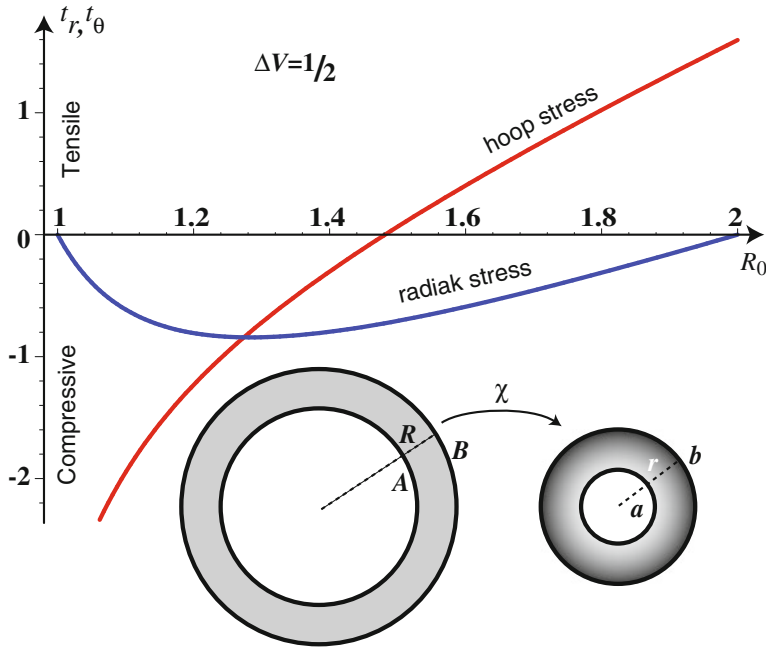


Figure 15.8 Radial and hoop stresses due to shrinking in a vacuum ($\Delta V = 1/2$, i.e., $\nu \approx -0.39$) for a neo-Hookean elastic shell with $A_0 = 1$, $B_0 = 2$ and $\mu_{sh} = 1$.

The pressure stretch curve $t_r(\alpha_b)$ as a function of α_a may present a maximum followed by a minimum at finite stretch as shown in Figure 15.10. Therefore, under controlled pressure, the stretch may jump for increasing pressure and present a hysteresis loop when the pressure is reduced leading to an *inflation jump*. This jump is more pronounced in thinner shells.

To understand the effect of thickness on this instability, we follow [465, 975] and consider

$$t_r(\alpha) = \int_{\alpha_a}^{\alpha} \frac{\widehat{W}'(\alpha)}{1 - \alpha^3} d\alpha, \quad \text{and} \quad -P = \int_{\alpha_a}^{\alpha_b} \frac{\widehat{W}'(\alpha)}{1 - \alpha^3} d\alpha. \quad (15.44)$$

We use the mean-value theorem and expand (15.44) to second order in $\delta = (B_0 - A_0)/A_0$ to obtain

$$t_r(\alpha) = \delta \frac{\widehat{W}'(\alpha)}{\alpha^2} + \frac{\delta^2}{2\alpha^4} \left[\frac{\alpha^3 - 2}{\alpha} \widehat{W}'(\alpha) - (\alpha^3 - 1) \widehat{W}''(\alpha) \right] + \mathcal{O}(\delta^3), \quad (15.45)$$

where α is now the position of the inner radius. Since the wall thickness is assumed to be small, this relation also describes the stress field at every point in the shell.

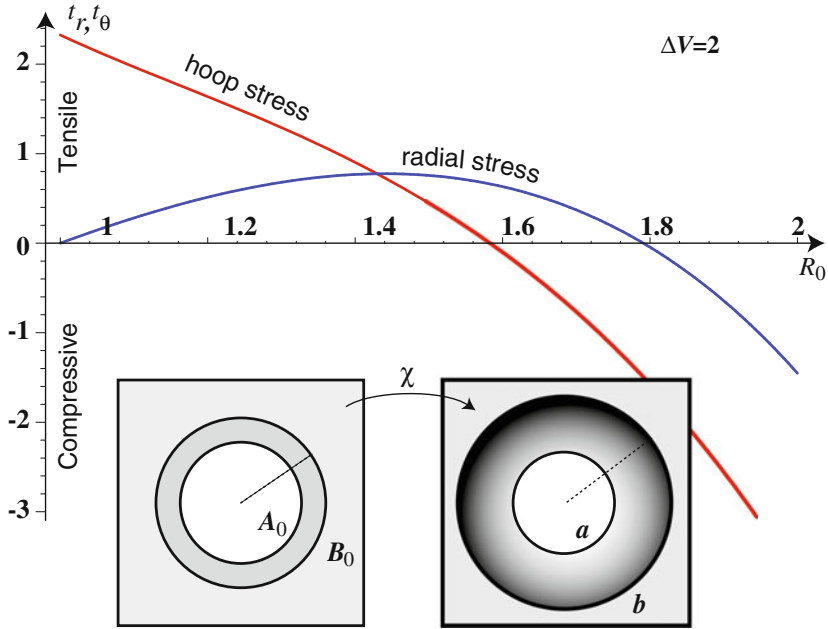


Figure 15.9 Radial and hoop stresses due to growth inside an elastic medium ($\Delta V = 2$, i.e., $\nu \approx 0.378$) for a neo-Hookean elastic shell with $A = 1$, $B = 2$ and $\mu_{\text{sh}} = \mu_{\text{me}} = 1$.

A limit-point instability occurs for α_{cr} such that $t'_r(\alpha_{\text{cr}}) = 0$. Writing $t'_r = 0$ to order $\mathcal{O}(\delta)$, we recover the condition for the critical hoop stretch for thin shells [551], that is,

$$\widehat{W}''(\alpha)\alpha - 2\widehat{W}'(\alpha) = 0. \quad (15.46)$$

For instance, in the case of a neo-Hookean strain-energy function, we have

$$W = \frac{\mu}{2}(\alpha_r^2 + \alpha_\theta^2 + \alpha_3^2 - 3), \quad \widehat{W} = \frac{\mu}{2}(\alpha^{-4} + 2\alpha^2 - 3), \quad (15.47)$$

and a limit-point instability appears at $\alpha = 7^{1/6}$.

To explore the dependence of the critical stretch with thickness, we expand α_{cr} to first order in δ as

$$\alpha_{\text{cr}} = \alpha_0 + \alpha_1\delta + \mathcal{O}(\delta^2), \quad (15.48)$$

where α_0 is chosen as the smallest solution of

$$\widehat{W}''(\alpha_0)\alpha_0 - 2\widehat{W}'(\alpha_0) = 0, \quad (15.49)$$

which is larger than one.

Using $t'_r = 0$ to order $\mathcal{O}(\delta^2)$, and making use of (15.49), we find that α_1 is given by

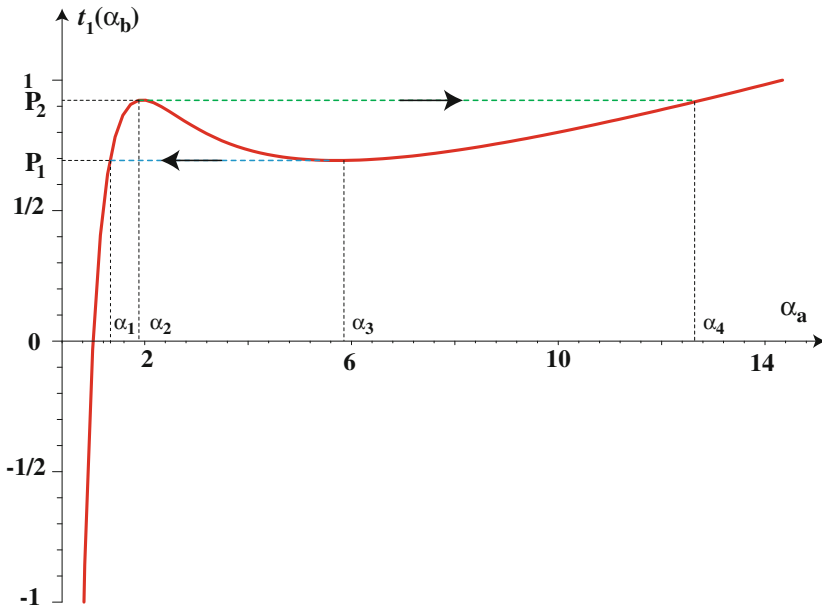


Figure 15.10 Inflation jump: For a Mooney–Rivlin material with $\mu = 1.886$, $\nu = -0.05$, the curve $t_r(\alpha_b)$ as a function of α_a has a minimum and a maximum ($A = 1$, $B = 2$, $\gamma_r = \gamma_\theta = 1$). If the internal pressure of the shell is raised to P_2 , a sudden inflation occurs through a jump from α_2 to α_4 . When pressure is decreased to P_1 , a second jump from α_3 to α_1 occurs.

$$\alpha_0^3 - 2\alpha_1\alpha_0^2 - 1 = 0. \quad (15.50)$$

It follows that

$$\alpha_{\text{cr}} = \alpha_0 + \frac{\alpha_0^3 - 1}{2\alpha_0^2} \delta + \mathcal{O}(\delta^2). \quad (15.51)$$

The first correction (15.51) shows that *universally* (independent of the constitutive relation), the critical stretch for the limit-point instability increases with thickness for thin shells. In other words, thicker membranes are always more stable against limit-point instabilities during inflation.

For a given model, we can identify the critical value of the parameters where this instability disappears. We start with the strain-energy function (15.43) for a Mooney–Rivlin material. The limit-point disappears as ν increases to ν_{cr} when the curve $t_r(\alpha)$ becomes strictly monotonic. This critical point is found by solving $t'_r = t''_r = 0$, which gives

$$\nu_{\text{cr}} = \frac{2\sqrt{11} - 3}{5(19 + 6\sqrt{11})^{1/3}} \approx 0.21446, \quad \alpha_{\text{cr}} = (19 + 6\sqrt{11})^{1/6} \approx 1.84073. \quad (15.52)$$

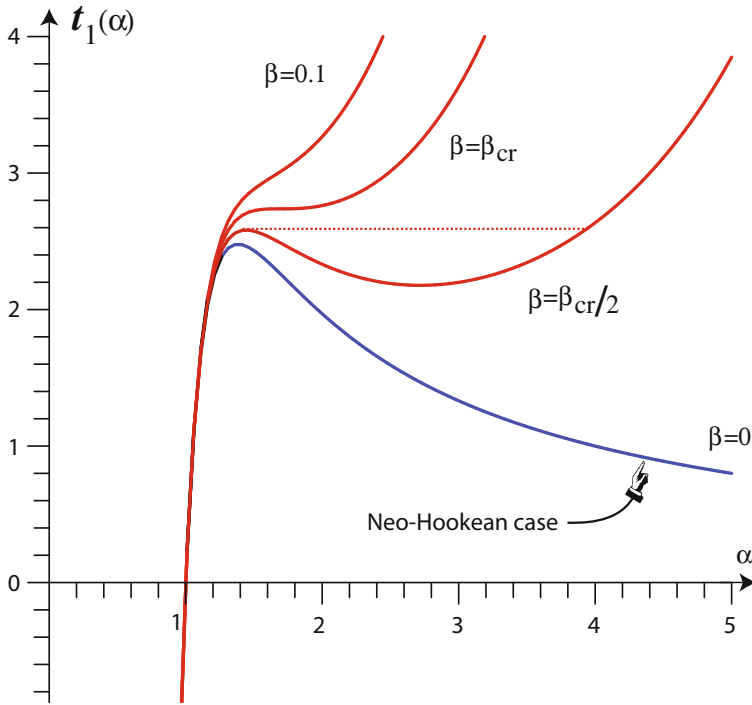


Figure 15.11 Pressure–stretch curve for a Fung material. The limit $\beta = 0$ corresponds to a neo-Hookean material. When $0 < \beta < \beta_{\text{cr}}$, the system exhibits a limit-point instability and an inflation jump (see dotted line when $\beta = \beta_{\text{cr}}/2$). For $\beta \geq \beta_{\text{cr}}$, the limit-point instability disappears.

The situation is similar for Fung materials

$$W_{\text{fu}} = \frac{\mu}{2\beta} [\exp \beta(I_1 - 3) - 1], \quad (15.53)$$

as shown in Figure 15.11, where we can readily identify the critical values of the parameters:

$$\beta_{\text{cr}} = \frac{1}{48} \frac{(92 + 12\sqrt{65})^{2/3} (3 + \sqrt{65})}{57 + 7\sqrt{65}} \approx 0.06685, \quad (15.54)$$

$$\alpha_{\text{cr}} = \frac{1}{\sqrt{2}} (92 + 12\sqrt{65})^{1/6} \approx 1.69355. \quad (15.55)$$

Hence, when $\beta > 0.067$, as is the case for soft biological tissues, there are no limit-point instabilities [72], in accordance with Osborne’s early observations [1000] depicted in Figure 11.1.

For Gent materials,

$$W_{\text{ge}} = -\frac{\mu}{2\beta} \log[1 - \beta(I_1 - 3)], \quad (15.56)$$

we find that the limit-point instability disappears when $\beta > \beta_{\text{cr}}$, given by

$$\beta_{\text{cr}} = \frac{1}{3} \frac{(10 + \sqrt{93})^{2/3} (3 + \sqrt{93})}{315 + 33\sqrt{93} - (10 + \sqrt{93})^{2/3} (3 + \sqrt{93})} \approx 0.05669, \quad (15.57)$$

and the corresponding critical stretch is

$$\alpha_{\text{cr}} = (10 + \sqrt{93})^{1/6} \approx 1.64262. \quad (15.58)$$

For elastomers, Gent [433] found experimentally limit-point instabilities (and inflation jumps) for inflated shells with $\beta = 0.01$ and $\beta = 0.03$. However, Horgan and Saccomandi [619] estimated that $\beta \approx 0.44$ for the aorta of a 21-year-old male and that $\beta \approx 2.4$ for the (stiffer) aorta of a 70-year-old male. In these instances, no limit-point instability is possible as the strain-stiffening property of the material prevents them from occurring.

The behavior for a one-term Ogden material

$$W_{\text{og1}} = \frac{2\mu}{\beta^2} (\lambda_1^\beta + \lambda_2^\beta + \lambda_3^\beta - 3), \quad (15.59)$$

is slightly different as shown in Figure 15.12. Here again, the limit-point instability disappears at $\beta_c = 3$, below any realistic physiological values. The asymptotic limits for $t_r(\alpha)$ as $\alpha \rightarrow \infty$ are, however, different (0, 2, and ∞ for $0 < \beta < 3$, $\beta = 3$, and $\beta > 3$, respectively). Note finally that there is no inflation jump for any value of $\beta > 3$.

We conclude that for soft biological tissues, the critical parameter values are far below any typical range of physiological values so that the limit-point instability is unlikely to be observed. As noted repeatedly by Humphrey and coworkers [262, 544, 635], this observation should be kept in mind when a strain-energy function is chosen in numerical simulations of soft tissues, and when designing artificial soft tissues for experiments. The choice of a rubber-like strain-energy function in the former case, or of an elastomer in the latter case, might lead to instabilities which do not actually exist in the naturally occurring soft tissue.

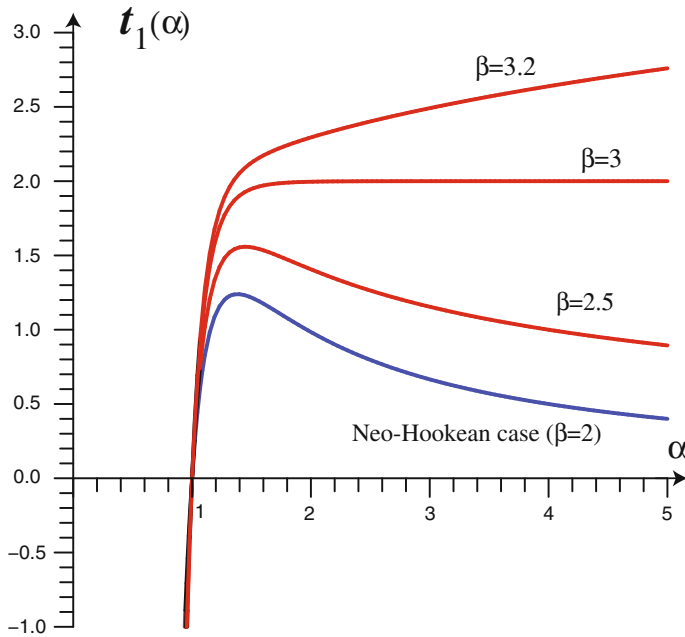


Figure 15.12 Pressure–stretch curve for a one-term Ogden material. The neo-Hookean material corresponds to $\beta = 2$. For $2 \leq \beta < 3$, the system exhibits a limit-point instability, and $t_r(\alpha) \rightarrow 0$ as $\alpha \rightarrow \infty$. For $\beta = 3$, $t_r(\alpha) \rightarrow 2$ as $\alpha \rightarrow \infty$. For $\beta > 3$, $t_r(\alpha) \rightarrow \infty$ as $\alpha \rightarrow \infty$ and the limit-point instability disappears.

15.3.1 The Effect of Growth on the Limit-point Instability

Growth can change the property of a material to allow or prevent inflation jumps. As an example, consider a nongrowing material and values of the parameters where there is no instability, that is, the strain is a continuous monotonic function of the applied pressure as shown in Figure 15.13A.

Now, for the same elastic material with radial growth, shown in Figure 15.13B, an inflation jump occurs if γ is large enough. To understand how growth, geometry, and elasticity control this effect, we compute the derivative of the pressure as a function of α_a from (15.29) to obtain

$$\left(\frac{\alpha_a}{\gamma} - \alpha_a^{-2}\right) \frac{dP}{d\alpha_a} = \frac{\partial_{\alpha_b} \widehat{W}(\alpha_b)}{\alpha_b^2} - \frac{\partial_{\alpha_a} \widehat{W}(\alpha_a)}{\alpha_a^2}. \quad (15.60)$$

We conclude that limit-point instabilities are controlled by the function $(\partial_{\alpha} \widehat{W}(\alpha))/\alpha^2$ as found in Equation (15.45) and that the only dependence on growth enters in the strain through relation (15.27). Therefore, the effect of constant radial or hoop growth

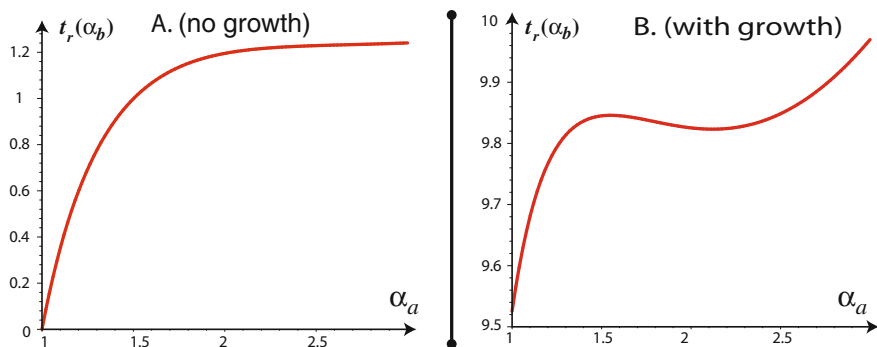


Figure 15.13 Limit-point instability for a growing Mooney–Rivlin material with $\mu = 5/3$, $\nu = -1/6$, $A_0 = 1$, $B_0 = 2$. A. The curve $t_r(\alpha_b)$ is monotonic for a non-growing material ($\gamma_1 = \gamma_2 = 1$). B. For a growing material ($\gamma_1 = 8$, $\gamma_2 = 1$) the curve $t_r(\alpha_b)$ has a minimum and a maximum and the strain becomes a discontinuous function of the pressure.

is to effectively change the geometry of the shell, that is, a thick shell with radial growth effectively behaves as a thin shell.

We can quantify the combined effects of growth and thickness for neo-Hookean materials undergoing anisotropic constant growth. The critical value of the stretch where such an instability occurs can be computed by taking a double expansion of (15.60) in the thickness δ and growth γ , to obtain

$$\alpha_a = 7^{1/6} \left\{ 1 + \frac{\delta \left[415513 - 157039 \sqrt{7} + (113960 - 43079 \sqrt{7}) (\gamma - 1) \right]}{14(55\sqrt{7} - 148)^2} + O(\delta^2, (\gamma - 1)^2) \right\}, \quad (15.61)$$

$$\approx 1.383 \{ 1 + \delta [0.311 - 0.189(\gamma - 1)] \} + O(\delta^2, (\gamma - 1)^2), \quad (15.62)$$

where $\delta = (B_0 - A_0)/A_0$ measures the thickness of the shell.

15.4 Singularities in Growing Solid Spheres

We consider growth within a solid sphere ($a = A_0 = 0$) under an external pressure P . In particular, we are interested in the behavior of the stress at the origin. We start by considering constant anisotropic growth of the form (15.11) controlled by $\gamma = \gamma_r/\gamma_\theta$. The integration of (15.16) with $a = A_0 = 0$ gives

$$r^3 = \gamma_r \gamma_\theta R^3, \quad (15.63)$$

which together with the definition of $\alpha = r/(R_0\gamma_\theta)$ gives the stretch $\alpha = \gamma^{1/3}$. Then, Equation (15.23) reads

$$\frac{\partial t_r}{\partial R_0} = \frac{\beta}{R_0}, \quad \text{where} \quad \beta = \gamma^{1/3} \partial_\alpha \widehat{W} \Big|_{\alpha=\gamma^{1/3}}. \quad (15.64)$$

With the boundary condition $t_r(B) = -P$, the stress profile is

$$t_r = -P + \beta \ln \left(\frac{R_0}{B} \right). \quad (15.65)$$

Assuming that the strain-energy function W has a single minimum for $\gamma \neq 1$, we have $\beta \neq 0$, and the radial stress exhibits a logarithmic singularity. Note, however, that the principal stretches and hence the strain-energy function are finite everywhere.

The presence of a singularity in elasticity may seem surprising and unphysical. However, it is known that anisotropy can lead to stress singularities even for bodies with smooth boundaries [780, 1074]. For instance, the study of radially symmetric equilibrium configurations of transversely isotropic solid cylinders and balls under constant pressure on their boundaries demonstrates the existence of a pressure singularity above a critical applied pressure [34, 939]. Singularities due to material anisotropy in cylindrical and spherical geometries were also observed by several authors [47, 413]. Similarly, anisotropic eigenstrains are responsible for singularities [1354, 1356].

The existence of a singularity is intimately related to the behavior of the growth tensor at the origin. Indeed, for an arbitrary growth tensor, since $\gamma_r(R_0)$ and $\gamma_\theta(R_0)$ are both bounded and strictly positive, we can define

$$\gamma = \lim_{R_0 \rightarrow 0} \frac{\gamma_r(R_0)}{\gamma_\theta(R_0)}. \quad (15.66)$$

Then, we have

$$\frac{\partial t_r}{\partial R_0} = \frac{\beta}{R_0} + \mathcal{O}(1), \quad \beta = \gamma^{1/3} \partial_\alpha \widehat{W} \Big|_{\alpha=\gamma^{1/3}}, \quad (15.67)$$

and, we conclude again that if $\gamma \neq 1$, the radial stress exhibits a logarithmic singularity at the origin.

15.5 Cavitation

Elastic cavitation is the phenomenon in which a cavity appears in the interior of an elastic body under tension. Consider for instance the poker chip experiment shown in Figure 15.14 where a cylinder of rubber with Young's modulus E is glued to two

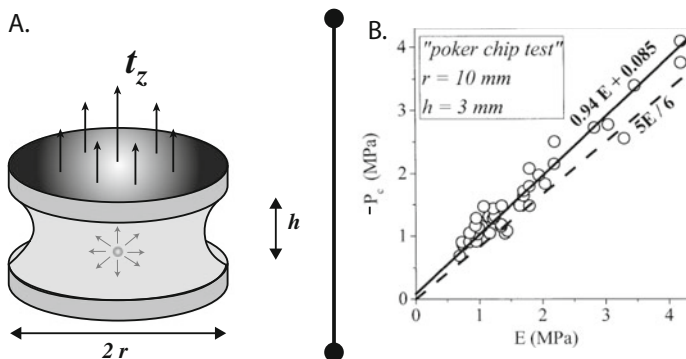


Figure 15.14 A. The poker-chip experiment. A cylinder of rubber is glued to two plates that are pulled apart. The deformation is supported by a nearly spherical tensile field at the center of the cylinder creating the conditions under which cavitation is predicted to happen. B. Experimental data for the poker-chip experiment (circles) compared to the theoretical prediction (dashed line) for a neo-Hookean material [371].

rigid plates that are pulled apart with stress t_z . The deformation creates a large tensile isotropic stress field at the center of the sample which is equivalent to a radial outward pressure P applied to a sphere. Experimental data show that the critical pressure at which a cavity first appears scales linearly with the Young's modulus.

This problem has received considerable interest in the literature, starting with the pioneering experimental work of Gent and Lindley [434] and the seminal mathematical analysis of Ball [53]. Gent and Lindley considered solid elastic spheres under uniform hydrostatic loads and found that the critical pressure at which radially symmetric configurations with an internal cavity emerge from the undeformed configuration is $P_{\text{crit}} = -5/6E$ for a neo-Hookean material with $W_{\text{nh}} = E/6(I_1 - 3)$.

Since the work of Ball, cavitation has received substantial attention and has been studied for various situations—compressibility versus incompressibility, anisotropy, and composite layers have all been analyzed in different combinations and for various material models [546, 613, 616, 800, 1028, 1040, 1168, 1169]. Further experimental and numerical works have validated the theoretical approaches of some of these theories [204, 290, 294, 371, 1263].

Within our framework, cavitation can easily be understood by looking for a solution of the boundary-value problem of a sphere ($A_0 = 0$) under tensile pressure such that the inner radius in the current configuration is strictly positive $a > 0$. The smallest value of the pressure for which such a solution exists is the critical pressure.

15.5.1 Cavitation Induced by Tensile Loading

We first integrate the equation for the radial stress (15.22) in the absence of growth:

$$\frac{\partial t_r}{\partial \alpha} = \frac{\partial_\alpha \widehat{W}}{1 - \alpha^3}, \quad t_r(\alpha_a) = 0, \quad t_r(\alpha_b) = -P, \quad (15.68)$$

to obtain

$$-P = \int_{\alpha_a}^{\alpha_b} \frac{\partial_\alpha \widehat{W}}{1 - \alpha^3} d\alpha. \quad (15.69)$$

In the limit $A_0 \rightarrow 0$, we have $\alpha_a \rightarrow \infty$ and $\alpha_b \rightarrow 1$ so that

$$P_{\text{crit}} = \int_1^\infty \frac{\partial_\alpha \widehat{W}}{1 - \alpha^3} d\alpha. \quad (15.70)$$

This integral is improper and the existence of a finite critical pressure depends on the behavior of $\widehat{W}$ as $\alpha \rightarrow \infty$. If, in that limit, $\widehat{W} \sim \alpha^n$ then

$$\frac{\partial_\alpha \widehat{W}}{1 - \alpha^3} \sim \alpha^{n-4}, \quad (15.71)$$

and the integral converges if $n < 3$ [616]. For instance, in the neo-Hookean case, taking the limit $\alpha_a \rightarrow \infty$ and $\alpha_b \rightarrow 1$ in (15.32) with $t_r(\alpha_b) = -P$, $\mu = E/3$ gives $P_{\text{crit}} = -5E/6$ as shown in Figure 15.14.

The fact that cavitation depends both on the material response and on the particular geometry; that it changes the topology of the material; and that it relies on the assumption that elasticity remains valid at the microstructure suggest that cavitation may not be a robust material feature. However, cavitation is an idealized concept. If there exists a microvoid in the material, cavitation is replaced by the problem of cavity opening, which does not suffer the topological instabilities encountered in pure cavitation. If the cavity is small enough, the bifurcation is essentially indistinguishable from the ideal cavitation problem and no experiment could differentiate between microvoid opening and pure cavitation.

15.5.2 Cavitation Induced by Growth

We showed that cavitation can occur as a consequence of external mechanical loading. However, growth or swelling can also induce cavitation [850, 1023, 1024] as we will now demonstrate. We study the possibility of growth-induced cavitation following [469] by looking at the existence of nontrivial solutions for given growth functions γ_r and γ_θ . We consider two complementary cases, first the case of anisotropic and homogeneous growth and second, the case of isotropic and inhomogeneous growth.

We restrict our attention to a neo-Hookean energy function and scale all forces by taking the elastic modulus to be $\mu = 1$, which corresponds to a Young's modulus of $E = 3$.

In the first case (anisotropic growth), we take, without loss of generality, an outer radius $B_0 = 1$ and $\gamma_r = 1$. Then, (15.23) can be integrated explicitly to obtain an implicit relationship between a and γ_θ . In Figure 15.15, we graph the solution $a = a(\gamma_\theta, A)$ for various initial inner radii.

The cavitated solution from the solid sphere corresponds to the choice $A_0 = 0$. A local analysis of the solution close to $\gamma_\theta = 1$ leads to

$$a \underset{\gamma_\theta \rightarrow 1}{\sim} \sqrt{3} \exp \left[\frac{\sqrt{3}\pi}{18} - \frac{66\gamma_\theta^2 + 183\gamma_\theta - 114}{36(5\gamma_\theta + 1)(\gamma_\theta - 1)} \right], \quad (15.72)$$

which clearly establishes the existence of a cavitated solution whose inner radius is exponentially small close to $\gamma_\theta = 1$, but nonvanishing for all values of $\gamma_\theta > 1$. This situation is in contrast to the classic cavitation case discussed previously for which the base solution exists for all pressure and a large value of the external traction is required to obtain a cavitated solution. Physically, the two problems are different due to the particular boundary conditions associated with the residual stress field. The effect of anisotropic growth and residual stress is to create large radial tension close to the inner radius. In the classic case, a large elastic energy is necessary to balance a large gradient of radial stress close to the inner boundary which jumps from a finite value for the base solution to zero on the bifurcated solution.

In Figure 15.15, the radial stress is plotted for some cavitated solutions. Notice that the magnitude of the stress and its gradient close to the origin are larger in the solution with the smaller cavity radius.

In the case of inhomogeneous growth), we set $\gamma_r = \gamma_\theta = 1 + \beta r$ with constant β . Then, a cavity opens for $\beta > \beta_{\text{crit}} \approx 0.8971637$ as shown in Figure 15.16. Here the radial tension at the origin increases with β up to the critical point where sufficient elastic energy has been built in the system to trigger cavitation. A similar mechanical environment could be created by considering an elastic sphere surrounded by a growing spherical shell. Again, for sufficiently large growth, the tension created by the shell pulling on the sphere would be enough to open a cavity.

Therefore, we conclude that growth, either inhomogeneous or anisotropic, could be a simple and universal mechanism to open cavities in elastic materials. Its potential relevance to biological matter and the opening of plant stem will be discussed in Section 16.2.

15.6 Instability Due to Anisotropic Growth

Buckling computations for pressurized spherical shells in the absence of growth have a long history going back to the work of Wesolowski [1313] and Wang and Ertepinar

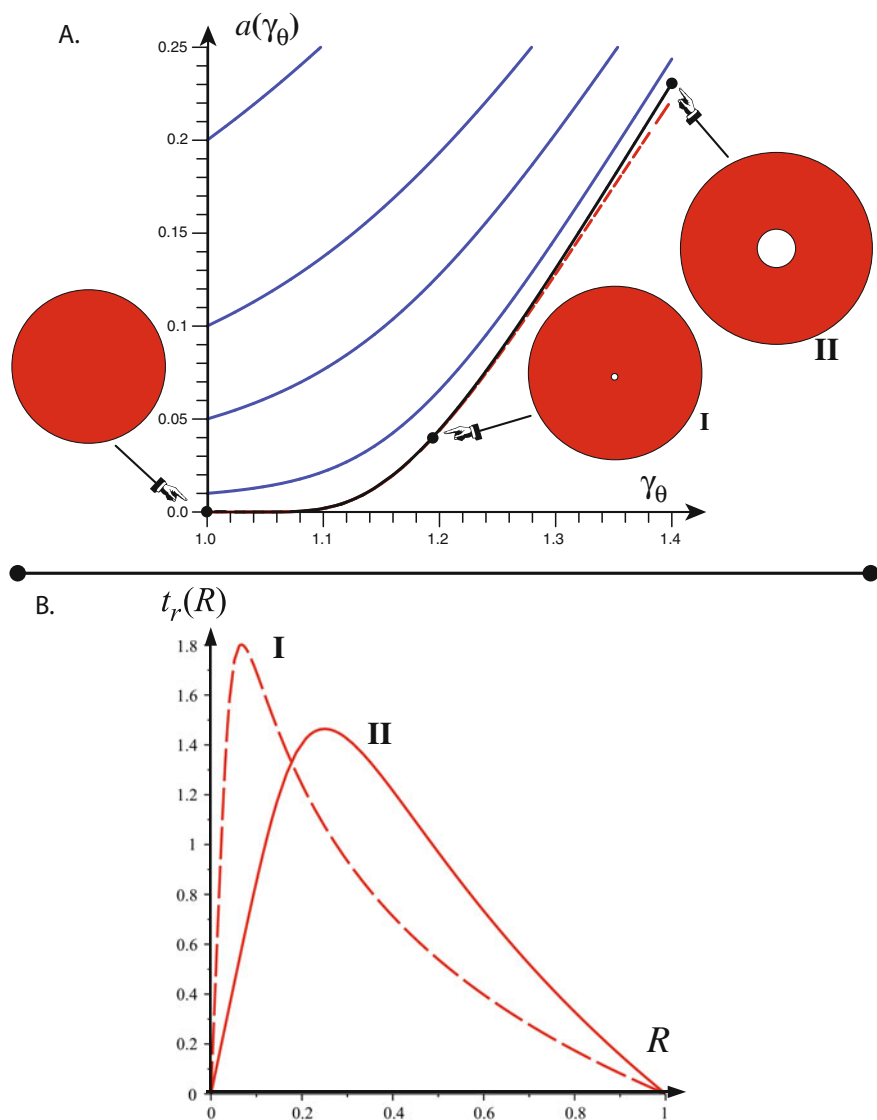


Figure 15.15 A. Growth-induced cavitation of a sphere of initial radius 1 with constant anisotropic growth ($\gamma_r = 1$, $\gamma_\theta \geq 1$). Dashed curve: asymptotic solution. Solid curves correspond to cavity opening of a shell of initial inner radius $A = 0.01, 0.05, 0.1, 0.2$ due to growth. B. Radial residual stress corresponding to the two highlighted solutions. The dashed curve corresponds to the solution with smaller cavity radius. In both cases the sphere is in radial tension, but as the cavity opens the magnitude of the radial tension decreases.

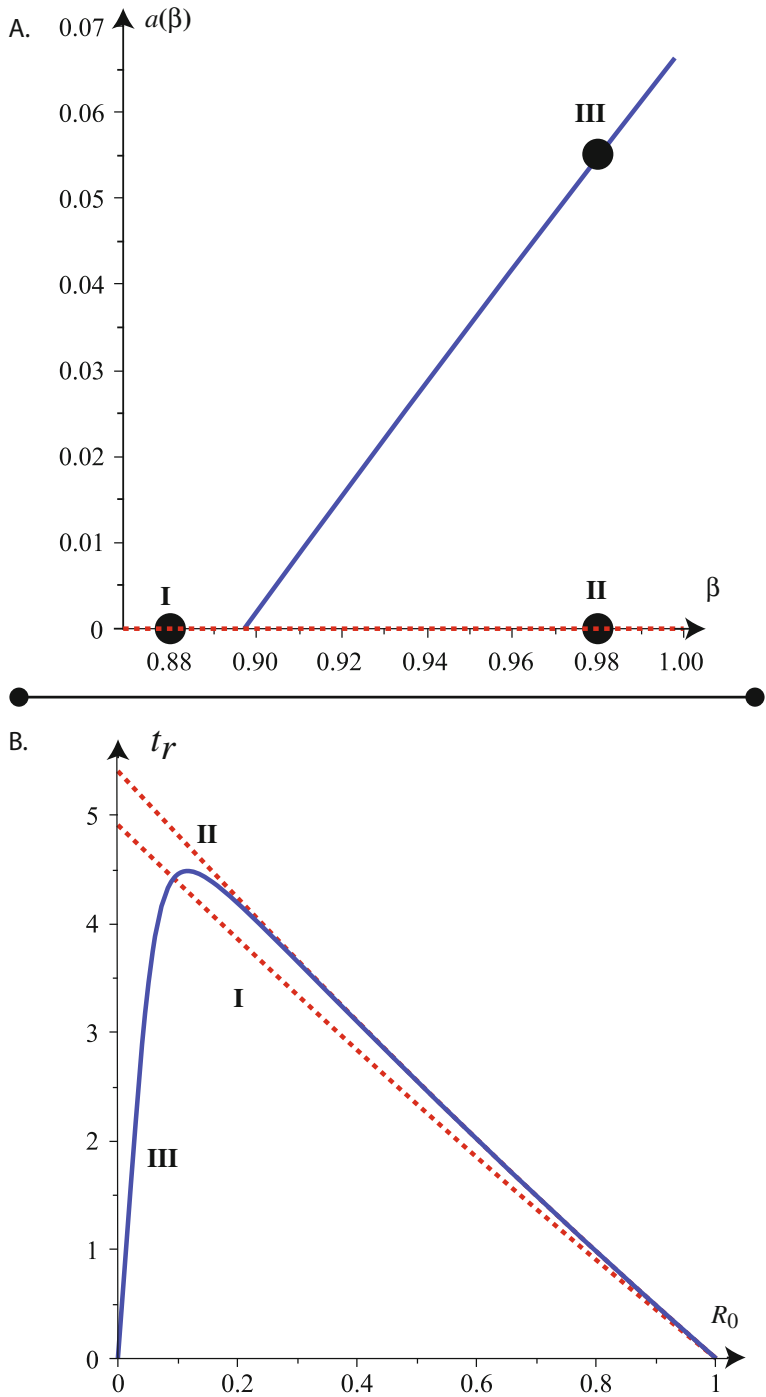


Figure 15.16 Growth-induced cavitation of a sphere of initial radius 1 with isotropic homogeneous growth ($\gamma_r = \gamma_\theta = 1 + \beta R$). A. Opening a as a function of β after the critical value β_{crit} . B. Radial stress as a function of initial radius R for $\beta = 0.88$ and $\beta = 0.98$; dashed curve: base solution, solid curves, the cavitated solution with zero radial tension at the boundaries.

[1290] on the neo-Hookean shell. Later on, Hill [575], Haughton and Ogden [551], Ogden [975], and Chen and Healey [198] obtained results for general strain-energy functions and thin pressurized shells (see also [465] for the role of strain-stiffening on the bifurcation condition). Work on asymptotic limits, the relationship with other stability criterion and the eversion problem include studies by Fu [397], Haughton and Kirkinis [547, 550], and Haughton and Chen [549].

We consider the possible bifurcations of a growing shell following the method outlined in Section 14.8. We start with the base solution obtained for the radially symmetric deformation of a growing shell under pressure. Once the change in radius due to growth and applied stress has been established, we study the existence of nearby non-radial deformation with respect to changes in the control parameters.

We first look at the case of an incompressible elastic shell subject to constant anisotropic growth and uniform hydrostatic pressure P . The base solution is given in Section 15.2.1 and we recall that

$$[\mathbf{G}] = \text{diag}(\gamma_r, \gamma_\theta, \gamma_\theta), \quad [\mathbf{A}^{(0)}] = \text{diag}(\alpha^{-2}, \alpha, \alpha), \quad (15.73)$$

so that

$$r' = \gamma_r / \alpha^2, \quad r/R_0 = \alpha \gamma_\theta, \quad (15.74)$$

and

$$\alpha^3 = \gamma \left(1 - \frac{A_0^3}{R_0^3} \right) + \frac{a^3}{\gamma_\theta^3 R_0^3}, \quad (15.75)$$

where $\gamma = \gamma_r / \gamma_\theta$. The elastic stretch at the outer boundary is

$$\alpha_b^3 = \gamma \left(1 - \frac{A_0^3}{R_0^3} \right) + \alpha_a^3 \left(\frac{A_0}{B_0} \right)^3. \quad (15.76)$$

The stretch α satisfies the equation

$$\frac{d\alpha}{dr} = \frac{\alpha}{r} - \frac{\alpha^4}{r\gamma}. \quad (15.77)$$

To lowest order, the base solution for the radial stress is

$$t_r^{(0)}(\alpha) = \gamma \int_{\alpha_a}^{\alpha} \frac{\partial_\alpha \widehat{W}}{(\gamma - \alpha^3)} d\alpha, \quad (15.78)$$

where, as before, $\widehat{W} = W(\alpha^{-2}, \alpha, \alpha)$. We further restrict our attention to the case of a growing neo-Hookean material for which we have

$$\widehat{W} = \frac{\mu}{2}(\alpha^{-4} + 2\alpha^2 - 3). \quad (15.79)$$

For a given set of fixed parameters $A, B, \gamma_r, \gamma_\theta$, the base solution is completely specified by the pressure P . The problem is now to establish the existence of solutions that are not radially symmetric for some values of these parameters.

Step 1: Kinematics of incremental deformations. The general form for the first-order deformation $\chi^{(1)}$ describing the bifurcation of a spherical shell is

$$\chi^{(1)} = u(r, \theta, \varphi)\mathbf{e}_r + v(r, \theta, \varphi)\mathbf{e}_\theta + w(r, \theta, \varphi)\mathbf{e}_\varphi. \quad (15.80)$$

The standard procedure is to expand the functions (u, v, w) in spherical harmonics and solve Equation (14.116) for each mode. However, in the determination of the parameters where a bifurcation occurs, it has been established in the classic case [1290, 1313], and verified in the case of a growing shell, that the equation for w decouples so that w does not play a role in the bifurcation. Furthermore, the equations for all spherical harmonics are identical. Therefore, the analysis to zeroth order, corresponding to Legendre polynomials, is sufficient to identify the bifurcation point.

We conclude that the bifurcation analysis of the spherical shell reduces to the analysis of axisymmetric deformations, that is,

$$\chi^{(1)} = u(r, \theta)\mathbf{e}_r + v(r, \theta)\mathbf{e}_\theta. \quad (15.81)$$

To compute the deformation gradient of $\chi^{(1)}$, we recall that if $f = f(r, \theta, \varphi)$, then

$$\text{grad}(f) = (\partial_r f)\mathbf{e}_r + \frac{1}{r}(\partial_\theta f)\mathbf{e}_\theta + \frac{1}{r \sin \theta}(\partial_\varphi f)\mathbf{e}_\varphi. \quad (15.82)$$

Using this identity to compute the gradient of $\chi^{(1)}$ leads to

$$[\mathbf{F}^{(1)}] = [\text{grad } \chi^{(1)}] = \begin{bmatrix} \partial_r u & (\partial_\theta u - v)/r & 0 \\ \partial_r v & (\partial_\theta v + u)/r & 0 \\ 0 & 0 & (u + v \cot \theta)/r \end{bmatrix}. \quad (15.83)$$

The condition (14.105) gives

$$r \partial_r u + 2u + \partial_\theta v + v \cot \theta = 0. \quad (15.84)$$

Step 2: Linearized equations. In order to compute the components of $\text{div } \mathbf{T}^{(1)} = \mathbf{0}$ given explicitly by (14.116), we also need the expression for the divergence of an arbitrary tensor $\mathbf{A}$ in spherical coordinates:

$$[\operatorname{div} \mathbf{A}]_r = \frac{1}{r^2} \partial_r (r^2 A_{rr}) + \frac{1}{r \sin \theta} \partial_\theta (A_{\theta r} \sin \theta) + \frac{1}{r \sin \theta} \partial_\varphi A_{\varphi r} - \frac{A_{\theta\theta} + A_{\varphi\varphi}}{r}, \quad (15.85)$$

$$[\operatorname{div} \mathbf{A}]_\theta = \frac{1}{r^2} \partial_r (r^2 A_{r\theta}) + \frac{1}{r \sin \theta} \partial_\theta (A_{\theta\theta} \sin \theta) + \frac{1}{r \sin \theta} \partial_\varphi A_{\varphi\theta} + \frac{A_{\theta r} - \cot \theta A_{\varphi\varphi}}{r}, \quad (15.86)$$

$$[\operatorname{div} \mathbf{A}]_\varphi = \frac{1}{r^2} \partial_r (r^2 A_{r\varphi}) + \frac{1}{r \sin \theta} \partial_\theta (A_{\theta\varphi} \sin \theta) + \frac{1}{r \sin \theta} \partial_\varphi A_{\varphi\varphi} + \frac{A_{\varphi r} + \cot \theta A_{\varphi\theta}}{r}. \quad (15.87)$$

Then, the third component of $\operatorname{div} \mathbf{T}^{(1)} = \mathbf{0}$, written in spherical coordinates, vanishes identically.

Step 3: Linearized constitutive equations. We adapt the general expressions of the connections (14.122–14.127) relating the linearized Cauchy stress tensor to the instantaneous elastic moduli to express the two remaining equations as

$$c_1 \frac{\partial^2 u}{\partial r^2} + c_2 \frac{\partial u}{\partial r} + c_3 \frac{\partial^2 u}{\partial \theta^2} + c_4 \frac{\partial u}{\partial \theta} + c_5 u = \frac{\partial}{\partial r} q^{(1)}, \quad (15.88)$$

$$c_6 \frac{\partial^2 v}{\partial r^2} + c_7 \frac{\partial v}{\partial r} + c_8 \frac{\partial^2 u}{\partial r \partial \theta} + c_9 \left(\frac{\partial u}{\partial \theta} - v \right) = \frac{1}{r} \frac{\partial}{\partial \theta} q^{(1)}, \quad (15.89)$$

with

$$c_1 = \mathcal{L}_{1111} - \mathcal{L}_{1122} - \mathcal{L}_{1212} + \alpha_1 W_1, \quad (15.90)$$

$$c_2 = \frac{1}{r} \left[r^{-1} \frac{\partial}{\partial r} (r^2 \mathcal{L}_{1111} - r^2 \mathcal{L}_{1122}) + \mathcal{L}_{2222} - 2\mathcal{L}_{1122} - 2\mathcal{L}_{1212} + \mathcal{L}_{2233} + 2\alpha_1 W_1 - \alpha_2 W_2 + r^{-1} \frac{\partial}{\partial r} (r^2 \alpha_1 W_1) \right], \quad (15.91)$$

$$c_3 = r^{-2} \mathcal{L}_{2121}, \quad c_4 = r^{-2} \cot(\theta) \mathcal{L}_{2121}, \quad c_5 = 2r^{-2} \mathcal{L}_{2121}, \quad (15.92)$$

$$c_6 = \mathcal{L}_{1212}, \quad c_7 = r^{-2} \frac{\partial}{\partial r} (r^2 \mathcal{L}_{1212}), \quad (15.93)$$

$$c_8 = \frac{1}{r} (\mathcal{L}_{1122} - \mathcal{L}_{2222} + \mathcal{L}_{1212} - \alpha_1 W_1), \quad (15.94)$$

$$c_9 = r^{-2} \left[r^{-1} \frac{\partial}{\partial r} (r^2 \mathcal{L}_{1212}) - \mathcal{L}_{2222} + \mathcal{L}_{2233} - \alpha_2 W_2 \right]. \quad (15.95)$$

Equations (15.84) and (15.88–15.89) form a system of three linear partial differential equations for $(u, v, q^{(1)})$. The standard method to solve (15.88–15.89) is to express all variables of r and θ into products of a function of r alone and a Legendre polynomial in $\cos(\theta)$. We write

$$u(r, \theta) = U_n(r) P_n(\cos \theta), \quad (15.96)$$

$$v(r, \theta) = V_n(r) \frac{d}{d\theta} P_n(\cos \theta), \quad (15.97)$$

$$q^{(1)}(r, \theta) = Q_n(r) P_n(\cos \theta), \quad (15.98)$$

where $P_n(\cos \theta)$ are the Legendre polynomials for which the following standard equality [2, Chap. 8] holds:

$$\frac{d^2}{d\theta^2} P_n(\cos \theta) + \cot \theta \frac{d}{d\theta} P_n(\cos \theta) + n(n+1) P_n(\cos \theta) = 0. \quad (15.99)$$

Step 4: The boundary-value problem. By substituting (15.97–15.98) into (15.84–15.89), together with identity (15.99), one can express V_n and Q_n as a function of U_n and its derivatives to obtain a closed fourth-order linear ordinary differential equation for U_n :

$$C_4 \frac{d^4 U_n}{dr^4} + C_3 \frac{d^3 U_n}{dr^3} + C_2 \frac{d^2 U_n}{dr^2} + C_1 \frac{dU_n}{dr} + C_0 U_n = 0. \quad (15.100)$$

In the case of constant anisotropic growth, these coefficients are

$$C_4 = r^4 \gamma^2, \quad (15.101)$$

$$C_3 = 8\alpha^3 r^3 \gamma, \quad (15.102)$$

$$C_2 = r^2 [(4 - \gamma^2(n^2 + n - 2)) \alpha^6 + 16\gamma\alpha^3 - \gamma^2(n^2 + n + 10)], \quad (15.103)$$

$$C_1 = r^2 [2\gamma(n^2 + n - 2)\alpha^9 - 4(\gamma^2(n^2 + n - 2) - 2)\alpha^6 - 4\gamma(n^2 + n + 8)\alpha^3 + 2\gamma^2(n^2 + n + 10)], \quad (15.104)$$

$$C_0 = (n^2 + n - 2) [4\gamma\alpha^9 + (\gamma^2(n^2 + n - 2) + 4)\alpha^6 - 16\gamma\alpha^3 + 10\gamma^2]. \quad (15.105)$$

The boundary conditions are

$$\mathbf{T}^{(1)} \mathbf{n} = 0 \quad \text{on } r = a, \quad (15.106)$$

$$\mathbf{T}^{(1)} \mathbf{n} = -P^{(1)} \mathbf{n} \quad \text{on } r = b. \quad (15.107)$$

With the help of (14.115), the boundary conditions for the incremental deformation take the form

$$\mathbf{T}^{(1)} \mathbf{n} = (\mathcal{L} : \mathbf{F}^{(1)} + \mathbf{F}^{(1)} \cdot \mathbf{A}^{(0)} \cdot \mathbf{W}_A - q^{(1)} \mathbf{1}) \mathbf{n}. \quad (15.108)$$

For the particular homogeneous isotropic case under consideration, the radial and hoop components of the traction provide two boundary conditions on $U(r)$ at $r = a, b$:

$$\begin{aligned} r^3 \gamma \frac{d^3 U_n}{dr^3} + 2r^2 (\gamma + 2\alpha^3) \frac{d^2 U_n}{dr^2} \\ + r \left[8\alpha^3 - 2\gamma(2 + n + n^2) - \gamma\alpha^6(n^2 + n - 2) \right] \frac{dU_n}{dr} \\ + (-2\gamma\alpha^6 + 4\alpha^3 - 2\gamma)(n^2 + n - 2)U_n = 0, \end{aligned} \quad (15.109)$$

$$\frac{d^2 U_n}{dr^2} + \frac{2}{r} \frac{dU_n}{dr} + \frac{(n^2 + n - 2)}{r^2} U = 0. \quad (15.110)$$

The integration of (15.100) takes place between $r = a$ and $r = b$ and the central problem of solving this equation lies in finding, for a given initial thickness A_0/B_0 , the value of a such that the boundary conditions are satisfied (the outer radius b being a function of a).

In the case of a growing shell, the outer radius b depends not only on the initial thickness A_0/B_0 , but also on the parameters γ_r and γ_θ that describe growth through Equation (15.75).

The mode $n = 0$ corresponds to a symmetric increase in shell radius and is not a true axisymmetric bifurcation but a limit-point instability as discussed in Section 15.3. The stability of a pressurized shell and the critical mode (the first unstable mode $n > 0$) depends on whether the pressure is applied internally ($P < 0$) or externally ($P > 0$), its thickness, and the choice of strain-energy functions. If the pressure is applied internally, a bifurcation analysis [975] shows that the unstable mode depends on the choice of strain-energy function and the thickness of the shell. However, neo-Hookean shells under internal pressure are always stable under axisymmetric perturbations. Therefore, this case will not be further discussed and, instead, we focus our attention on the case of a growing material subject to external pressure ($P \geq 0$).

15.6.1 A Numerical Scheme

The first step in the analysis of the linearized equation (15.100) is to develop a numerical scheme that will help us identify the critical values of the parameters where a bifurcation takes place.

The general problem is to find the values of a parameter (say, λ) for which there is a solution of a fourth-order equation with mixed boundary values. Let $\mathbf{y} = [U, U', U'', U''']^T$ be the vector of variables and derivatives. The fourth-order problem can be written as a system of four first-order equations:

$$\mathbf{y}' = \mathbf{f}(\mathbf{y}; r), \quad (15.111)$$

where r is the independent variable. The boundary-value conditions are given by a set of four linear functions $\{c_i(\mathbf{y}(r); r), i = 1, 2, 3, 4\}$, that vanish at one of the boundaries, namely

$$c_{1,2}(\mathbf{y}(a); a) = 0, \quad c_{3,4}(\mathbf{y}(b); b) = 0. \quad (15.112)$$

In order to find values of the parameter for which a solution of the equation with the proper boundary conditions exists, the general strategy of the *determinant method* [80, 553, 554] is used. We consider two copies of system (15.111), that is,

$$(\mathbf{y}^{(1)})' = \mathbf{f}(\mathbf{y}^{(1)}; r), \quad (\mathbf{y}^{(2)})' = \mathbf{f}(\mathbf{y}^{(2)}; r). \quad (15.113)$$

The parameter λ in the system is given by the relationship between the endpoints a and b through relations such as (15.76). We integrate (15.113) with two linearly independent conditions $\mathbf{y}^{(1)}(a), \mathbf{y}^{(2)}(a)$ that satisfy both conditions at $r = a$ (that is, $c_{1,2}(\mathbf{y}^{(1,2)}(a); a) = 0$). Then, we carry the integration up to a point $r = b$, at which the determinant

$$\Delta(r) = \begin{vmatrix} c_3(\mathbf{y}^{(1)}(r); r) & c_3(\mathbf{y}^{(2)}(r); r) \\ c_4(\mathbf{y}^{(1)}(r); r) & c_4(\mathbf{y}^{(2)}(r); r) \end{vmatrix}, \quad (15.114)$$

vanishes identically. By the linear superposition principle, if $\Delta(b) = 0$, then there exists a linear combination of $\mathbf{y}^{(1)}$ and $\mathbf{y}^{(2)}$ that satisfies System (15.111) with boundary values (15.112).

Note that the value of b is not known a priori and the integration proceeds with a stop condition on $\Delta(b) = 0$. However, once b is known, we deduce the value of A_0/B_0 from (15.76).

As an application of this method, we consider the case of an internally pressurized shell ($P < 0$) in the absence of growth. A typical plot of the strain α_a , required to excite different modes for various thicknesses, is shown in Figure 15.17 for a neo-Hookean material. Once the critical strain α_a is known for the n th mode, α_b can be computed from (15.27) and the critical pressure necessary to excite the mode n is given by (15.44).

The following features appear:

- Thin shells are more prone to instabilities than thicker shells since the critical strain increases with thickness;
- Unstable modes are not ordered. In particular, as the thickness decreases or increases, higher modes can become unstable first;
- For thick shells, a detailed numerical analysis reveals that the limit $A_0/B_0 \rightarrow 0$ the $n = 10$ is the most unstable mode [465].

This computational analysis suggests that there are two regimes where further analytical progress is possible, the thin-shell limit $A/B \rightarrow 1$ and the thick-shell limit $A_0/B_0 \rightarrow 0$. We consider these two limits separately and look at the effect of the growth parameters on the stability of the shell.

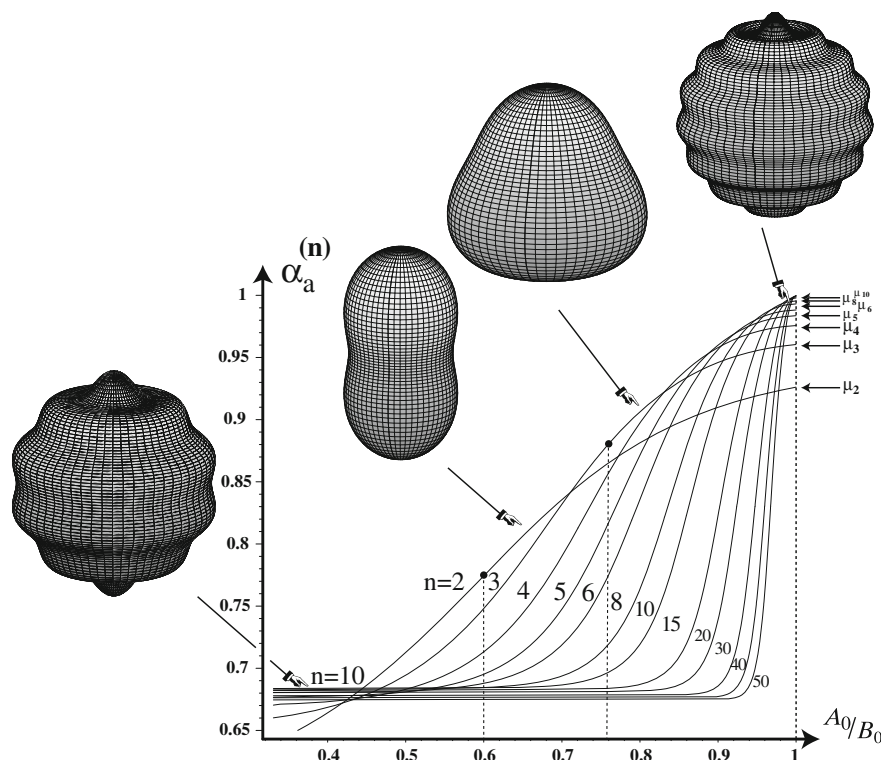


Figure 15.17 Critical strains α_a for the n th mode of a neo-Hookean shell as a function of the thickness A_0/B_0 . Only the modes $n = 2, 3, 4, 5, 6, 8, 10, 15, 20, 30, 40, 50$ are shown. For a given thickness A_0/B_0 , as the external pressure is increased, the inner boundary of the shell moves inward and the strain α_a decreases until it reaches a critical curve. The critical mode is the first unstable mode. For instance, at $A_0/B_0 = 6/10$ the critical mode is $n = 2$, whereas for a thinner shell at $A_0/B_0 = 3/4$, the critical mode is $n = 3$ (both indicated by a black dot). Note that the amplitude of the modes is arbitrary and has been chosen to show the structure of the solution.

15.6.2 Thin-Shell Limit

The numerical procedure for the calculation of the critical values at which bifurcations occur can be adapted for the calculation of asymptotic solutions in the thin-shell limit [397]. For thin shells, one can obtain analytic results by introducing the small parameter $\epsilon = (b - a)$ and the stretched variable

$$\rho = \frac{r - a}{\epsilon}. \quad (15.115)$$

System (15.113) now reads

$$\frac{d\mathbf{z}}{d\rho} = \mathbf{g}(\mathbf{z}; \rho; \epsilon), \quad (15.116)$$

where $\mathbf{z} = [\mathbf{y}^{(1)}, \mathbf{y}^{(2)}]^\top$, $\mathbf{g} = [\mathbf{f}(\mathbf{y}^{(1)}), \mathbf{f}(\mathbf{y}^{(2)})]^\top$, and the integration takes place between $\rho = 0$ and $\rho = 1$. We seek solutions of this system of eight equations with initial values $\mathbf{z}(\rho = 0; \epsilon) = [\mathbf{y}_0^{(1)}, \mathbf{y}_0^{(2)}]^\top = \mathbf{z}_0(\epsilon)$ where we choose $\mathbf{y}_0^{(1)}$ and $\mathbf{y}_0^{(2)}$ to be linearly independent such that the conditions

$$c_{1,2}(\mathbf{y}_0^{(1)}; \rho = 0; \epsilon), \quad c_{1,2}(\mathbf{y}_0^{(2)}; \rho = 0; \epsilon), \quad (15.117)$$

given by (15.112) are identically satisfied. We look for solutions analytic in ϵ

$$\mathbf{z} = \sum_{i=0}^k \mathbf{z}_i \epsilon^i + \mathcal{O}(\epsilon^{k+1}), \quad (15.118)$$

where each $\mathbf{z}_i$ satisfies an equation of the form

$$\frac{d\mathbf{z}_i}{d\rho} = \mathbf{g}_i(\mathbf{z}_1, \mathbf{z}_2, \dots, \mathbf{z}_i), \quad \mathbf{z}(0)_i = \mathbf{z}_{0,i}, \quad (15.119)$$

where the linear vector fields $\mathbf{g}_i$ and the initial values $\mathbf{z}_{0,i}$ are, respectively, the coefficients of the expansions $\mathbf{g} = \sum_i \mathbf{g}_i \epsilon^i$ and $\mathbf{z}_0 = \sum_i \mathbf{z}_{0,i} \epsilon^i$. This hierarchy of linear systems can be integrated explicitly for increasing values of i and the solution $\mathbf{z}_{1,i}$ at $\rho = 1$ can be computed.

The solution at the outer boundary $\mathbf{z}_1 = \sum_i \mathbf{z}_{1,i} \epsilon^i$ is a function of the unknown parameter a (or, equivalently, the parameter α_a) and the condition for the existence of a solution of the original problem is the vanishing of the determinant

$$\Delta = \begin{vmatrix} c_3(\mathbf{y}^{(1)}(1)) & c_3(\mathbf{y}^{(3)}(1)) \\ c_4(\mathbf{y}^{(1)}(1)) & c_4(\mathbf{y}^{(2)}(1)) \end{vmatrix}, \quad (15.120)$$

where $[\mathbf{y}^{(1)}(1), \mathbf{y}^{(2)}(1)]^\top = \mathbf{z}_1$. We expand α_a in powers of ϵ and solve $\Delta = 0$ to each order. To third order, the solution reads

$$\alpha_a^{(n)} = \alpha_0(n) + \tilde{\alpha}_1(\gamma, n)\epsilon + \tilde{\alpha}_2(\gamma, n)\epsilon^2 + \mathcal{O}(\epsilon^3), \quad (15.121)$$

where α_0 is the first positive root of

$$(n+2)(n-1)\alpha_0^{12} + 2(n^2+n+7)\alpha_0^6 - 3n(n+1) = 0, \quad (15.122)$$

and

$$\tilde{\alpha}_1 = \frac{\alpha_0^3}{2\gamma\gamma_\theta^3} - \frac{1}{2}, \quad (15.123)$$

$$\begin{aligned} \tilde{\alpha}_2 = & -\frac{1}{72\gamma_\theta^3\gamma^2} \left[\right. \\ & -462\alpha_0^6\gamma^2\gamma_\theta^3 - 342n^2\gamma\alpha_0^9 + 33n^2\gamma^2\gamma_\theta^9 + 98n\gamma^2\gamma_\theta^9 + 6n^4\alpha_0^9\gamma \\ & -330\gamma_\theta^3n\alpha_0^6 + 90n^4\gamma\alpha_0^3\gamma_\theta^6 - 41n^4\gamma^2\gamma_\theta^9 + 672\gamma\alpha_0^9 + 24n^5\gamma^2\gamma_\theta^9 \\ & -180\gamma n\alpha_0^3\gamma_\theta^6 - 348n\gamma\alpha_0^9 + 345n\gamma^2\alpha_0^6\gamma_\theta^3 - 57n^4\alpha_0^6\gamma_\theta^3\gamma^2 \\ & +288\alpha_0^6\gamma_\theta^3n^2\gamma^2 + 180n^3\gamma\alpha_0^3\gamma_\theta^6 - 90n^2\gamma\alpha_0^3\gamma_\theta^6 - 122n^3\gamma^2\gamma_\theta^9 \\ & +90\gamma_\theta^9n^3 + 12\alpha_0^9n^3\gamma + 45\gamma_\theta^9n^4 + 315\gamma_\theta^9n - 150\gamma_\theta^3n^3\alpha_0^6 - \\ & -75\gamma_\theta^3n^4\alpha_0^6 + 8n^6\gamma^2\gamma_\theta^9 - 1470\gamma_\theta^3\alpha_0^6 - 114n^3\alpha_0^6\gamma_\theta^3\gamma^2 \\ & \left. +360\gamma_\theta^9n^2 + 405\gamma_\theta^3n^2\alpha_0^6 \right] \\ & \times \left[-3\gamma_\theta^6n^2 - \alpha_0^6n^4 - 2\alpha_0^6n^3 + 14\alpha_0^6 - 6n^2\alpha_0^6 \right. \\ & \left. -5n\alpha_0^6 - 6\gamma_\theta^6n + 6n^3\gamma_\theta^6 + 3n^4\gamma_\theta^6 \right]^{-1}. \quad (15.124) \end{aligned}$$

Higher order coefficients can be computed in a similar manner. To obtain the critical curves in terms of the parameter $\delta = (B_0 - A_0)/A_0$, we use the expression for the volume of the deformed shell given by (15.16):

$$b^3 - a^3 = \gamma\gamma_\theta^3(B_0^3 - A_0^3). \quad (15.125)$$

To second order, this relation reads $\epsilon = \gamma\gamma_\theta^3\delta/\alpha_0^2$ and the expansion of the critical curves in terms of δ becomes

$$\alpha_a^{(n)} = \alpha_0(n) + \alpha_1(\gamma, n)\delta + \alpha_2(\gamma, n)\delta^2 + \mathcal{O}(\delta^3), \quad (15.126)$$

where

$$\alpha_i = \tilde{\alpha}_i \left(\frac{\gamma\gamma_\theta^3}{\alpha_0^2} \right)^i, \quad \text{for } i > 0. \quad (15.127)$$

In Figure 15.18, the comparison between the numerical curves and the expansion for thin shells in the absence of growth is given. In this case, we have

$$\alpha_a^{(n)} = \alpha_0(n) + \alpha_1(1, n)\delta + \alpha_2(1, n)\delta^2 + \alpha_3(1, n)\delta^3 + \mathcal{O}(\delta^4). \quad (15.128)$$

The thin-shell expansion gives a satisfactory approximation of the numerical curves. Moreover, the limiting value, corresponding to $\epsilon = \delta = 0$, is the exact critical strain. We can also calculate an expression for the envelope of the critical curves

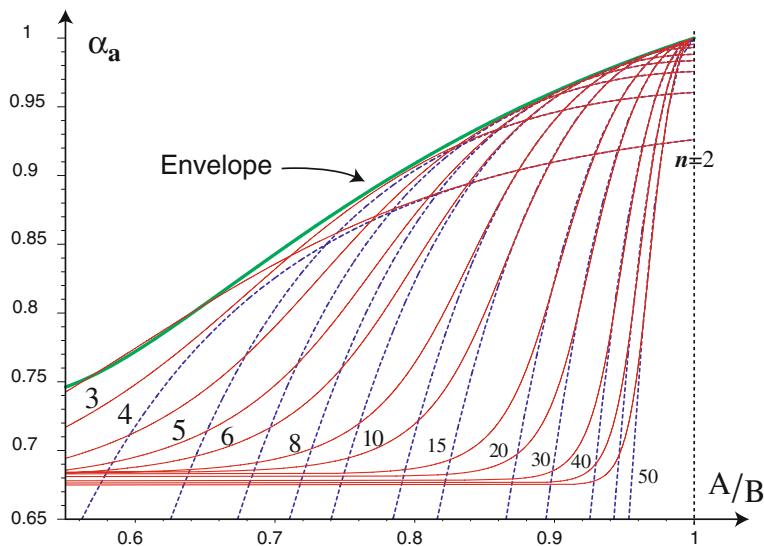


Figure 15.18 Blow-up of the critical curves (solid lines) of Figure 15.17 together with the asymptotic curves (dotted lines) valid for thin shells and the critical envelope given by (15.129).

$$\alpha_a = 1 - \frac{1}{3}\delta - \frac{7}{36}\delta^2 + \frac{235}{864}\delta^3 + \mathcal{O}(\delta^3). \quad (15.129)$$

This envelope shown in Figure 15.18 is particularly important as it gives the critical value of the bifurcation parameter at which the spherical shell becomes unstable.

15.6.3 Thick-Shell Limit

Equation (15.100) with boundary conditions (15.109) and (15.110) also admits a WKB expansion [82] valid in the large n limit. Such solutions have been computed in the classic case [397]. This expansion can be captured by setting

$$U(r) = \exp\left(\int_a^r S(r)dr\right), \quad (15.130)$$

with

$$S = n \sum_{i=0}^{\infty} S_i(r)n^{-i}. \quad (15.131)$$

The functions $S_i(r)$ can be obtained by substituting (15.130) in (15.100) and the resulting systems of equations can be solved to each order in n . Since the problem

is of fourth order, the equation to order n^{-4} has four distinct solutions given by

$$S_0^{(1,2)} = \pm \frac{1}{r}, \quad S_0^{(3,4)} = \pm \frac{\alpha^3}{r}. \quad (15.132)$$

Each of these branches gives rise to a separate solution

$$U^{(k)} = \exp \left(\int_a^r S^{(k)} dr \right) = \exp \left[\int_a^r \left(n \sum_{i=0}^{\infty} S_i^{(k)} n^{-i} \right) dr \right]. \quad (15.133)$$

The equations for $S_i^{(k)}$ with $i > 0$ are linear with coefficients depending only on $\{S_0^{(k)}, \dots, S_{i-1}^{(k)}\}$.

We test the existence of a solution to the boundary-value problem by looking for a linear combination of the four fundamental solutions satisfying the boundary conditions. Such a solution exists when the determinant of the matrix built on the four boundary conditions (15.109–15.110) evaluated on the four solutions vanishes identically.

Let $c_{1,2}(U)$ and $c_{3,4}(U)$ be the boundary conditions (taken respectively at $r = a$ and $r = b$) and

$$M_{ij} = c_i(U^{(j)}), \quad i, j = 1, \dots, 4. \quad (15.134)$$

Then, the condition for the existence of a solution to the boundary-value problem in the large n limit is simply given by the vanishing of

$$\Delta = \det(M_{ij}). \quad (15.135)$$

However, the values of the parameters at which this determinant vanishes have to be evaluated numerically.

Further theoretical progress can be achieved for thick shells, that is, for shells such that $(B_0 - A_0)/A_0 = \mathcal{O}(1)$. In such a case, the expansion of the determinant is itself an asymptotic series. An excellent approximation of the critical curves can be obtained by finding the roots of the exponentially dominant term. This analysis leads to

$$\alpha_a = \alpha_0 + \alpha_1 \frac{1}{n} + \alpha_2 \frac{1}{n^2} + \alpha_3 \frac{1}{n^3} + \mathcal{O}\left(\frac{1}{n^4}\right), \quad (15.136)$$

where α_0 is the first positive root of

$$\begin{aligned} \alpha_0 = \frac{1}{12} \left[576 \left(26 + 6\sqrt{33} \right)^{1/3} + 234 \left(26 + 6\sqrt{33} \right)^{2/3} \right. \\ \left. - 576 - 54 \left(26 + 6\sqrt{33} \right)^{2/3} \sqrt{33} \right]^{1/3} \\ \approx 0.6661423391, \end{aligned} \quad (15.137)$$

and

$$\alpha_1 = \frac{-(3\gamma + 11)\alpha_0^6 - (32 + 4\gamma)\alpha_0^3 + 9 + 5\gamma}{12\gamma\alpha_0^5(\alpha_0^3 + 2)}, \quad (15.138)$$

$$\alpha_2 = \left[(-70752\gamma - 31349 - 3111\gamma^2)\alpha_0^6 - (164574 + 73724\gamma - 45474\gamma^2)\alpha_0^3 - 13163\gamma^2 + 27972\gamma + 51387 \right] \times \left[18(\alpha_0^3 + 2)^3 \gamma^2 \alpha_0^{14} (\alpha_0 - 1)^3 (\alpha_0 + 1)^2 (\alpha_0^2 + 1 + \alpha_0)^3 (\alpha_0^2 + 1 - \alpha_0)^2 \right]^{-1}. \quad (15.139)$$

The limit from thick shell to the sphere can be obtained by taking the limit $A_0 \rightarrow 0$ at fixed B_0 or, alternatively, by taking A_0 constant and $B_0 \rightarrow \infty$. This last limit corresponds to a half-space under pressure and we recover the limiting value $\alpha_a \approx 0.66614$ in the absence of growth obtained in Section 11.10.1 for such an instability.

15.6.4 Bifurcation of the Growing Shell

We now consider the effect of anisotropic growth on stability. We focus our attention on radial growth and resorption. The effect of hoop growth is equivalent to radial resorption up to an isotropic change of volume that can be taken into account by a rescaling of the pressure (15.12).

15.6.4.1 Mechanical Versus Geometric Effects

In a growth process, there are two main effects that can influence the stability of a structure. The first effect is due to geometry. When the volume of the spherical shell changes, the relative thickness with respect to its radius also changes, affecting its stability. For instance at a given pressure, a reduction in thickness after resorption tends to destabilize the shell, since thinner shells are more unstable than thicker ones. Likewise, an increase in the thickness after growth stabilizes the shell.

The second effect is related to mechanics through changes in residual stress. Radial growth induces a compressive radial stress as observed in Figure 15.5A. This stress tends to further destabilize the shell under pressure. Similarly, we see in Figure 15.5B that radial resorption (or hoop growth) induces a tensile radial stress that stabilizes the shell.

To illustrate these two opposing effects, we show the critical pressure P_{crit} for the mode $n = 10$ as a function of thickness and for small values of radial growth and resorption in Figure 15.19.

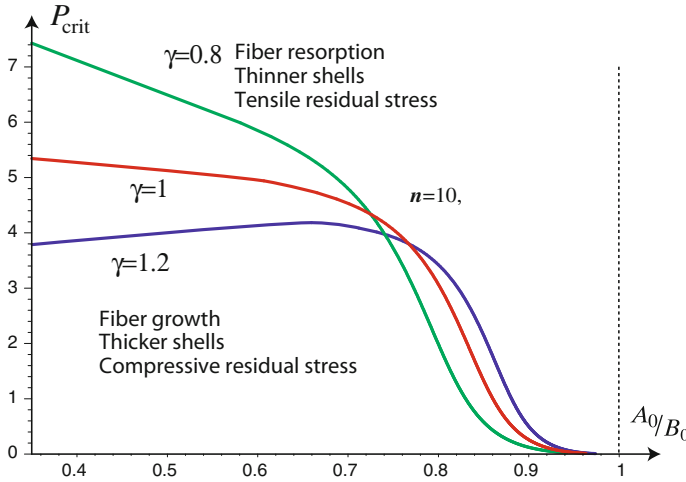


Figure 15.19 Critical pressure for mode $n = 10$ as a function of the initial thickness for radial growth and resorption. Geometric effect of growth: For thin shells (A_0/B_0 close to 1), radial growth is stabilizing (larger critical pressure) and radial resorption is destabilizing (smaller critical pressure). Mechanical effect of growth: For thick shells, radial growth is destabilizing and radial resorption is stabilizing.

For thin shells (A_0/B_0 close to 1), radial growth is stabilizing. A small change in thickness has a direct effect on the critical strain that produces an instability (see Figure 15.17 in the thin shell regime).

For thick shells, a change in thickness does not significantly change the critical strain needed for the existence of an axisymmetric solution (see Figure 15.17 for $A_0/B_0 < 1/2$).

The effect of growth on thin shells can be explicitly understood by using the thin-shell approximation and computing asymptotically the critical displacement for each mode:

$$\alpha_a^{(n)} = \alpha_0(n) + \alpha_1(\gamma, n)\delta + \alpha_2(\gamma, n)\delta^2 + \alpha_3(\gamma, n)\delta^3 + \mathcal{O}(\delta^4), \quad (15.140)$$

where $\delta = (B_0 - A_0)/A_0$ and the coefficients $\alpha_i(\gamma, n)$ are explicitly given in (15.126). The critical mode number, n_{crit} , is the unstable mode number n with the largest value of $\alpha_a^{(n)}$. It is found, as a first approximation, by the solution of $\partial\alpha_a/\partial n = 0$. Once n_{crit} is known, the envelope giving the critical value of the strain for instability can be computed explicitly as $\alpha_a(n_{\text{crit}})$. In our case, it is given by

$$\begin{aligned} \alpha_a = & 1 + \left(\frac{1}{2} - \frac{5}{6}\gamma\right)\delta + \left(\frac{5}{24} - \frac{3\gamma}{4} + \frac{25}{72}\gamma^2\right)\delta^2 \\ & - \frac{\gamma}{864}(21 - 168\gamma - 88\gamma^2)\delta^3 + \mathcal{O}(\delta^4). \end{aligned} \quad (15.141)$$

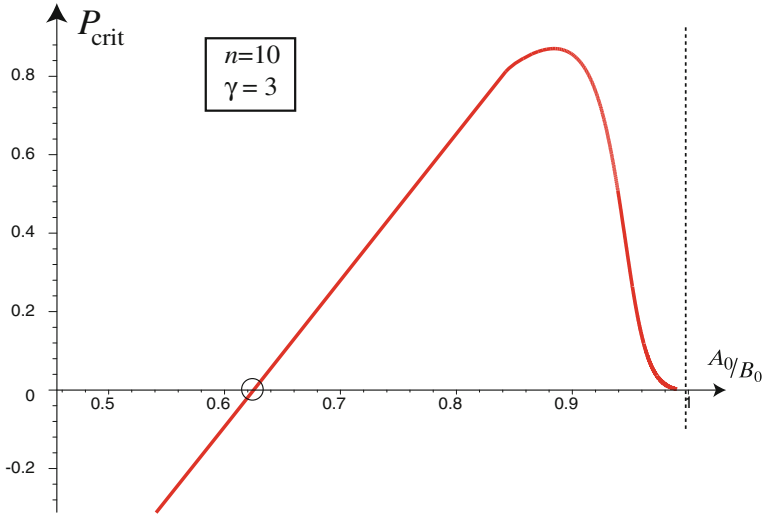


Figure 15.20 Growth-induced buckling: For larger values of γ , there exists a value of A_0/B_0 such that the mode $n = 10$ is unstable in the absence of external pressure

From this envelope, the critical pressure can be calculated explicitly by integrating (15.44) for a neo-Hookean energy:

$$P_{\text{crit}} = 8(\gamma\delta)^2 + \frac{2}{3}(\gamma\delta)^3 + \mathcal{O}(\delta^4), \quad (15.142)$$

and, recalling that $\gamma = \gamma_r/\gamma_\theta$, we have

$$\left. \frac{dP_{\text{crit}}}{d\gamma_r} \right|_{(\gamma_r=1, \gamma_\theta=1)} = 16\delta^2 + 2\delta^3 + \mathcal{O}(\delta^4), \quad (15.143)$$

$$\left. \frac{dP_{\text{crit}}}{d\gamma_\theta} \right|_{(\gamma_r=1, \gamma_\theta=1)} = -16\delta^2 - 2\delta^3 + \mathcal{O}(\delta^4). \quad (15.144)$$

We conclude that for thin shells, radial growth or hoop resorption has a stabilizing effect, whereas radial resorption or hoop growth is destabilizing.

15.6.4.2 Spontaneous Instabilities

Another feature of interest can be seen in Figure 15.19. For thick shells and radial growth, the pressure necessary to destabilize the shell decreases with the thickness. This trend is due to the residual compressive stress associated with radial growth. It suggests that, for sufficient growth, the shell might become unstable without any external applied load. Indeed, for large enough values of γ , we find that there exists

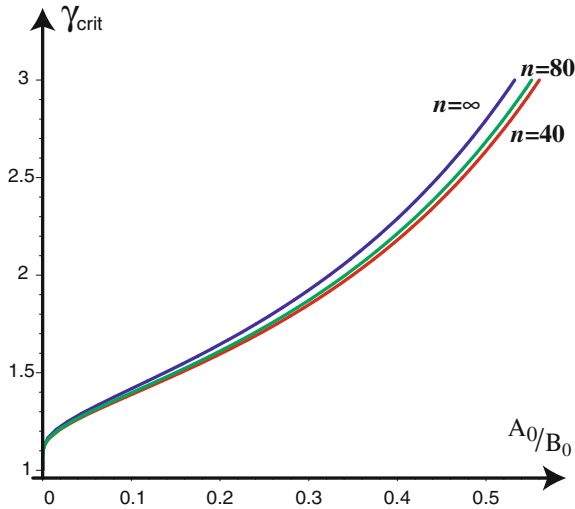


Figure 15.21 The critical value of radial growth necessary to induce a spontaneous instability in a shell of initial thickness A_0/B_0 for the modes $n = 40, 80, \infty$. Note that the WKB expansion is not valid for low modes so the value of γ_{crit} given by the mode $n = \infty$ is an upper bound for the instability.

a value of A_0/B_0 such that the mode $n = 10$ becomes unstable *in the absence of an external pressure*, as shown in Figure 15.20.

Therefore, we can compute for a given A_0/B_0 the value of $\gamma = \gamma_{crit}$ necessary to induce an instability. To do so, we consider thick shells and high-mode numbers so that the WKB expansion given in (15.136) is valid. In this regime, we compute γ_{crit} leading to an instability at zero pressure. In Figure 15.21, we plot the critical radial growth γ_{crit} as a function of the initial thickness for high-mode numbers (including $n = \infty$ obtained by taking $\alpha_a = \alpha_0$ in the WKB expansion (15.136)). The exact threshold for an instability is not known since the WKB expansion is only valid for high-mode numbers and the first instability for thick shells occurs at mode $n = 10$. Nevertheless, the value of γ_{crit} provides an upper bound for the instability.

15.7 Instability Due to Differential Growth

Isotropic and inhomogeneous growth also produces residual stress. This stress field may be sufficient to create an instability. Following the method presented in the previous two sections, we consider the possibility of a bifurcation for the two cases of differential growth discussed in Section 15.2.2.

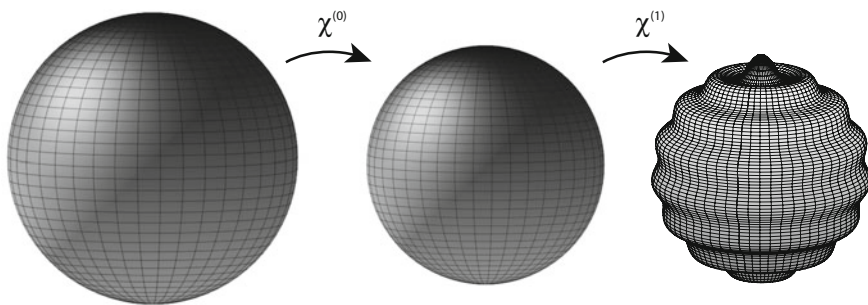


Figure 15.22 The shell is first shrinking through differential growth until it builds enough residual stress and becomes unstable (here, mode $n = 15$).

15.7.1 Instability in a Shrinking Shell

We first consider the case of a shell of initial radii A_0, B_0 and current radii a, b that shrinks according to the law

$$\gamma_r = \gamma_\theta = g(r) = 1 + \nu(r - a), \quad (15.145)$$

as shown in Figure 15.22. The constant ν is directly related to the change of volume

$$\Delta V = \frac{b^3 - a^3}{B_0^3 - A_0^3}, \quad (15.146)$$

through

$$B_0^3 - A_0^3 = 3 \int_a^b \frac{\rho^2}{g^3(\rho)} d\rho. \quad (15.147)$$

The strain and stress for the radially symmetric solution are given by

$$\alpha(r) = \frac{r}{g(r)R_0(r)}, \quad (15.148)$$

$$t_r^{(0)}(r) = \int_a^r \frac{\alpha}{\rho} \partial_\alpha \widehat{W}_{\text{sh}}(\alpha) d\rho, \quad (15.149)$$

where we choose $\widehat{W}_{\text{sh}}$ to be the auxiliary function for a neo-Hookean strain-energy function.

We follow the same steps as before to obtain a linearized system of equations. We use the spherical coordinates (r, θ, φ) and consider axisymmetric deformations of the shell in the form

$$\chi^{(1)} = u(r, \theta)\mathbf{e}_r + v(r, \theta)\mathbf{e}_\theta. \quad (15.150)$$

The nonvanishing components of $\text{div } \mathbf{T}^{(1)} = 0$ and the incompressibility condition form a system of three coupled PDEs of second order for u , v and $q^{(1)}$ as a function of (r, θ) with coefficients depending on the base finite-strain solution. Again, we expand this solution in Legendre polynomials $P_n(\cos \theta)$, that is, we write

$$u(r, \theta) = U_n(r) P_n(\cos \theta), \quad (15.151)$$

$$v(r, \theta) = V_n(r) \frac{d}{d\theta} P_n(\cos \theta), \quad (15.152)$$

$$q^{(1)}(r, \theta) = Q_n(r) P_n(\cos \theta), \quad (15.153)$$

and obtain, after simplification, a fourth-order differential equation describing the amplitude of the field u with respect to the n th Legendre polynomial.

For each mode n , a solution of this boundary-value problem exists only for particular combinations of parameters $a = a(\nu, \delta, n)$ where $\delta = (b - a)$ is the width of the shell in the current configuration. These values of a are the critical values of the inner radius where the n th mode first appears.

For small δ , these curves in parameter space can be obtained by a perturbation expansion of the form

$$a = a_0 + a_1 \delta + a_2 \delta^2 + \mathcal{O}(\delta^3), \quad (15.154)$$

where a_0 is the first positive solution of

$$(n+2)(n-1)a_0^{12} + 2(n^2 + n + 7)a_0^6 = 3n(1-n), \quad (15.155)$$

and

$$a_1 = \frac{1}{2} a_0^3 + \frac{\nu}{2} a_0 - \frac{1}{2}. \quad (15.156)$$

The coefficient a_2 is given by a similar expression in terms of ν and a_0 . Once the bifurcation of each individual mode is known, the critical value a_{crit} where the shell first bifurcates (independently of the mode number) is

$$a_{\text{crit}} = 1 - \left(\frac{1}{3} - \frac{1}{2} \nu \right) \delta - \frac{1}{24} (2 + 4\nu + 5\nu^2) \delta^2 + \mathcal{O}(\delta^3). \quad (15.157)$$

For a given δ , the value of a_{crit} and $b_{\text{crit}} = a_{\text{crit}} + \delta$ can be used in Equation (15.149) to solve $t_r^{(0)}(b_{\text{crit}}) = -P$ with respect to ν . The value of $\nu_{\text{crit}} = \nu(a_{\text{crit}}, b_{\text{crit}})$ can then be used to compute the initial radii A_0 and B_0 , and hence, the current thickness.

The selected modes shown in Figure 15.23 are given by the largest integer n less than

$$N = \sqrt{\frac{3}{\delta}} \left(1 - \sqrt{\frac{\delta}{12}} + \frac{8 + 3\nu}{24} \delta - \frac{29\nu^2 + 220\nu + 282}{384} \delta^2 \right). \quad (15.158)$$

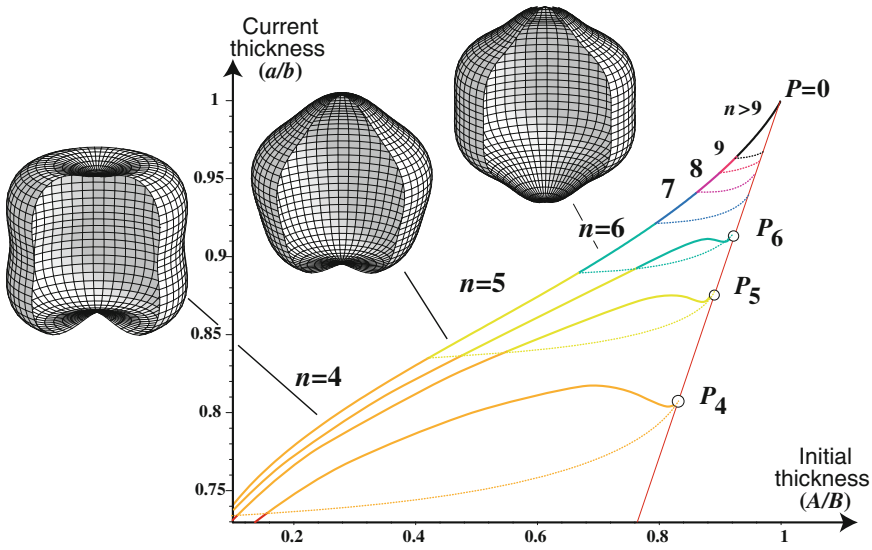


Figure 15.23 Instability of the shrinking shell. For an initial thickness A_0/B_0 , the shell first becomes unstable due to residual stress when the current thickness a/b reaches the critical value given by the solid curves. The solid curves are obtained at constant pressure P_i given by the critical value for instability of the i th mode without growth. The dashed lines denote the regions of the mode of deformation n found at the bifurcation. The corresponding configurations $n = 4, 5, 6$ are shown, but their amplitudes are not predicted by the theory.

The mode selected at the bifurcation depends on the initial thickness in such a way that thinner shells become unstable with increasingly high-mode numbers, as discussed in the previous section.

The basic physical process of the instability shown in Figure 15.23 is as follows: A shell of thickness A_0/B_0 becomes unstable when both its current thickness a/b is small enough and sufficient compressive residual stress has built up in the shell. Under a pressure P_n chosen to be the critical pressure for mode n , the shrinking shell becomes unstable with possible mode $2 \leq m \leq n$.

15.7.2 Instability of a Shell Growing Inside a Medium

We now turn our attention to the case of a growing shell inside an incompressible elastic medium. The stability analysis in such interfacial problems is delicate due to the matching of stresses at the interface in the deformed configuration. Nevertheless, some insight can be gained by modeling the problem with the assumption that the outside medium creates a hydrostatic compressive force equivalent to the one created through growth and contact. In this context, we compute a lower bound for instability

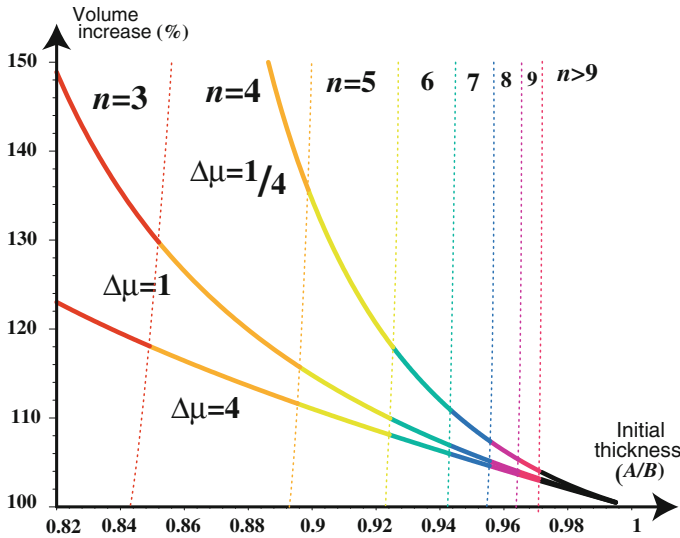


Figure 15.24 Instability of a growing embedded shell. For an initial thickness A_0/B_0 , the shell first becomes unstable due to contact stress when the volume increase ($100v/V$) reaches the critical value given by the solid curves (with different relative medium responses $\Delta\mu = 1/4, 1, 4$). The dashed lines represent the different instability modes.

in terms of the initial thickness and the volume increase for different relative medium responses $\Delta\mu = \mu_{me}/\mu_{sh}$.

The linearized equation for the instability threshold is the same one as in the previous section and the same estimate for small current thicknesses can be used. For each δ , the value of ν necessary for the radial problem to satisfy the boundary values can be computed. Once this value is known, the initial thickness and volume of the current configuration can be found for different values of $\Delta\mu$ as shown in Figure 15.24.

This analysis shows the effect of differential growth on the stability of shells. In a shrinking shell, two effects drive the instability: The shell thickness decreases and the residual stress is compressive. Not surprisingly, in the absence of hydrostatic pressure, the neo-Hookean shell is stable under moderate shrinking and only becomes unstable when a large portion of the initial volume has been resorbed. Under compressive loads, the shell can rapidly become unstable with lower or equal mode number than the one given by the initial thickness.

In the case of a growing shell creating compressive stress through contact, the instability for a thin shell is driven rapidly by the volume increases and the rigidity of the external medium.

Chapter 16

Growing Cylinders

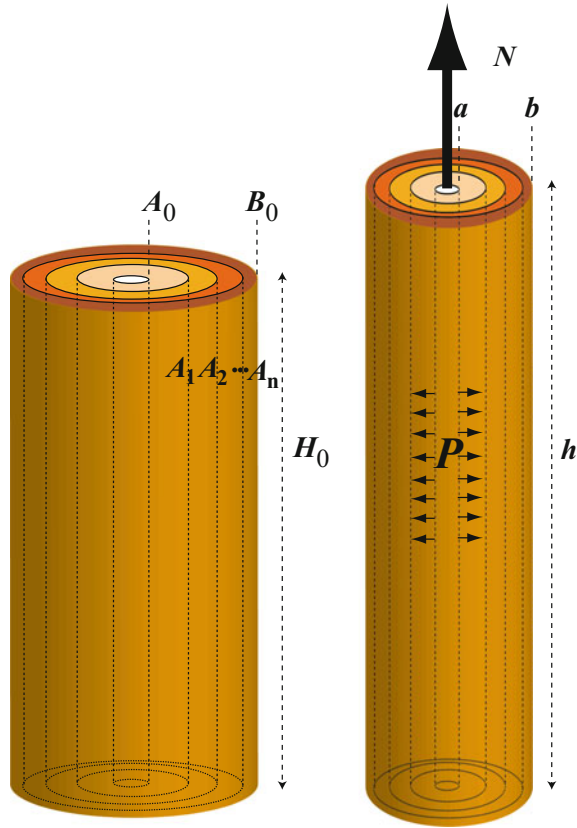


Among the many typical biological structures, tubular structures such as hollow stems and blood vessels abound in nature. Tubes are typically used for transport, to carry information, or for mechanical support. Their morphogenesis usually involves complex genetic and biochemical processes [1018] mediated by mechanical forces.

Residual stress plays a particularly important role in tubular structures: It regulates hoop stress gradients in blood vessels [407], it is used to improve the rigidity of growing plant stems [1274], it mechanically stabilizes arteries [485], and it is known to assist in the proper functioning of airways and oesophagus [534]. In this chapter, we study different aspects of growing tubular structures.

First, we look at the problem of cavity opening that transforms cylinders into tubes. Second, we consider several types of instability in growing structures and from their applications in nature. Third, we study the surprising rotation of some tubular fungi. We start with a general study of growing incompressible cylindrical structures.

Figure 16.1 A. Geometry of the deformation under axial force N and pressure P , the tube on the left is in its initial configuration, the tube on the right is in the current configuration, due to both growth and elasticity.



16.1 Kinematics of the Growing Cylinder

We consider the general problem of a growing cylindrical structure consisting of N different elastic, isotropic, and incompressible cylinders each defined by a diagonal growth tensor and with, possibly different, but homogeneous, material properties. The deformation and the interpretation of the growth tensor are sketched in Figure 16.1.

When the growth tensor is taken to be piecewise constant, the problem is a generalization of the inclusion problem which consists in inserting pieces of elastic materials inside an elastic body by deforming both the inclusions and the body itself [348, 1354]. The cylindrical growth problem is the generalization of the circular shrink-fit problem which consists in fitting a disk in a circular opening with a different radius [35, 692]. It is highly relevant in biology where many cylindrical structures can be described as multiple cylindrical layers with residual stresses. The overall properties of these structures are inherited both from the elastic response of the individual layers and from their relative geometric arrangement. The relative geometry of the different layers is fully described by the growth of an initial stress-free multilayer cylinder.

In the initial configuration $\mathcal{B}_0$, the structure has inner and outer radii A_0 and $A_n \equiv B_0$, and height H_0 . This cylinder is further divided into n cylindrical shells labeled by i from 1 to n so that the inner and outer radii of the i th cylindrical shell is A_{i-1} and A_i , respectively, as shown in Figure 16.1. Each shell is homogeneous, isotropic, and incompressible.

We assume that the cylinder retains its integrity and cylindrical geometry in all deformations. Following Section 11.8.3, the total deformation from the initial to the current configuration, $\mathbf{x} = \chi(\mathbf{X}_0, t)$, in cylindrical coordinates, $\{r, \theta, z\}$ and $\{R_0, \Theta_0, Z_0\}$ reads

$$r = r(R_0), \quad \theta = \Theta_0, \quad z = \zeta Z_0, \quad (16.1)$$

where ζ is the constant axial stretch of the cylinder such that $h_0 = \zeta H_0$, and the continuous function $r(R_0)$ gives the location of circles of radius R_0 after deformation. The total deformation gradient is then

$$\mathbf{F} = r' \mathbf{e}_r \otimes \mathbf{e}_r + \frac{r}{R_0} \mathbf{e}_\theta \otimes \mathbf{e}_\theta + \zeta \mathbf{e}_z \otimes \mathbf{e}_z, \quad (16.2)$$

where the prime denotes differentiation with respect to R_0 . Since the cylindrical geometry is respected in all configurations, we can use the same bases vectors: $\mathbf{E}_{R_0} = \mathbf{e}_r$ and so on. We introduce the deformation gradient in terms of the principal stretches

$$\boldsymbol{\lambda}_i(R_0) = (\lambda_{i,r}, \lambda_{i,\theta}, \lambda_{i,z}), \quad (16.3)$$

where $R_0 \in [A_{i-1}, A_i)$, for $i = 1, \dots, n-1$ and $R_0 \in [A_{n-1}, A_n]$, when $i = n$. The deformation gradient reads:

$$[\mathbf{F}(R_0)] = \sum_{i=1}^n \text{diag}(\boldsymbol{\lambda}_i) [\mathbf{H}(R_0 - A_{i-1}) - \mathbf{H}(R_0 - A_i)], \quad R_0 \in [A_0, A_n], \quad (16.4)$$

where $\mathbf{H}(\cdot)$ is the Heaviside function.

Using the multiplicative decomposition, we assume that $\mathbf{F} = \mathbf{A}\mathbf{G}$ where the elastic deformation tensor is defined in terms of the elastic stretches $\boldsymbol{\alpha}_i(R_0) = (\alpha_{i,r}, \alpha_{i,\theta}, \alpha_{i,z})$, so that

$$[\mathbf{A}(R_0)] = \sum_{i=1}^n \text{diag}(\boldsymbol{\alpha}_i) [\mathbf{H}(R_0 - A_{i-1}) - \mathbf{H}(R_0 - A_i)], \quad R_0 \in [A_0, A_n]. \quad (16.5)$$

Similarly, the growth tensor is defined in each shell by a growth vector $\boldsymbol{\gamma}_i$

$$\boldsymbol{\gamma}_i = (\gamma_{i,r}, \gamma_{i,\theta}, \gamma_{i,z}). \quad (16.6)$$

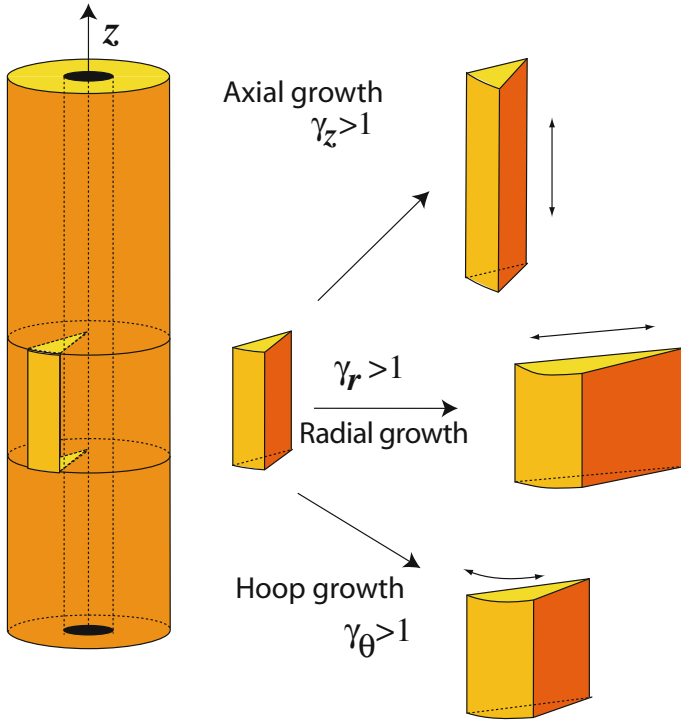


Figure 16.2 Local deformation of a cylindrical element due to the three growth functions considered. A cylindrical element in the initial configuration is transformed into another cylindrical element in the virtual state by increasing its height, depth, or angular span.

The geometric interpretation of this special choice of growth tensor is depicted in Figure 16.2. For the entire tube, we define the growth function

$$g(R_0) = \sum_{i=1}^n \text{diag}(\gamma_i) [H(R_0 - A_{i-1}) - H(R_0 - A_i)], \quad R_0 \in [A_0, A_n]. \quad (16.7)$$

Due to the incompressibility constraint, we have

$$\det \mathbf{F} = \det(\mathbf{A}\mathbf{G}) = \det \mathbf{G} = g. \quad (16.8)$$

That is,

$$\frac{dr}{dR_0} r = \frac{1}{\zeta} g(R_0) R_0, \quad (16.9)$$

which can be solved to give

$$r^2 = a^2 + \frac{2}{\zeta} \int_{A_0}^{R_0} g(\rho) \rho d\rho. \quad (16.10)$$

For a given growth function $g(R_0)$, we define the position of the i th radius as $a_i = r(A_i)$ in the current configuration.

The deformation is diagonal in cylindrical coordinates and only depends on R_0 . Therefore, it follows from Equation (11.156) that the Cauchy stress tensor is also diagonal in these coordinates:

$$[\mathbf{T}] = \text{diag}(t_r, t_\theta, t_z), \Leftrightarrow \mathbf{T} = t_r \mathbf{e}_r \otimes \mathbf{e}_r + t_\theta \mathbf{e}_\theta \otimes \mathbf{e}_\theta + t_z \mathbf{e}_z \otimes \mathbf{e}_z. \quad (16.11)$$

The Cauchy equation, $\text{div } \mathbf{T} = \mathbf{0}$, in cylindrical coordinates, reduces to

$$\frac{dt_r}{dr} + \frac{1}{r}(t_r - t_\theta) = 0. \quad (16.12)$$

It is then possible to solve for the radial stress using the expression for the single cylinder given by Equation (13.54), that is

$$t_r(R_0) = \sum_{i=1}^n [\tau(R_0; A_{i-1}, a, \zeta)H(R_0 - A_{i-1}) - \tau(R_0; A_i, a, \zeta)H(R_0 - A_i)] \quad (16.13)$$

with

$$\tau(R_0; A_{i-1}, a, \zeta) \equiv \frac{g_i}{\zeta} \int_{A_{i-1}}^{R_0} w(R_0) R_0 dR_0, \quad (16.14)$$

and where

$$w(R_0) = \frac{t_\theta - t_r}{r^2}. \quad (16.15)$$

For a strain-energy function $W = W(\alpha_r, \alpha_\theta, \alpha_z)$, we have

$$w(R_0) = \frac{1}{r^2} \left(\alpha_\theta \frac{\partial W}{\partial \alpha_\theta} - \alpha_r \frac{\partial W}{\partial \alpha_r} \right), \quad (16.16)$$

where

$$\alpha_r = \frac{R_0}{r(R_0)\zeta} \gamma_\theta \gamma_z, \quad \alpha_\theta = \frac{r(R_0)}{R_0 \gamma_\theta}, \quad \alpha_z = \frac{\zeta}{\gamma_z}, \quad (16.17)$$

so that $w(R_0)$ is a piecewise function of R_0 .

Once the radial component of the stress is known, the hoop stresses are given by

$$t_\theta = t_r + \alpha_\theta \frac{\partial W}{\partial \alpha_\theta} - \alpha_r \frac{\partial W}{\partial \alpha_r}, \quad (16.18)$$

$$t_z = t_r + \alpha_z \frac{\partial W}{\partial \alpha_z} - \alpha_r \frac{\partial W}{\partial \alpha_r}. \quad (16.19)$$

Note that since $t_r(R_0)$ is given by the integral of a piecewise continuous function, it is also continuous. Continuity for the radial component of the stress tensor is expected

since we require, physically, continuity of the traction vector at the interface between two cylindrical shells. However, in general, both the hoop and axial stress components given by (16.18–16.19) will be discontinuous at the interfaces.

The boundary conditions have been discussed in Section 11.11.4. For given pressure P and axial force N , they are given by

$$C_1 : \int_a^b \frac{t_\theta - t_r}{r} dr = P, \quad (16.20)$$

$$C_2 : \pi \int_a^b (2t_z - t_r - t_\theta)r dr = N - \chi P \pi a^2, \quad (16.21)$$

where $\chi = 1$ for a capped cylinder, and $\chi = 0$ for an open cylinder. These conditions provide, for given P and N , the values of the current inner radius $a = r(A_0)$ and the axial stretch ζ that fully determine the deformation and stress at all points in the structure.

As an example, we consider the case where the growth tensor is piecewise constant in a four-layer cylinder and plot the resulting stress components in Figure 16.3. We observe the continuity of the radial stress and discontinuity of the hoop and axial stresses.

16.2 Application: Cavitation in Plants

We first consider the possible role of mechanical stress in the opening of cavities in elastic tissues. In Section 15.5.2, we observed that cavitation can be triggered by either anisotropic or inhomogeneous growth in spherical geometry. However, for typical materials, elastic cavitation is not possible in cylindrical geometry, since a similar computation to the one performed in Section 15.5.2 reveals that cavitation is only possible for cylinders if $W \sim \alpha^n$ with $n < 2$ which rules out the neo-Hookean case. Nevertheless, the same conditions that create cavitation in spheres will create large tensile stress at the core of a cylinder. These stresses may be sufficient to rupture the material. We investigate this possibility in the context of cavity opening in the world of plants following [469].

16.2.1 Background

Most people are familiar with the simple observation that many plants such as dandelions, chives, and bamboo have hollow stems. Similarly, many roots and water plants have tissues with large airy tissues known as *aerenchyma* as shown in Figure 16.4.

These pockets of gas in the plant tissues fulfill many functions such as mechanical economy and rigidity for hollow stems [583], buoyancy for hydrophytes, increased

gas transport and sap flow, change in the scattering of light for chlorophyll production, and seed projection [1064].

In the nineteenth century, Sachs [946, 1107] characterized the formation of aerenchyma as being either *lysigenous*, that is, created through uniform growth and cell death, or *schizogenous*, that is, air spaces are created through a process of differential growth creating tension in tissues that leads to the mechanical tearing of adjoining cells [352].

Schizogenous formation is associated with large and regular structures in plant tissues such as hollow stems of which Sachs writes [1107]: “*I will refer only to the one obvious fact that while the pith is no longer able to grow in proportion, it*

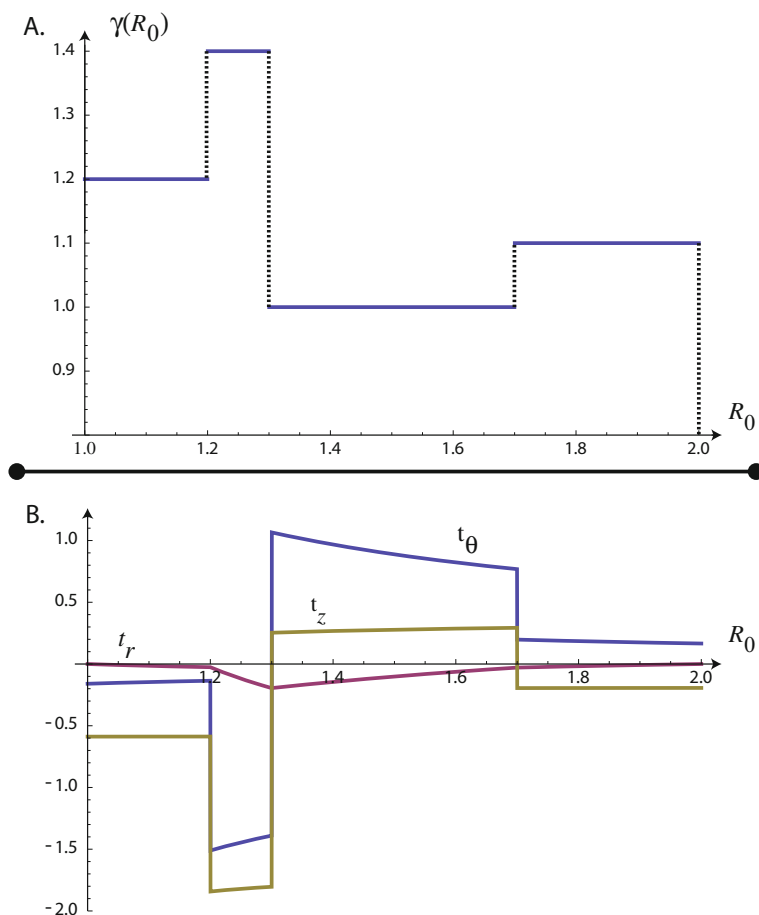


Figure 16.3 Residual stress in a four-layer cylinder. Here, we choose $N = P = 0$, isotropic growth in all layers ($\gamma_i = \gamma_{i,r} = \gamma_{i,z} = \gamma_{i,\theta}$) with $\gamma_1 = 1.2$, $\gamma_2 = 1.4$, $\gamma_3 = 1$, $\gamma_4 = 1.1$ and $\mu = 1$, $\zeta = 1$, $A_0 = 1$, $A_1 = 1.2$, $A_2 = 1.3$, $A_3 = 1.7$, $A_4 = 2$.

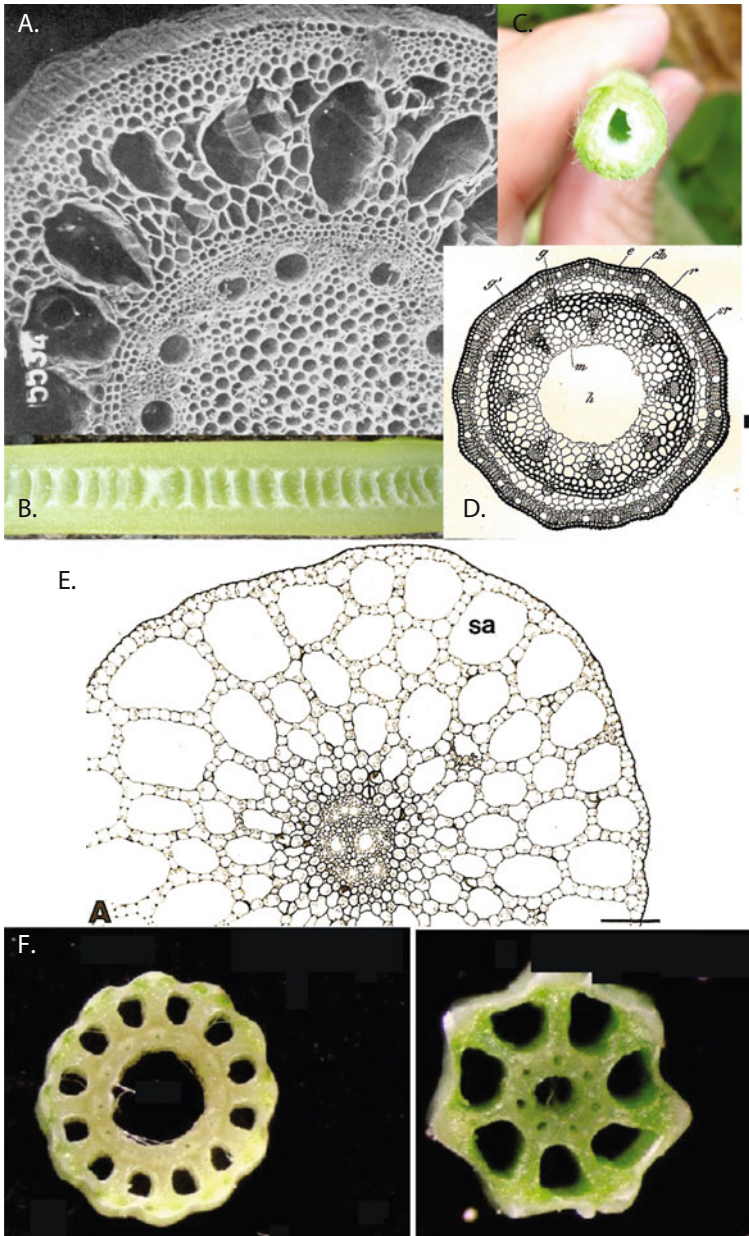


Figure 16.4 A. Aerenchyma tissue in the roots of corn (*Zea mays* L., from Kramer [726]), B. Diaphragms in a sliced stem, C. Hollow stem in hollyhock *Althaea rosea*., D. Transverse section of the flowering scape of chive (*Allium Schoenoprasum*, from Sachs [1107]), E. Aerenchyma in water plant helps buoyancy (cat-tail: *Sparganium emersum*). F. Patterns in the stems of horsetail (*Equisetum*, picture courtesy of Thomas Schoepke).

becomes ruptured while a cavity arises in the interior. This may easily be observed in the flower stems of the Teazel and Dandelion.” While lysigenous aerenchyma formation has received considerable attention by plant physiologists [725], schizogenous aerenchyma formation with its combined mechanical and developmental regulation is not well understood [657].

In a beautiful study, Takano et al. [1219] analyzed the effect of mechanical stress and gibberellins on stem hollowing in bean plants (see also [173]). *Gibberellins* are a well-known class of plant growth hormones involved in stem elongation [930]. In Takano’s experiment, the application of gibberellin to bush bean plants, which are naturally not hollow, increases the length of the stem, reduces its diameter, and induces stem hollowing. Conversely, in bean pole plants, which are naturally hollow, the inhibition of gibberellin or mechanical stresses induced by rubbing the stem cause an increase in the thickening, a reduction in axial length, and prevent stem hollowing [660, 1043].

While Takano’s experiment suggests a connection between stem hollowing and differential growth, other authors have argued that cavity opening is the result of a chemical lysing process acting on the cell wall [173]. It is therefore of interest to study the possible role of mechanical stresses in this process.

16.2.2 The Model

We consider a simple model of stem growth where the stem is an incompressible neo-Hookean cylinder with initial outer radius B_0 subject to radial, angular, and axial deformation and growth along the three cylindrical coordinates (r, θ, z) . As discussed above, cavitation is not possible for a neo-Hookean cylinder. Therefore, we explore whether growth-induced stresses can be sufficient to induce rupture. Assuming that the cylinder retains its symmetry during deformation, the deformation tensors given in the previous section reduce to

$$[\mathbf{F}] = \text{diag}(r', r/R, \zeta), \quad (16.22)$$

$$[\mathbf{G}] = \text{diag}(\gamma_r, \gamma_\theta, \gamma_z), \quad (16.23)$$

$$[\mathbf{A}] = \text{diag}(1/(\alpha\zeta), \alpha, \zeta), \quad (16.24)$$

where $\alpha = \alpha_\theta$. The radial stress is then given by

$$t_r(R) = t_r(0) + \int_0^R \frac{\gamma_r \gamma_z w_\alpha}{\zeta \gamma_\theta \alpha \rho} d\rho, \quad (16.25)$$

where $w(\alpha) = W(1/(\alpha\zeta), \alpha, \zeta)$. Added to this last equation are the usual boundary conditions $t_r(B) = 0$ and zero resultant load on the top and bottom, leading to the condition

$$\int_0^b r t_z(r, \zeta) dr = 0. \quad (16.26)$$

Together, these conditions fix the strains α , ζ and the tension at the origin, $t_r(0)$.

Following known patterns of growth in stems [1029], we assume that on a given cross section, growth is isotropic and inhomogeneous using a linear dependence with respect to the radius R_0 . Further, we assume that axial growth creates tissue tension by being larger in the pith than the epidermis [1030, 1274], that is,

$$\gamma_r = \gamma_\theta = \nu_1 + \nu_2 R_0, \quad \gamma_z = \mu_1 + \mu_2 (B_0 - R_0). \quad (16.27)$$

Keeping the growth gradients ν_2 and μ_2 constant, an increase of the parameter μ_1 corresponds to axial growth and an increase of ν_1 induces stem thickening which theoretically reproduce the changes in growth patterns corresponding to Takano's experiments.

16.2.3 Analysis

We compute the maximal radial stresses in the cylinder cross section for various situations. The axial stress is always compressive due to the fact that the pith grows faster than the outer layers [1030, 1274]. However, both hoop and radial stresses at the origin ($t_r(0)$ and $t_\theta(0)$) are equal and positive (i.e., tensile) for most realistic values of the growth parameters.

Due to the zero load boundary condition on the outer edge and the form of the imposed growth laws, cross-sectional rings expand in the virtual state, but are restricted by the solid cylinder geometry in the current configuration creating a tensile radial stress. It follows that the hoop and radial stresses are maximal at the origin.

In Figure 16.6, we plot this maximal value as a function of the axial and sectional growth parameters (μ_1 and ν_1 respectively). In addition, we plot the value of breaking stress for pith tissue estimated from [955] in which the Young's modulus for the pith is around 1 Mpa (Figure 1 in [955]) and values of the breaking stresses are around 0.3 MPa (Figure 2 in [955]). Since we have rescaled the stresses by setting the Young's modulus $E = 3$, the breaking stress is around $t_{\text{break}} = 1$ in rescaled variables.

16.2.4 Discussion

The analysis shows that the sign (compressive or tensile) and magnitude of the mechanical stresses acting on the cross section of a stem are consistent with the hypothesis that aerenchyma is the result of mechanical tearing. In the case of stem elongation, a faster elongation promotes hollowing by increasing the stress at the cylinder core.

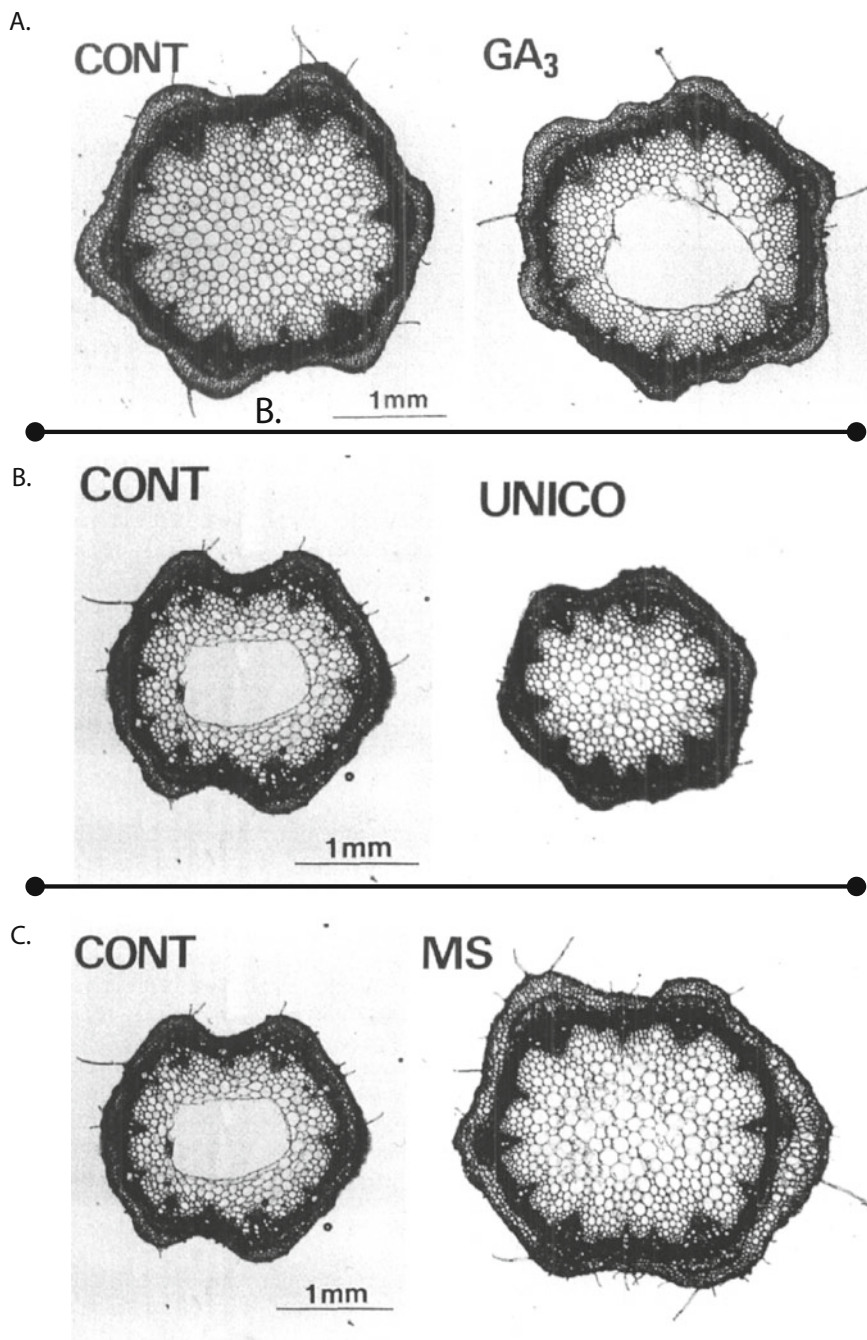


Figure 16.5 Takano's experiment on bean plants. A. In bush bean plants, addition of gibberellins induces elongation and hollowing in a species with a naturally full stem. B. In pole bean plants, a species that has naturally a hollow stem, the addition of uniconazole inhibits GA₃ and prevents hollowing. C. In pole bean plants, mechanical stress induced by moderate rubbing with the thumb and forefinger back and forth 19 times, once daily for 5 days (adapted from [1219]).

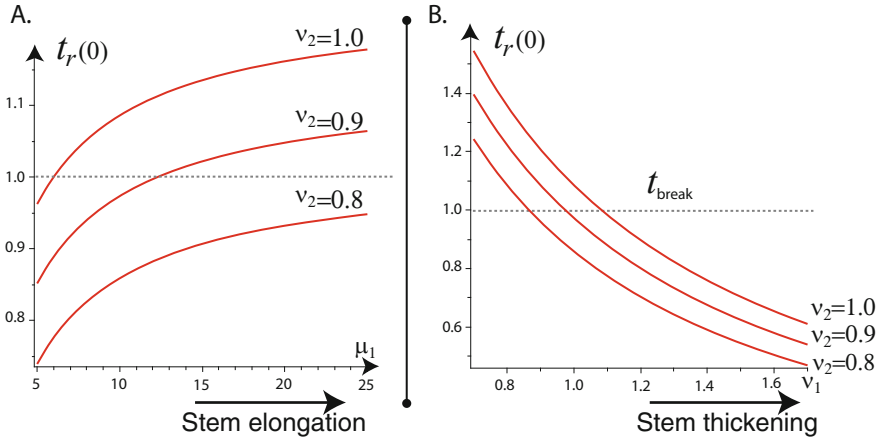


Figure 16.6 Radial stress at the origin of a growing cylinder with constant inhomogeneous and anisotropic growth ($g_r = g_\theta = \nu_1 + \nu_2 R_0$, $g_z = \mu_1 + \mu_2(B_0 - R_0)$) with parameter $\mu_2 = 2$. A. The growth parameter $\nu_1 = 1$ is constant and the axial growth parameter μ_1 is varied. B. The axial growth parameter $\mu_1 = 10$ is constant and the constant sectional growth parameter is varied. The dashed line corresponds to an estimate of the breaking strength. The material is assumed to be elastic with a strain-energy function W_{nh} .

Indeed, in Figure 16.6A, an increase of μ_1 implies an increases of the stress at the origin. This increase is consistent with the observation of Takano shown in Figure 16.5A.

Similarly, the inhibition of gibberellins corresponds to a decrease of μ_1 consistent with the non-hollowing of pole plants observed in Figure 16.5B.

Conversely, in the second case shown in Figure 16.6B, an increase of the stem thickness reduces the stress at the origin below the critical rupture stress. This trend is consistent with the observation of Takano shown in Figure 16.5C where thickening induced by mechanical stresses prevents cavity formation.

The key effect that allows for tissue separation is cross-sectional differential growth, that is the coefficient ν_2 describing the relative rate of growth of the outer layers versus the inner layers. However, in general, the effect of differential growth may not be sufficient to initiate tearing and a local decrease of the breaking stress due to cell wall degradation is also necessary. Indeed, based on similar experiments on celery and tomato pithiness, Jaffe and coworkers have argued that chemical lysis play a dominant role in aerenchyma [666]. Yet another possible mechanism for the opening of cavity is not through tearing, but through cell–cell separation by introducing intercellular space at tricellular junctions [665]. This separation requires either weakening of the pectin in the middle lamina or large compressive stresses. However, the mechanical compressive axial stresses generated by differential growth are not sufficient by themselves to initiate cell separation and we conclude that a full understanding of cavity opening in plants requires the coupling of both chemical and mechanical effects.

16.3 Bifurcation of Growing Cylinders

We now consider the possibility of buckling in a growing elastic cylinder. Before doing so, it is of interest to recall the basic mechanisms through which a cylindrical structure can become unstable in the absence of growth.

16.3.1 Buckling Versus Barreling

It is well known from daily experience that under a large enough compressive axial load an elastic beam will buckle. This phenomenon known as *elastic buckling* or *Euler buckling* is a paradigmatic instability of mechanics. The critical load for buckling was first derived by Euler in 1744 [350, 351, 984] and further refined for higher modes by Lagrange in 1770 [748, 1234]. Both authors obtained their result on the basis of simple beam equations first derived by Bernoulli [1240] (see Figure 16.7). Since then, Euler buckling has played a central role in the stability and mechanical properties of slender structures from nano- to macro-structures in physics, engineering, biochemistry, and biology [954, 1236].

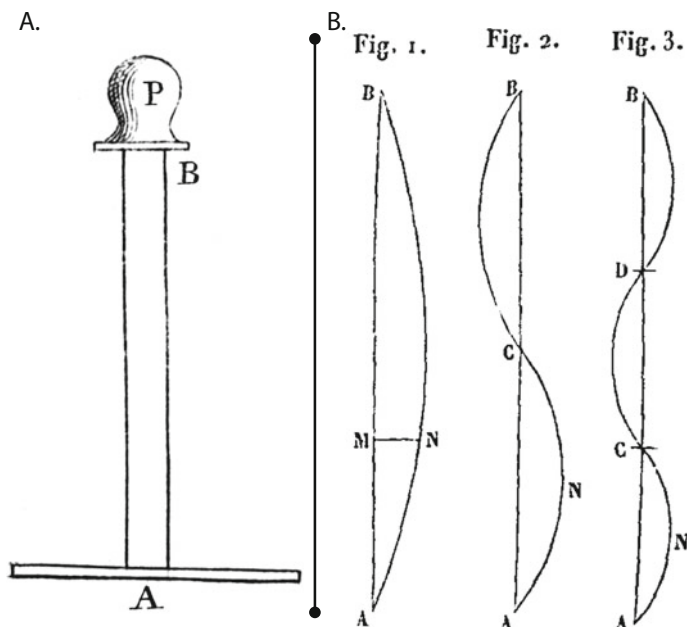


Figure 16.7 Axial buckling. A. Illustrations from Euler manuscript [350]. B. Lagrange solutions for modes $n = 1, 2$, and 3 [748].

We can use the theory of the planar elastica developed in Section 5.8 to look at the possibility of a bifurcation for an elastic rod of length L . Recalling that $\theta = \theta(s)$ is the angle between the tangent to the rod's centerline and the direction of a compressive load $\mathbf{N} = N\mathbf{e}_x$, the equation for the transverse deflection $y = y(s)$ and for the angle are

$$y' = \sin \theta, \quad (16.28)$$

$$\theta'' + \alpha \sin \theta = 0, \quad (16.29)$$

where the prime denotes the derivative with respect to the arc length, and $\alpha = N/EI$ is positive for compressive forces, i.e., $N > 0$. Here, EI is the beam's bending stiffness, where E is the Young's modulus, and I is the second moment of area. Following Section 5.5, the second moment of area, in the case of a cylindrical shell of inner radius A and outer radius B , is

$$I = \pi \frac{B^4 - A^4}{4}. \quad (16.30)$$

For a hinged-hinged beam as shown in Lagrange's drawings in Figure 16.7B, the boundary conditions are

$$\theta'(0) = \theta'(L) = 0, \quad y(0) = y(L) = 0. \quad (16.31)$$

Linearizing the equations around the base solution, $y(s) = \theta(0) = 0$, leads to

$$y' = \theta, \quad (16.32)$$

$$\theta'' + \alpha \theta = 0. \quad (16.33)$$

This boundary-value problem has nontrivial solutions of the form

$$\theta = \cos \left(\frac{n\pi s}{L} \right), \quad (16.34)$$

$$y = \sin \left(\frac{n\pi s}{L} \right), \quad (16.35)$$

with $\alpha L/\pi = n^2 \in \mathbb{N} \setminus \{0\}$. The smallest load N for which there exists a nontrivial solution corresponds to $n = 1$ and is the celebrated Euler buckling load

$$N_{\text{Euler}} = \frac{\pi^2 EI}{L^2}, \quad (16.36)$$

where, according to Euler, " π is the circumference of a circle whose diameter is one" [351].

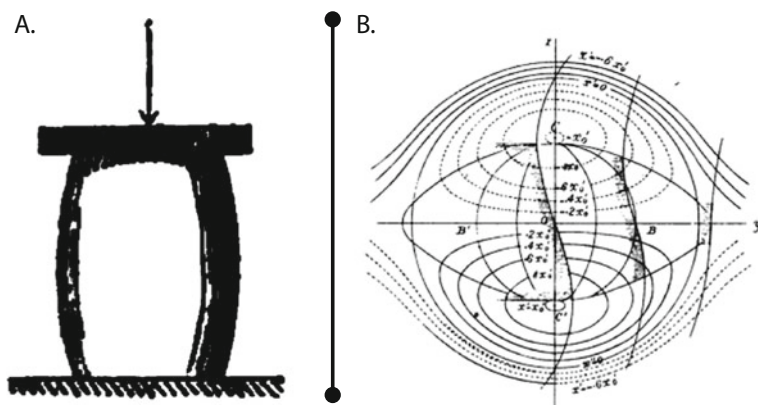


Figure 16.8 Navier and Saint-Venant description of a barreling instability [938] and computations of a distorted cross-section of beams under flexure [1239].

Many other approaches in the theory of one-dimensional structures lead to the same conclusion. For instance, one can analyze the exact solutions of the planar elastica, as given in Section 5.8, or use an energy argument [1236].

The one-dimensional theory can be used with a variety of boundary conditions. It is particularly easy to generalize and it can be used for large geometric deflections of the axis [33]. However, since material cross sections initially perpendicular to the axis remain undeformed and perpendicular to the tangent vector, no information on the elastic deformation around the central curve can be obtained. In particular, other modes of instability such as the barreling instability shown in Figure 16.8A, cannot be obtained. *Barreling* is an axisymmetric deformation mode of a cylinder or a cylindrical shell. These modes will typically occur for sufficiently short structures, where the assumptions used in deriving the Kirchhoff equations fail.

The two-dimensional theory of shells can be used when the thickness of the cylindrical shell is small enough. Then the stability analysis of shell equations such as the Donnell-von Kármán equations leads to detailed information on symmetric instability modes, their localization, and selection [642]. However, the theory cannot be directly applied to obtain information on the buckling instability (asymmetric buckling mode).

The three-dimensional theory of nonlinear elasticity provides a full description of the different instability modes. In the case of long slender structures under loads, the buckling instability can be captured by assuming that the object is either a rectangular beam [102, 787, 967] or a cylindrical shell under axial load. Then, the buckling instability can be recovered by a bifurcation argument following the general theory given in Section 11.10.

This problem was first addressed in 1955 within the framework of nonlinear elasticity by Wilkes [1325] who showed that the linearized system around a finite axial strain can be solved exactly in terms of Bessel functions. While Wilkes only analyzed the first axisymmetric mode ($n = 0$, see Figure 16.9), he noted in his

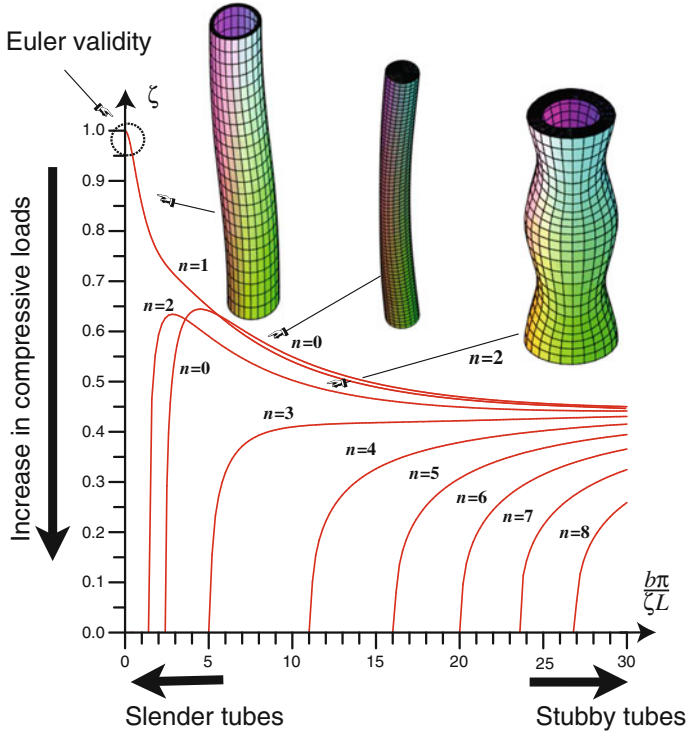


Figure 16.9 Bifurcation curves (stretch as a function of stubbiness) of an homogeneous neo-Hookean ($W = (I_1 - 3)/2$) cylindrical tube for different *circumferential number* $n = 0, 1, 2, \dots, 9$, with $b/a = B/A = 2$. For a given geometry, a bifurcation point is reached when the axial stretch ζ reaches a bifurcation curves. The selected mode is the mode with the largest value of ζ (adapted from [486]).

conclusion that the asymmetric mode ($n = 1$) corresponds to the Euler strut and doing so, opened the door to further investigation by Fosdick and Shield [374] who recovered Euler's criterion asymptotically from Wilkes' solution.

These initial results constitute the basis for much of the modern theory of elastic stability of cylinders within the framework of three-dimensional nonlinear elasticity [96, 295, 311, 552, 553, 1008, 1166]. The experimental verification of Euler's criterion was considered by Southwell [1180] and by Beatty and Hook [73].

A complete bifurcation analysis of cylindrical shells and cylinders is given by Destrade et al. [267, 486] and is summarized here. First, an example of different types of instabilities found in an incompressible neo-Hookean cylindrical shell of different length is shown in Figure 16.9. The known standard features of the stability problem for the cylindrical shell are recovered, namely: For slender tubes, the Euler buckling ($n = 1$) is dominant and becomes unavoidable as slenderness increases; there is a critical slenderness value at which the first barreling mode, $n = 0$, is the first unstable mode (in a thought experiment where the axial strain would be incrementally

increased until the tube becomes unstable); and for very large $b\pi/(\zeta L)$, the critical compression ratio tends asymptotically to the value $\zeta \approx 0.44375$, which corresponds to the surface instability of a half-space under uniaxial compression discussed in Section 11.10.1.

We observe in Figure 16.9 that the Euler buckling criterion is only valid for slender structures and we wish to make that statement more precise. Therefore, we focus on the Euler buckling instability by taking the limit $\zeta \rightarrow 1$ for a cylindrical shell of initial radii A and B . We consider a Mooney–Rivlin strain-energy function, which for λ close to 1, corresponds to the most general form of third-order incompressible elasticity:

$$W_{\text{mr}} = \frac{\mu}{2} \left[\left(\frac{1}{2} + \alpha \right) (I_1 - 3) + \left(\frac{1}{2} - \alpha \right) (I_2 - 3) \right], \quad (16.37)$$

where $\alpha \in [-1/2, 1/2]$. In the limit $\zeta \rightarrow 1$, an asymptotic expression in $\nu = B/L$ can be obtained:

$$N_{\text{crit}} = \frac{3}{4} \frac{\pi^3 B^2 \mu (\rho^4 - 1) \nu^2}{\rho^4} - \frac{1}{48} \frac{\pi^5 B^2 \mu (\rho^2 - 1) (18\alpha(\rho^2 + 1)^2 - 17(\rho^2 - 1)^2) \nu^4}{\rho^6} + \mathcal{O}(\nu^6), \quad (16.38)$$

where $\rho = B/A$ and $\mu = E/3$. We recover to order ν^2 the classic Euler buckling formula (16.36) and we note that to order $\mathcal{O}(\nu^4)$, higher order elasticity effects, controlled by the parameter α , first appear.

The largest correction to the Euler criterion is obtained when $\alpha = -1/2$ and in the limit of a solid circular cylinder ($A \rightarrow 0$ at fixed B). In this case, the ratio of the fourth- to second-order corrections is $13\pi^2\nu^2/12 \approx 10.7\nu^2$ and amount of about 10% for a rod of length $L = 10B$.

For a neo-Hookean material ($\alpha = 1/2$), the maximal deviation from Euler's criterion is found in the limit of thin shells $B \rightarrow A$ in which the ratio of the fourth- to second-order corrections is $-3\pi^2\nu^2/4 \approx -7.4\nu^2$ and amount of about -7% for a rod of length $L = 10B$. In general, for any third-order elastic materials we have, up to corrections of order $\mathcal{O}(\nu^6)$,

$$N_{\text{Euler}} \left(1 - \frac{3}{4} \pi^2 \nu^2 \right) \leq N_{\text{crit}} \leq N_{\text{Euler}} \left(1 + \frac{13}{12} \pi^2 \nu^2 \right). \quad (16.39)$$

We see that the maximal error drops below 1% for rods of length $L \gtrsim 33B$.

It is also of interest to understand which bifurcation will first appear depending on the geometry of the initial cylindrical shell. Here, we restrict our attention to the neo-Hookean case. We want to identify the geometric values at which there is a transition between buckling and barreling modes. We refer to this transition as a *dimensional transition*, in the sense that the material mostly behaves as a slender one-dimensional structure when it buckles according to mode $n = 0$ and mostly

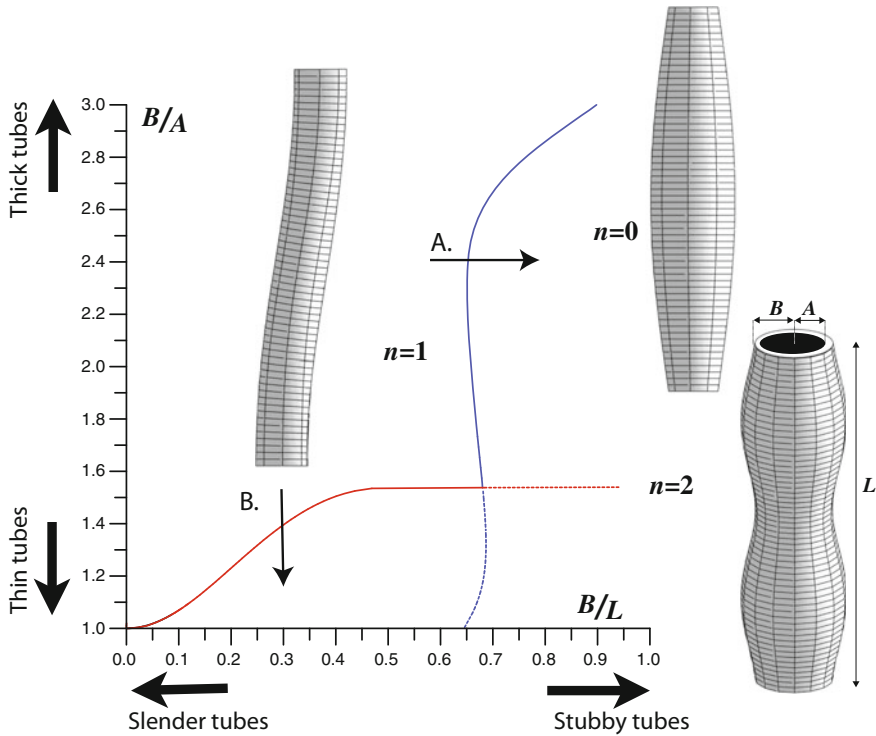


Figure 16.10 Dimensional transition for a neo-Hookean cylindrical tube of initial length L and initial radii A and B . All tubes in the $n = 1$ region become unstable through Euler buckling. As the tube gets stubbier or thinner (arrows), it will not buckle, but it will be subject to a barrelling instability. Note that only the transition curve from mode $n = 0$ are shown. Tubes in the barrelling regions may be susceptible to other unstable modes. Adapted from [486].

as a two-dimensional structure when it barrels with mode $n = 2$. Both modes of instability can be captured by, respectively, a one- or a two-dimensional theory. The results in Figure 16.10 show that for sufficiently slender and thin tubes (B/L small, B/A large), the Euler buckling mode is the dominant instability mode. At a given thickness, the Euler buckling mode disappears in favor of a barrelling mode when the tube is stubby enough (shorter tube at fixed radius) as indicated by the arrow A in Figure 16.10.

For short tubes, at a fixed stubbiness, the Euler buckling mode disappears at the expense of the $n = 2$ barrelling mode as indicated by the arrow B in Figure 16.10. This analysis guarantees that for slender enough tubes ($\nu = B/L$ small enough), the Euler buckling mode is always dominant as long as [486]

$$\frac{B}{A} > \rho^* = 1 + \frac{3}{4} \pi^2 \nu^2 - \frac{17}{32} \pi^4 \nu^4 + \frac{161}{384} \pi^6 \nu^6 + \mathcal{O}(\nu^8). \quad (16.40)$$

Therefore, as long as this inequality is satisfied, we can focus further bifurcation analyses on the Euler buckling mode only. Finally, we note that a local bifurcation analysis does not prevent the cylinder from becoming unstable through global dynamical bifurcation as found in thin stubby cylinders through the formation of diamond patterns [492, 764].

16.3.2 Bifurcation and Buckling in Growing Cylinders

We apply the bifurcation scheme given in Section 14.8 to the problem of computing bifurcations in growing cylinders. The computations are tedious, but the main steps are conceptually simple. Following Section 16.1, we assume that, for a given diagonal growth tensor $\mathbf{G} = \mathbf{G}(R_0)$, there exists a family of cylindrical solutions. We denote by $\chi^{(0)}$ this deformation and by $\mathbf{A}^{(0)}$ and $\mathbf{F}^{(0)}$ the corresponding base solution for the elastic and geometric deformation tensors. The problem is then to write the boundary-value problem for the linearized equations around that base solution.

Step 1: Kinematics of incremental deformations. We expand the deformation $\chi = \chi^{(0)} + \epsilon \chi^{(1)}$, where the $\chi^{(0)}$ is the finite deformation, and $\chi^{(1)}$ is given by the vector

$$\chi^{(1)} = [u(r, \theta, z), v(r, \theta, z), w(r, \theta, z)]. \quad (16.41)$$

Let $\mathbf{F}^{(0)} = \text{Grad}(\chi^{(0)})$, then the incremental deformation tensor $\mathbf{F}^{(1)}$, defined through $\mathbf{F} = (\mathbf{1} + \epsilon \mathbf{F}^{(1)}) \cdot \mathbf{F}^{(0)}$, is given by

$$[\mathbf{F}^{(1)}] = \begin{bmatrix} u_r & (u_\theta - v)/r & u_z \\ v_r & (u + v_\theta)/r & v_z \\ w_r & w_\theta/r & w_z \end{bmatrix}, \quad (16.42)$$

where the (r, θ, z) subscripts denote partial derivatives. The elastic stress tensors are given by

$$\mathbf{A}^{(0)} = \mathbf{F}^{(0)} \mathbf{G}^{-1}, \quad \mathbf{A}^{(1)} = \mathbf{F}^{(1)}. \quad (16.43)$$

The incompressibility constraint is

$$\text{tr}(\mathbf{F}^{(1)}) \equiv u_r + (u + v_\theta)/r + w_z = 0. \quad (16.44)$$

Step 2-3: Linearized equations. The Cauchy stress tensor is expanded around the base solution to give

$$\mathbf{T} = \mathbf{T}^{(0)} + \epsilon \mathbf{T}^{(1)} + \mathcal{O}(\epsilon^2), \quad (16.45)$$

and the constitutive relationship to leading and first order reads

$$\mathbf{T}^{(0)} = \mathbf{A}^{(0)} W_{\mathbf{A}}^{(0)} - p^{(0)} \mathbf{1}, \quad (16.46)$$

and

$$\mathbf{T}^{(1)} = \mathcal{L} : \mathbf{F}^{(1)} + \mathbf{F}^{(1)} \mathbf{A}^{(0)} W_{\mathbf{A}}^{(0)} - p^{(1)} \mathbf{1}, \quad (16.47)$$

where $p = p^{(0)} + p^{(1)}\epsilon$, the derivatives of W with respect to $\mathbf{A}$ are evaluated at $\mathbf{A}^{(0)}$, and $\mathcal{L}$ is the fourth-order tensor of instantaneous elastic moduli defined by

$$\mathcal{L} : \mathbf{F}^{(1)} = \mathbf{A}^{(0)} W_{\mathbf{A}\mathbf{A}}^{(0)} : \mathbf{F}^{(1)} \mathbf{A}^{(0)}. \quad (16.48)$$

The explicit form for an isotropic material is given in Section 14.8. The condition $\text{div } \mathbf{T}^{(1)} = \mathbf{0}$ leads to

$$\text{div } (\mathcal{M}) + (\mathbf{F}^{(1)})^T \text{grad } (p^{(0)}) - \text{grad } (p^{(1)}) = \mathbf{0}, \quad (16.49)$$

where $\mathcal{M} \equiv \mathcal{L} : \mathbf{F}^{(1)}$. In cylindrical coordinates, these three equations are given by

$$\frac{\partial \mathcal{M}_{11}}{\partial r} + \frac{1}{r} \frac{\partial \mathcal{M}_{21}}{\partial \theta} + \frac{\partial \mathcal{M}_{31}}{\partial z} + \frac{1}{r} (\mathcal{M}_{11} - \mathcal{M}_{22}) + F_{11}^{(1)} \frac{dp^{(0)}}{dr} - \frac{\partial p^{(1)}}{\partial r} = 0, \quad (16.50)$$

$$\frac{\partial \mathcal{M}_{12}}{\partial r} + \frac{1}{r} \frac{\partial \mathcal{M}_{22}}{\partial \theta} + \frac{\partial \mathcal{M}_{32}}{\partial z} + \frac{1}{r} (\mathcal{M}_{21} + \mathcal{M}_{12}) + F_{12}^{(1)} \frac{dp^{(0)}}{dr} - \frac{\partial p^{(1)}}{\partial \theta} = 0, \quad (16.51)$$

$$\frac{\partial \mathcal{M}_{13}}{\partial r} + \frac{1}{r} \frac{\partial \mathcal{M}_{23}}{\partial \theta} + \frac{\partial \mathcal{M}_{33}}{\partial z} + \frac{1}{r} \mathcal{M}_{13} + F_{13}^{(1)} \frac{dp^{(0)}}{dr} - \frac{\partial p^{(1)}}{\partial z} = 0. \quad (16.52)$$

Substituting (16.42) into the incremental equations given in (16.49) results in

$$\begin{aligned} & (r(\mathcal{L}'_{2211} - \mathcal{L}'_{3311}) - \mathcal{L}_{2222} + \mathcal{L}_{2233} - \mathcal{L}_{2121} + \mathcal{L}_{1331}) v_{\theta}/r^2 \\ & + (\mathcal{L}_{1111} - \mathcal{L}_{3311} - \mathcal{L}_{1331}) u_{rr} \\ & (r(\mathcal{L}'_{1111} + (p^{(0)})' - \mathcal{L}'_{3311}) + \mathcal{L}_{1111} - 2\mathcal{L}_{3311} + \mathcal{L}_{2233} - \mathcal{L}_{1331}) u_r/r \\ & + (\mathcal{L}_{2112} + \mathcal{L}_{2211} - \mathcal{L}_{1331} - \mathcal{L}_{3311}) v_{r\theta}/r + \mathcal{L}_{2121} u_{\theta\theta}/r^2 + \mathcal{L}_{3131} \\ & + (r(\mathcal{L}'_{2211} - \mathcal{L}'_{3311}) - \mathcal{L}_{2222} + \mathcal{L}_{2233} + \mathcal{L}_{1331}) u/r^2 - (p^{(1)})_r = 0, \end{aligned} \quad (16.53)$$

$$\begin{aligned} & (r\mathcal{L}'_{1212} + \mathcal{L}_{1212} + \mathcal{L}_{2222} - \mathcal{L}_{2233} - \mathcal{L}_{3223}) u_{\theta}/r - (r\mathcal{L}'_{1212} + \mathcal{L}_{1212}) v/r \\ & + (\mathcal{L}_{2222} - \mathcal{L}_{2233} - \mathcal{L}_{3223}) v_{\theta\theta}/r + \mathcal{L}_{3232} r v_{zz} + \mathcal{L}_{1212} r v_{rr} \\ & + (\mathcal{L}_{2211} - \mathcal{L}_{2233} - \mathcal{L}_{3223} + \mathcal{L}_{1221}) u_{r\theta} + (r\mathcal{L}'_{1212} + \mathcal{L}_{1212}) v_r - (p^{(1)})_{\theta} = 0, \end{aligned} \quad (16.54)$$

$$\begin{aligned} & \mathcal{L}_{2323} w_{\theta\theta}/r^2 + (r\mathcal{L}'_{1313} + r(p^{(0)})' + \mathcal{L}_{1331} - \mathcal{L}_{2332}) u_z/r \\ & + \mathcal{L}_{1313} w_{rr} + (\mathcal{L}_{3333} - \mathcal{L}_{2332} - \mathcal{L}_{2233}) w_{zz} + (r\mathcal{L}'_{1313} + \mathcal{L}_{1313}) w_r/r \\ & + (\mathcal{L}_{3311} + \mathcal{L}_{1331} - \mathcal{L}_{2332} - \mathcal{L}_{2233}) u_{rz} - (p^{(1)})_z = 0, \end{aligned} \quad (16.55)$$

where the prime denotes differentiation with respect to r .

Step 4: The boundary-value problem. The set of partial differential equations for the variables $u, v, w, p^{(1)}$ can be further simplified to a boundary-value problem for a set of differential equations in the variable r by Fourier expanding the dependence in θ and z , that is

$$u = f(r) \cos n\theta \cos \psi z, \quad v = g(r) \sin n\theta \cos \psi z, \quad (16.56)$$

$$w = h(r) \cos n\theta \sin \psi z, \quad p^{(1)} = k(r) \cos n\theta \cos \psi z. \quad (16.57)$$

In order that the incremental displacements be single-valued, we take the mode number n to be an integer $n \geq 0$. Since the incremental end displacement w must vanish on the ends, we have

$$\psi = \frac{m}{l} \pi = \frac{m}{\lambda L} \pi, \quad m = 1, 2, 3, \dots \quad (16.58)$$

where m is set to unity, without loss of generality, so that ψ is inversely proportional to the length of the cylinder. The expressions in (16.56–16.57) are substituted in (16.53–16.55) and $h(r)$ can be eliminated by means of the incompressibility constraint (16.44). The resulting incremental equilibrium equations are

$$\begin{aligned} k' = & (r(\mathcal{L}'_{2211} - \mathcal{L}'_{3311}) - \mathcal{L}_{2222} + \mathcal{L}_{2233} - \mathcal{L}_{2121} + \mathcal{L}_{1331}) ng/r^2 \\ & + (\mathcal{L}_{2112} + \mathcal{L}_{2211} - \mathcal{L}_{1331} - \mathcal{L}_{3311}) ng'/r + (\mathcal{L}_{1111} - \mathcal{L}_{3311} - \mathcal{L}_{1331}) f'' \\ & + (r(\mathcal{L}'_{1111} + (p^{(0)})' - \mathcal{L}'_{3311}) + \mathcal{L}_{1111} - 2\mathcal{L}_{3311} + \mathcal{L}_{2233} - \mathcal{L}_{1331}) f'/r \\ & + (r(\mathcal{L}'_{2211} - \mathcal{L}'_{3311}) - \mathcal{L}_{2222} + \mathcal{L}_{2233} + \mathcal{L}_{1331}) f/r^2 \\ & - n^2 \mathcal{L}_{2121} f/r^2 - \psi^2 \mathcal{L}_{3131} f, \end{aligned} \quad (16.59)$$

$$\begin{aligned} r\mathcal{L}_{1212}g'' = & -nk + (r\mathcal{L}'_{1212} + \mathcal{L}_{1212} + \mathcal{L}_{2222} - \mathcal{L}_{2233} - \mathcal{L}_{3223})nf/r \\ & + (r\mathcal{L}'_{1212} + \mathcal{L}_{1212})g/r + (\mathcal{L}_{2222} - \mathcal{L}_{2233} - \mathcal{L}_{3223})n^2g/r \\ & + r\psi^2 \mathcal{L}_{3232}g + (\mathcal{L}_{2211} - \mathcal{L}_{2233} - \mathcal{L}_{3223} + \mathcal{L}_{1221})nf' - (r\mathcal{L}'_{1212} + \mathcal{L}_{1212})g', \end{aligned} \quad (16.60)$$

$$\begin{aligned} \mathcal{L}_{1313}f''' = & n^2 f' + (ng + f)/r \mathcal{L}_{2323}/r^2 - (r\mathcal{L}'_{1313} + r(p^{(0)})' + \mathcal{L}_{1331} - \mathcal{L}_{2332}) \psi^2 f/r \\ & - \mathcal{L}_{1313} ((f'' + ng'')/r - 2(r' + ng')/r^2 + 2(f + ng)/r^3) \\ & + (\mathcal{L}_{3333} - \mathcal{L}_{2332} - \mathcal{L}_{2233}) \psi^2 (f + ng)/r + (\mathcal{L}_{3333} + \mathcal{L}_{3311} - \mathcal{L}_{1331}) \psi^2 f' \\ & - (r\mathcal{L}'_{1313} + \mathcal{L}_{1313}) (f'' + (f' + ng')/r - (f + ng)/r^2)/r - \psi^2 k. \end{aligned} \quad (16.61)$$

The corresponding incremental boundary conditions on the inner and outer wall $r = a, b$ is $\mathbf{T}^{(1)} \mathbf{n} = P^{(1)} \mathbf{n}$ which takes the form

$$(\mathcal{L} : \mathbf{F}^{(1)} + \mathbf{F}^{(1)} \mathbf{A}^{(0)} W_{\mathbf{A}}^{(0)} - p^{(1)} \mathbf{1}) \mathbf{n} = P^{(1)} \mathbf{n}, \quad (16.62)$$

where the incremental internal pressure, $P^{(1)}$, is taken to be $P^{(1)} = 0$.

The three boundary condition equations on $r = a, b$ are given by

$$(\mathcal{L}_{1122} - \mathcal{L}_{1133})(f + ng) + (\mathcal{L}_{1111} - \mathcal{L}_{1133} + \alpha_r W_1) r f' - r k = P^{(1)}, \quad (16.63)$$

$$r g' - g - n f = 0, \quad (16.64)$$

$$r^2 f'' + r f' + (\psi^2 r^2 + n^2 - 1) f = 0. \quad (16.65)$$

The growth dependence comes about through the coefficients of the above system of equations. The position vector depends on $\mathbf{G}$ through (16.10) and the instantaneous elastic moduli depend on $\alpha = \alpha_\theta$ and its derivatives through the relation

$$\frac{d\alpha}{dr} = \frac{\alpha}{r} - \frac{\zeta \alpha^3 \gamma_\theta^2}{r g} - \frac{\alpha \gamma'_\theta}{\gamma_\theta}. \quad (16.66)$$

For a given growth tensor $\mathbf{G}$ and strain-energy function W , the bifurcation points corresponds to the critical value of $P = P_{\text{crit}}$ such that a nontrivial solution for this boundary-value exists. This critical value can be solved by the determinant method as explained in Section 15.6.1.

16.3.3 The Effective Rigidity of a Growing Cylinder

During growth, the effective property of a structure may change. Due to the residual stress field, it may support larger loadings before buckling, or, on the contrary, be prone to buckling under its own weight. Here, we are interested in quantifying the effective rigidity of a growing cylinder in the presence of residual stress. We are considering a grown hyperelastic incompressible cylinder through a growth process $\mathbf{G}$. Since the cylinder is in large deformation and supports residual stress, the classic notion of Young's modulus does not apply directly and an explicit computation of the rigidity is not possible.

We can perform the following thought experiment to obtain an effective Young's modulus: Consider the grown cylinder and measure all its geometric parameters (inner and outer radii a_0 and b_0 and height l_0 being the geometric parameters for zero load) and subject it to a normal load N until it buckles at N_{crit} . The critical buckling pressure

$$P_{\text{crit}} = \frac{N_{\text{crit}}}{\pi(b_0^2 - a_0^2)}, \quad (16.67)$$

can be used to compute the effective Young's modulus, defined as the Young's modulus of an equivalent homogeneous elastic cylinder with the same geometry, but with no residual stress, and buckling at the same pressure, that is

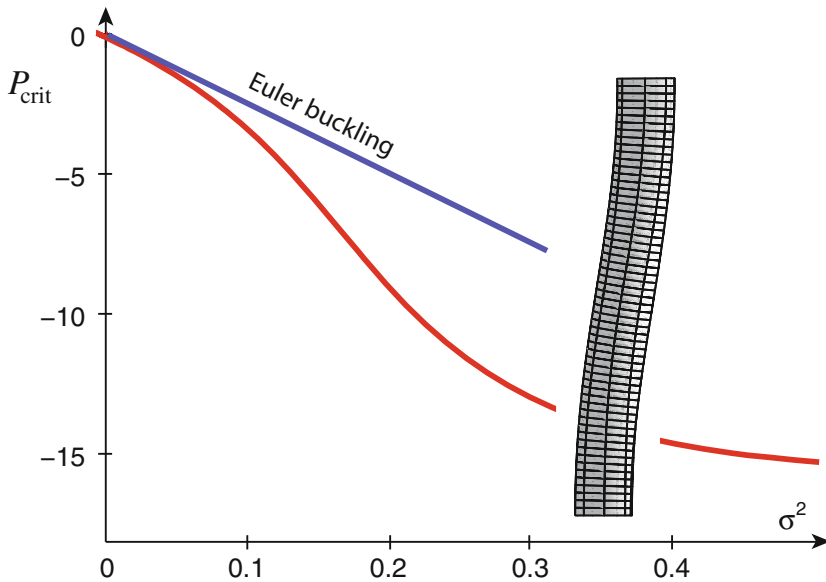


Figure 16.11 Bifurcation modes of a cylindrical tube ($A = 0.0001$, $B = 1$). The buckling mode $n = 1$ is shown. The curve gives the value of the parameters where buckling occurs and the line indicates the prediction given by the Euler buckling formula (where $\mu = 1 = E/3$).

$$E_{\text{eff}} = \frac{4P_{\text{crit}}}{\pi^2\sigma^2}, \quad (16.68)$$

where $\sigma = \sqrt{b_0^2 + a_0^2}/l_0$ is the stubbiness ratio (the inverse of the slenderness ratio).

We saw in Section 16.3.1 that the Euler buckling formula is valid for cylinders that are sufficiently slender. Therefore, in order to obtain an estimate of the cylinder rigidity through an effective Young's modulus, we compute the critical pressure P_{crit} as a function of σ and obtain the effective Young's modulus, E_{eff} , from the slope k of the graph

$$P_{\text{crit}}(\sigma^2) = k\sigma^2, \quad k = \frac{\pi^2}{4} E_{\text{eff}}. \quad (16.69)$$

This procedure is validated and illustrated in the absence of growth in Figure 16.11, where the critical pressure for the buckling mode ($n = 1$) of a neo-Hookean cylinder is plotted as a function of σ^2 together with the Euler buckling criterion. Therefore, we conclude that the bifurcation analysis provides a method to define an effective Young's modulus.

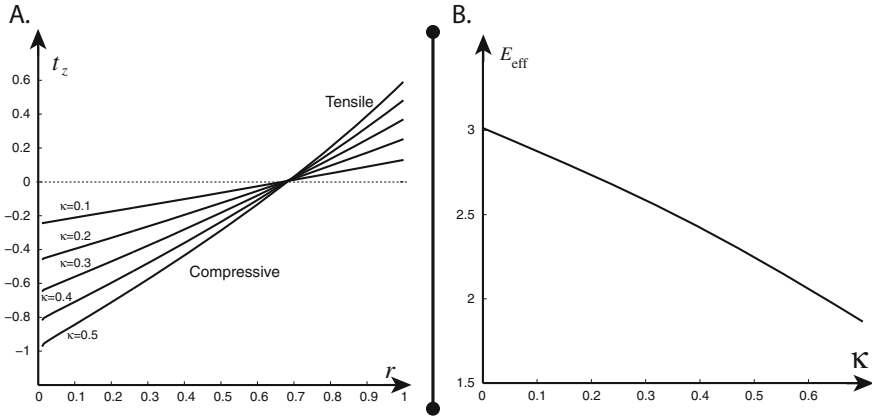


Figure 16.12 A. Axial stress profiles for neo-Hookean cylinders ($\mu = 1$) undergoing axial growth, $\gamma_z = 1 + \kappa(b - r)$. B. The effective modulus as a function of the growth parameter κ , where $\gamma_z = 1 + \kappa(b - r)$. For $\kappa = 0$, we recover the Young's modulus $E = 3$.

16.3.4 An Example

We apply this method to the case of an isotropic neo-Hookean cylinder with radial-dependent growth. The growth tensor $\mathbf{G}$ is a function of the radial position r in the current configuration. We assume a simple, linear growth law in the axial direction,

$$\gamma_r = \gamma_\theta = 1, \quad \gamma_z = 1 + \kappa(r - a), \quad (16.70)$$

where κ is a parameter characterizing growth in the system. It is interesting to consider the residual stresses created in the grown material in the absence of loads, $N = 0$, for various values of the growth parameter. As axial growth increases, a large compressive zone develops along the longitudinal direction as shown in Figure 16.12A. We can now determine the overall rigidity of the grown cylinder. We assume that the cylindrical shell has grown axially by a given amount and we test the stability of the resulting residually stressed cylindrical shell. In Figure 16.12B we observe that the effect of axial growth is to reduce the stability of the structure. This effect can be understood as follows. Differential growth creates a large zone of compression in the cylinder. The cylinder is pre-compressed due to growth and will therefore buckle under smaller loads.

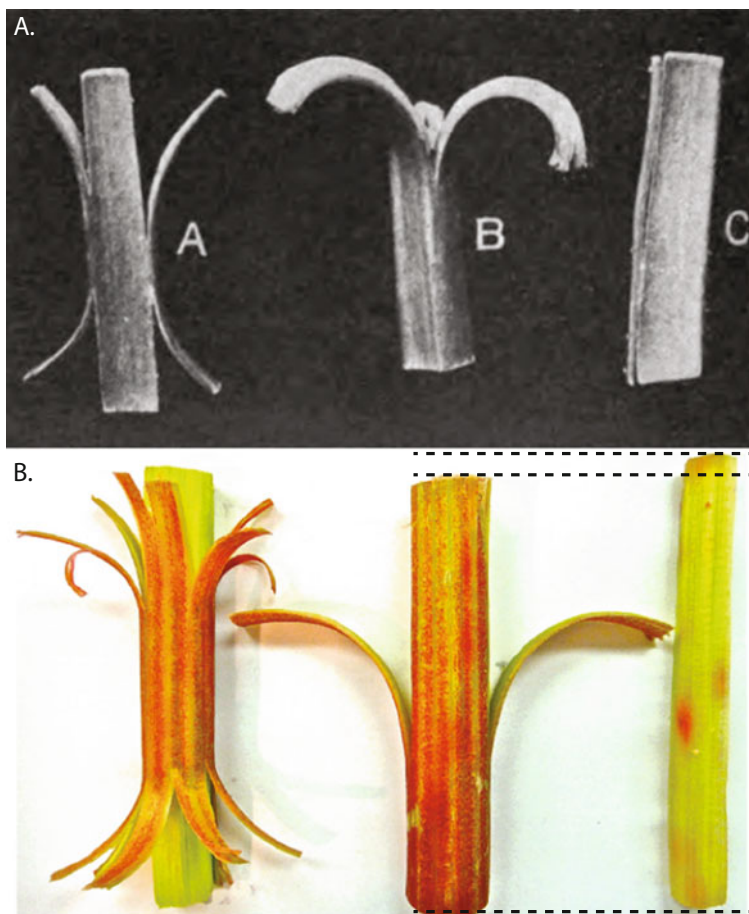


Figure 16.13 Growth-induced longitudinal tissue tension in a stalk of rhubarb. When partially peeled, the epidermis bends backward demonstrating the presence of residual stress and surface tension in the original configuration. When completely peeled (last picture on the right), the pith increases in length, as shown by the dashed lines. A. from Gager’s “Fundamental of Botany” [412]. B. Picture courtesy of Ellen Kuhl (adapted from [591]).

16.4 Application: Tissue Tension in Plants

16.4.1 Background

We briefly recall the problem of tissue tension first discussed in Section 2.2.1 and illustrated in Figure 16.13.

When the stem of a flower, such as a dandelion, is cut axially, it bends backwards as shown in Figure 16.14. This change of shape is due to the presence of residual stress



Figure 16.14 Left: When the stem of a dandelion is cut axially, it bends backward. Right: When a section is completely cut, it relieves stress by curving (held with suspicion by Zakkai, the author's second son).

in the original cylindrical configuration. This residual stress, called *tissue tension* by plant physiologists from the nineteenth century, is induced by a differential resting length of the outer tissue, the *epidermis*, with respect to the inner softer tissue. For instance, when the epidermis of a rhubarb stalk is completely peeled, it is markedly shorter than the *pith*, its inner tissue, as shown in Figure 2.14.

We conclude that, in their original configuration, the epidermis is in tension and the pith in compression. Many authors [562, 739, 741] have argued that this differential length originates from the differential extensional growth of the cell walls in outer and inner layers, creating an irreversible change in the resting lengths of both tissues. Note, however, that when a tissue is immersed in a bath with solutes of different concentration, it may also change its resting length, indicating that there is a hydraulic component to the relative extension of the tissues.

Mechanically, each separate rhubarb tissue is soft and cannot support its own weight without buckling. However, the combined configuration is rigid and allows the plant to shoot upwards. Experiments have established that the outer tissue plays a

substantial role in the overall rigidity, accounting for as much as 70% of the rigidity for less than 10% of the cross-sectional area [954, p. 300]. Therefore, the overall flexural rigidity of the residually stressed structure is much larger than the rigidity of each component. The problem is then to understand how axial differential growth and/or difference in tissue stiffness change the overall flexural rigidity. We note that in order to understand the mechanics of these structures, the biological origin of the residual stresses is not relevant as we take their existence as a starting point.

16.4.2 The Model

We use a simple model of a stem viewed as a cylindrical shell composed of two material layers with different growth and elastic properties. We are interested in understanding the specific role of axial growth, therefore, we neglect the possible effect of anisotropic reinforcement by assuming that the tissue is made out of a material that is hyperelastic, incompressible, homogeneous, isotropic and subject to growth solely along the axial direction (taken to be the z -axis).

Since typical ranges for elongation or compression can be as much as 6 to 40% of the original length [659], the material should be considered as being in large deformations. We take growth as a *fait accompli* by postulating that each cylindrical shell has grown axially by a given amount and study the grown structure at that time. Following the discussion in the previous section, we analyze the stability of the grown residually stressed cylindrical shell to obtain an effective Young's modulus.

We use the general setup of Section 16.1 and assume that in its initial configuration, the cylindrical shells have height L_0 and radii A_0, A_1, A_2 . Since growth is purely axial, we assume that the growth tensor has the form

$$[\mathbf{G}] = \begin{cases} \text{diag}(1, 1, \gamma_1) & R_0 \in [A_0, A_1], \\ \text{diag}(1, 1, \gamma_2) & R_0 \in [A_1, A_2], \end{cases} \quad (16.71)$$

with γ_1 and γ_2 constant.

Next, we model the two tissues separately based on experiments [564] in which tests were performed on the inner and outer tissues of the hypocotyl of the sunflower (*Helianthus annuus*). The data for the inner tissue (data points in Figure 16.15A) shows that the stress–strain curve for the inner tissue is nearly linear within the range of forces applied (0–0.4 N). Therefore, we model the inner tissue as a neo-Hookean material with strain-energy function

$$W_1 = \frac{\mu_1}{2} (I_1 - 3). \quad (16.72)$$

We consider elastic deformations of the form $[\mathbf{A}] = \text{diag}(\alpha, \alpha, 1/\alpha^2)$. Following the discussion in Section 11.8.1, the axial stress for a strip of neo-Hookean material is given by (taking $\lambda = 1/\alpha^2$ in Equation (11.190))

$$t_z = \mu_1 \left(\frac{1}{\alpha^4} - \alpha^2 \right). \quad (16.73)$$

A nonlinear regression can be performed to fit this relation to the experimental data while solving for the parameter μ_1 . Doing so, we obtain $\mu_1 = 1.25$ MPa with an R-squared value of 0.991. Figure 16.15A compares the approximate experimental data points [564] and the corresponding stress-strain fit.

The outer tissue is a complex tissue containing both the epidermis and one or two layers of cortical parenchyma. Uniaxial extension data, shown in Figure 16.15B, shows a very strong strain-stiffening effect. Therefore, we model the outer layer as a Fung material with

$$W_2 = \frac{\mu_2}{2\nu} (e^{\nu(I_1-3)} - 1), \quad (16.74)$$

where μ_2 is the elastic material constant and ν controls the strain-stiffening property of the outer layer. The data points were fitted to the axial stress

$$t_z = \alpha_z \frac{\partial W_2}{\partial \alpha_z} - p. \quad (16.75)$$

In a uniaxial test on a rectangular strip of tissue along the z -direction, the elastic tensor is again given by $[\mathbf{A}] = \text{diag}(\alpha, \alpha, 1/\alpha^2)$ and the boundary condition $t_x = t_y = 0$ implies $p = \alpha \partial_x W_2$. Substituting the strain-energy function W_2 into the stress-strain relationship, the axial stress is given by

$$t_z = \mu_2 \left(\frac{1}{\alpha^4} - \alpha^2 \right) \exp \left[\nu \left(2\alpha^2 + \frac{1}{\alpha^4} - 3 \right) \right]. \quad (16.76)$$

A nonlinear regression analysis produces values $\mu_2 = 6.7$ MPa and $\nu = 195$ with an R-squared value of 0.992. This large value of ν is needed to recover the observed exponential behavior at small strains. Figure 16.15 compares the approximate experimental data points and the corresponding stress-strain fit. Both models are shown to be very good fits to the data.

The relevant part of this analysis is not the precise values of the constants, but the overall qualitatively different properties of the two tissues in the elastic regime. Therefore, for the rest of our analysis, we adopt a neo-Hookean model for the inner tissue and a Fung model for the outer tissue and perform a general analysis of the response of the overall structures for arbitrary values of the material and geometric constants.

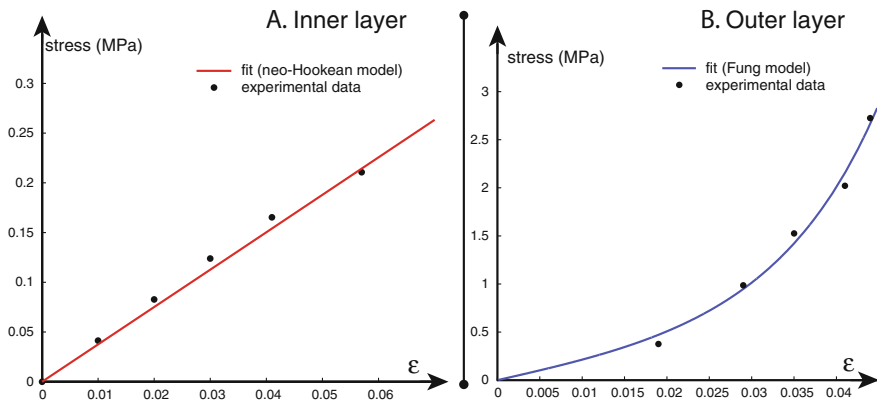


Figure 16.15 The experimental data from a uniaxial test on the tissue of a sunflower hypocotyl [564]. A. The data points for the inner layer are fitted to the constitutive relationship using a neo-Hookean strain-energy function (R-squared value is 0.991). B. The outer layer data and a fit to the constitutive relationship using a Fung-type strain-energy function (R-squared value is 0.992).

16.4.3 Analysis

16.4.3.1 The Base Solution

First, we consider the semi-inverse problem consisting in computing the deformation of the two-layer cylinder into another two-layer cylinder for given material, geometric, load, and growth parameters. The general solution is given in Section 16.1 with the particular choice $P = 0$, $n = 2$ and the form of the strain-energy functions given in the previous section. It is particularly interesting to consider the residual stresses created in the grown material in the absence of loads, that is by choosing $N = 0$. In Figure 16.16, we show the axial stress profile as we vary the ratio of the inner layer stiffness to the outer layer stiffness and the ratio of the inner layer width to the outer layer width (w_1/w_2) where $w_i = (A_i - A_0)$ and $w_2 = (A_2 - A_1)$. As the thickness of the inner layer decreases, large stress gradients are created in the outer layer.

16.4.3.2 Estimates

Before performing a stability analysis of the residually stressed cylinders, we derive estimates based on simple considerations from linear elasticity.

First, we consider a cylinder made out of two cylinders of different materials in the absence of growth with respective radii A_0 , A_1 and A_2 and length L as before. Then, a standard way to estimate the Young's modulus [1236] of the assembly is to consider the sum of the flexural rigidities, that is

$$E_{\text{est}} I = E_1 I_1 + E_2 I_2, \quad (16.77)$$

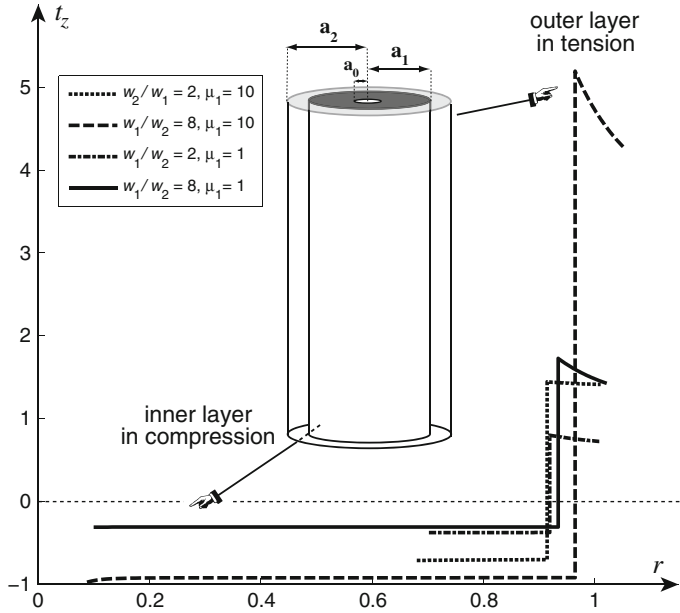


Figure 16.16 Tissue tension in two-layer cylinders with varying thickness and shear moduli ($A_1 = 0.9$, $A_2 = 1$, $\nu = 20$, $\gamma_2 = 1$, $\gamma_1 = 1.2$).

where E_{est} is an estimate for the effective Young's modulus provided by the linear theory of elasticity. Explicitly, since the moments of area for each cylindrical shells are known, we have

$$E_{\text{est}} = 3 \frac{\mu_1(A_1^4 - A_0^4) + \mu_2(A_2^4 - A_1^4)}{A_2^4 - A_0^4}. \quad (16.78)$$

This estimate provides a linear relationship with respect to changes in the rigidity of the outer layer. However, it fails to take into account the effect of strain-stiffening since the parameter ν does not appear explicitly.

Second, we consider a grown two-layer cylinder with a neo-Hookean material inside and a Fung material outside. We assume that the cylinder in the current configuration has height l_0 and radii a_0, a_1, a_2 where $a_0 \ll 1$ so that a_0^2, a_0^4 can be neglected. Before we consider an estimate of the flexural rigidity, we need to model the Fung material under extension. To do so, we consider the first approximation that captures both the exponential behavior and the small deformation limit, that is we express the axial tension as

$$T_2 = 3\mu_2\epsilon_2 e^{3\nu\epsilon_2^2}, \quad (16.79)$$

where ϵ_2 is the axial strain, computed with respect to the unstressed grown configuration of the outer cylinder. The apparent Young's modulus of the outer cylinder is obtained as the slope of the tangent to this curve as a function of ϵ_2 , that is, we estimate the Young's modulus of the outer cylinder as

$$E_2 = \frac{\partial T_2}{\partial \epsilon_2} = 3\mu_2(6\nu\epsilon_2^2 + 1)e^{3\nu\epsilon_2^2}. \quad (16.80)$$

Similarly, we have, for the inner cylinder $T_1 = 3\mu_1\epsilon_1$ and $E_1 = 3\mu_1$, where ϵ_1 is the strain with respect to the unstressed configuration of the inner cylinder. Next, we compute the rest shape of the grown cylinders by considering the case where no net traction is applied at the two caps, that is, we have

$$\begin{aligned} N &= 0 \\ &= \pi [T_1 a_1^2 + T_2(a_2^2 - a_1^2)] \\ &= 3\pi [\mu_1 \epsilon_1 a_1^2 + \mu_2 e^{3\nu\epsilon_2^2}(a_2^2 - a_1^2)], \end{aligned} \quad (16.81)$$

where $\epsilon_i = l_0/\gamma_i - 1$ and the two cylinders are assumed, without loss of generality, to have height 1 before they start growing. The equation $N = 0$ can be solved for l_0 to obtain the residual strain. Since the equation is transcendental in l_0 , no useful estimates of l_0 can be obtained, except in the case $\nu = 0$ which is an upper bound, l_{est} for the length l_0 :

$$l_{\text{est}} = \gamma_1 \gamma_2 \frac{\mu_1 a_1^2 + \mu_2(a_2^2 - a_1^2)}{\mu_1 \gamma_2 a_1^2 + \mu_2 \gamma_1(a_2^2 - a_1^2)}. \quad (16.82)$$

We can use again Equation (16.77) to obtain an estimate

$$E_{\text{est}} = 3 \frac{\mu_1 a_1^4 + \mu_2(6\nu\epsilon_2^2 + 1)e^{3\nu\epsilon_2^2}(a_2^4 - a_1^4)}{a_2^4}, \quad (16.83)$$

where $\epsilon_i = l_{\text{est}}/\gamma_i - 1$ and a_1, a_2 are obtained using the assumption $a_0 \ll 1$ and from the conservation of volume of each cylindrical layer, namely $A_1^2 \gamma_1 = b_0^2 l_{\text{est}}$ and $(A_2^2 - A_1^2) \gamma_2 = (a_2^2 - a_1^2) l_{\text{est}}$. This estimate is compared with the results of the numerical analysis of the stability equation in the next section.

16.4.3.3 Bifurcation Analysis and Effective Rigidity

We consider a grown two-layer cylinder with a neo-Hookean material inside and a Fung material outside and compute the effective Young's modulus as a function of the parameters by performing a full stability analysis and extracting the critical value of the axial load leading to buckling when parameters are varied. Without loss of

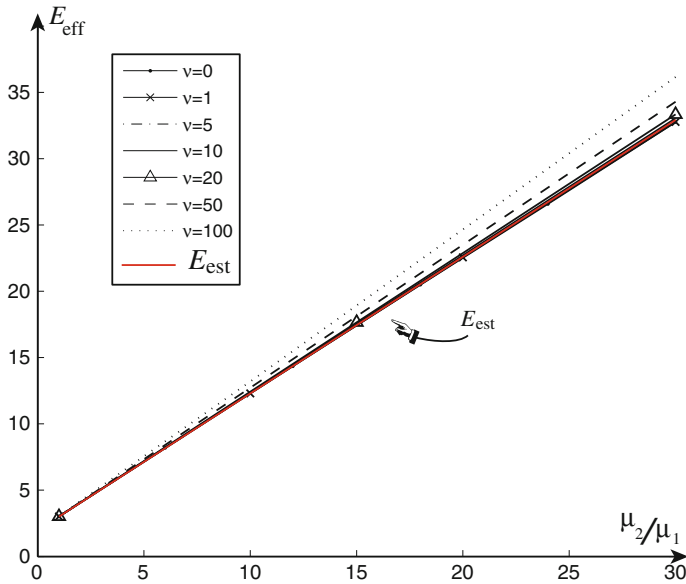


Figure 16.17 The effect of outer wall stiffness and strain-stiffening properties on the stability of a two-layer cylinder in the absence of residual stress. $A = 0.0001$, $B = 0.9$, $C = 1$. The solid line corresponds to the estimate (16.78).

generality, we take $\gamma_2 = \mu_1 = 1$. For comparison, we scale the effective Young's modulus by the Young's modulus of a neo-Hookean one-layer cylinder E_{nh} .

First, we study the effect of differential stiffness between layers in the absence of growth. In Figure 16.17, we observe that the stiffness of the outer layer μ_2 provides a substantial improvement on the overall rigidity of the structure, which is essentially linear in the ratio of moduli and well approximated by the estimate (16.78). Note that the correction due to the nonlinearity of the Fung model cannot be captured since, in the regime considered, the estimate (16.78) does not depend explicitly on the strain-stiffening parameter ν . However, the strain-stiffening property of the outer wall has very little, if any, effect. Essentially, in this regime, the outer layer is in a regime where it behaves as a neo-Hookean material.

Second, we fix the value of μ_2 and consider the effect of growth by varying the parameter γ_1 . In Figure 16.18, we observe that in the absence of strain-stiffening, the effect of growth is to reduce the stability of the structure. Indeed, growth creates a large zone of compression in the inner tissue, as observed in Figure 16.16, so that the cylinder is pre-compressed due to growth and therefore buckles for a smaller load. Therefore, there is no gain in stiffness due to growth in a homogeneous, isotropic, incompressible, two-layer neo-Hookean cylinder. For a strain-stiffening outer layer, the situation is radically different and even modest differential axial growth has a dramatic effect on the rigidity of the structure. After growth, large stresses are needed for the small changes in strains that would occur on the concave side of the

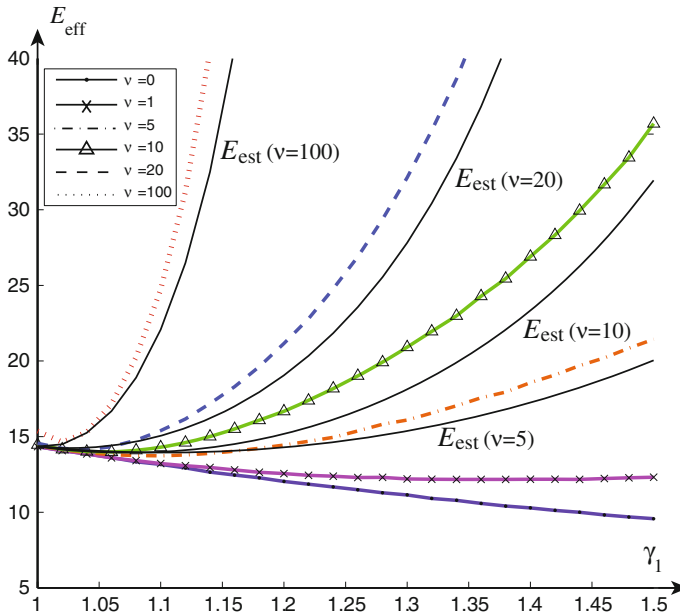


Figure 16.18 The effect of axial differential growth on the rigidity of a two-layer cylinder for different strain-stiffening properties (initial size $A = 0.0001$, $B = 0.9$, $C = 1.0$, $\mu_2 = 12$). The estimate given by (16.83) captures most of the exponential increase of the rigidity as the relative growth between outer and inner layer increases.

cylinder during bending. The exponential increase of the effective Young's modulus is qualitatively captured by the estimate (16.83) that predicts an exponential term of the form $\exp[\kappa\nu(\gamma_1 - 1)^2]$, where κ depends on the moduli μ_1 and the geometric parameters.

We conclude that the main effect of differential growth is to bring the outside layer in a regime where the nonlinear stiffening response can be fully utilized.

16.4.4 Discussion

The increase in flexural rigidity of cylindrical structures through differential axial growth and nonlinear strain-stiffening appears to be a simple generic mechanism through which structural properties is controlled in biological systems. In plants, this differential axial extension is only a component of a complex mechanical and growth environment [377–379]. In particular, for trees, apart from primary vertical growth, a secondary cambial radial growth also takes place. *Cambial growth* allows branches and trunks to gain in girth, but it also takes place differentially to allow the overall tree structure to attain a complicated mechanical balance. The net mechanical effect of

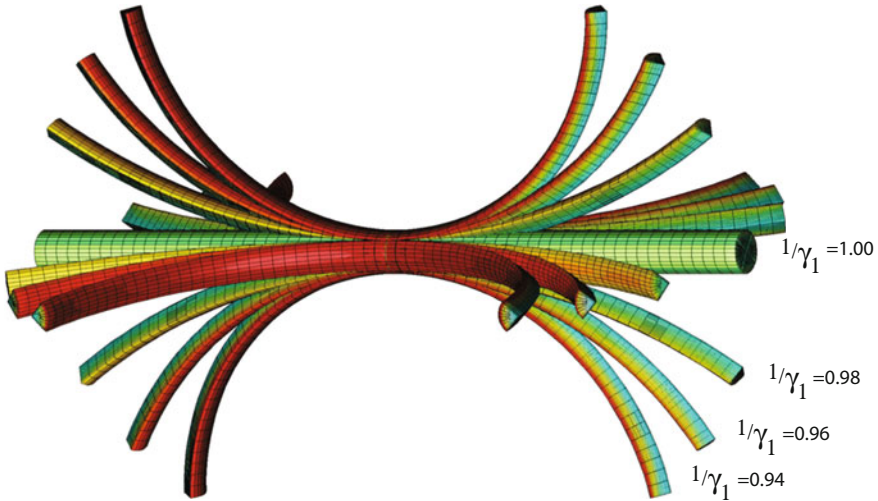


Figure 16.19 Growth-induced longitudinal tissue tension in a stalk of rhubarb. The stalk is modeled by assuming growing volume and surface elastic elements. As the relative shrinkage of the surface increases, the surface tension creates higher curvatures for quarter slices [591] (figure courtesy of Ellen Kuhl).

this combined growth is a complicated stress field with a combination of tension and compression wood [910]. However, the cellular mechanism sensing residual stresses during the differentiation process of the wood cells remains elusive [55].

The outer layer in tension is usually very thin and can be approximated by a surface condition [591]. The idea is to consider a cylinder with an external surface. Both volumes and surface can grow independently. The inner volume follows the usual rule of volumetric growth whereas surface growth appears as a boundary condition. This construction leads to an elegant formulation of the problem that can be used for analytical and computational purposes. For instance, Figure 16.19 shows the result of the computation of equilibrium solution of a shrinking skin on a quarter cylinder.

In order to isolate and understand the effect of differential axial growth, we have neglected important effects necessary to obtain a precise picture of the material properties of specific biological structures, notably, anisotropic response and inhomogeneity. However, the analysis presented here was performed using the general framework of nonlinear elasticity which can easily be generalized to include these effects. In particular, axial growth is also found in arteries [601], a system which crucially depends on anisotropy as we show next.

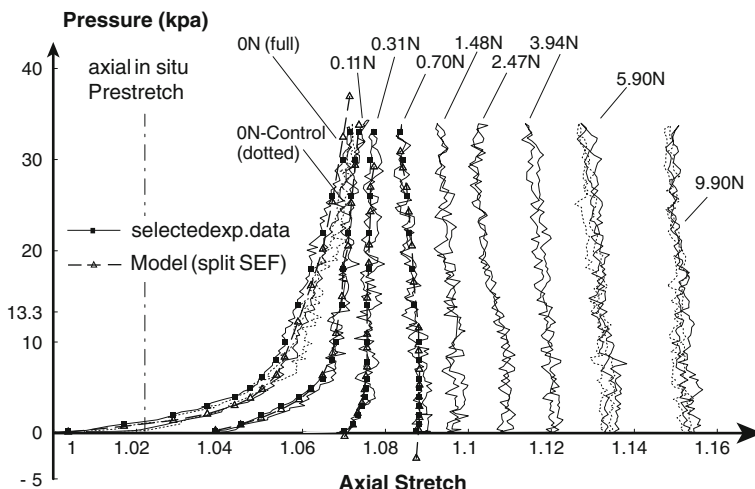


Figure 16.20 Pressure-axial stretch plot for a human iliac artery. At a fixed axial tension, the pressure is varied and the axial stretch measured [1133]. (picture courtesy of Gerhard Holzapfel.)

16.5 Application: The Buckling of Arteries

16.5.1 Background

As discussed in Section 2.1.3, the arterial system is a highly complicated and regulated mechanical system dedicated to carry blood from the heart to organs while sustaining varying pressures, loads, and stresses. Starting in the 1960s many different puzzling experimental observations revealed that large arteries have mechanical responses that cannot be readily understood by elementary mechanics:

- As early as 1881, Roy demonstrated that the elastic response of arteries is nonlinear [1101].
- During regular homeostatic functions, arteries are tethered to other tissues and they operate under a large stretch of about 1.3 to 1.6 [773]. They will therefore naturally retract to their preferred rest length when cut.
- Patel and Fry showed that during the cardiac cycle, and despite large variations of pressure, the end-to-end distance of major dog arteries remains mostly unchanged [248, 1019]. This property is also observed in human arteries. In Figure 16.20, we show the axial stretch of a human iliac artery obtained by fixing the axial tension and varying the pressure. It is observed that close to the homeostatic axial stretch, no axial stretch is observed while the pressure is varied.
- Even after cutting, in their rest length and in the absence of pressure, Bergel noted that arteries are still *axially* stressed [168] showing that the resting lengths of different layers are different [605] as shown in Figure 16.21B.

- Fung and, independently, Vaishnav and Vossoughi in the 1980s showed that arteries are also residually stressed *radially*. This observation is obtained by first slicing a ring out of an artery and by observing how this ring opens when a radial cut is made. The opening that results from the cut is measured by the so-called *opening angle*, a kinematic measure of residual strains [408] as discussed in Section 12.4.
- Arteries respond to sustained increase in axial loading by lengthening [264, 659] in order to attain a homeostatic state [448].

The stresses associated with the opening angle are known to play a fundamental role in regulating transmural stress gradient and lowering hoop stress at the inner walls [184, 635]. For instance, we showed, in Section 13.8.3.1, that radial differential growth can be tuned to reduce hoop stress gradient. Most models of arteries [601, 635, 1054] include the effect of radial residual stress but fail to properly account for differences in axial stresses.

Experimental observations [605, 607] show that arteries exhibit axial residual stress and that these stresses may be important in the regulation of homeostatic properties. For instance, Jackson et al. [658] showed that partial unloading of axial tension can induce arterial tortuosity. They studied the relationship between the development of tortuosity and mechanical forces imposed on arterial tissue. The axial strain in rabbit carotid arteries was reduced from $62 \pm 2\%$ and maintained at $33 \pm 2\%$ for twelve weeks. After this time period, all vessels became tortuous due to tissue growth and remodeling, as shown in Figure 16.22. They concluded that substantial axial strains are necessary to maintain arterial stability.

Arterial tortuosity is a well-known condition, shown in Figure 16.23, that can occur in response to abnormal growth stimuli or genetic defects [7, 146, 250, 260, 382, 420].

The stability of arteries under axial loads is essential to maintaining normal arterial function. Instability can lead to serious complications including stroke, vertigo, blackout, fainting, and persistent tinnitus [16, 1009, 1304], yet the biomechanical

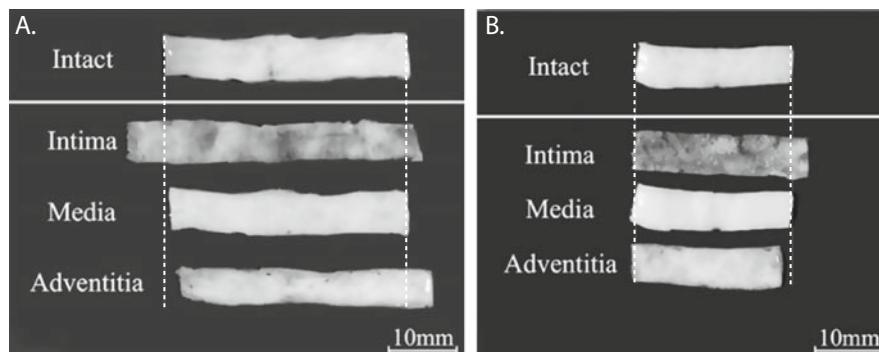


Figure 16.21 Differential resting length in arteries. The separation of the three tissue components of fresh human aortic patches demonstrate the existence of different resting length in the hoop (A) and axial (B) directions (picture courtesy of Gerhard Holzapfel [606]).

basis of why arterial buckling occurs is not well understood. Further experimental studies on the instability of arteries were conducted by Han [535] who set porcine carotid arteries at a fixed axial stretch and gradually pressurized the arteries until significant mechanical buckling occurred. The results supported by a linear stability analysis [536] showed that the critical pressure leading to buckling is directly related to the axial stretch ratio and is very close to a linear relationship in the tested range.

Here, following [485], we study the mechanics and stability of arteries including radial and axial residual stresses and we investigate the possibility of mechanical buckling in large deformations. We use the theoretical framework of large deformation morphoelasticity together with a bifurcation analysis to answer the following questions:

- What are the mechanical factors (anisotropy, residual stress, ...) responsible for the constancy of artery length in normal physiological regime?
- Could axial off-loading of an artery result in mechanical buckling?
- What is the role of residual stresses in arterial stability?

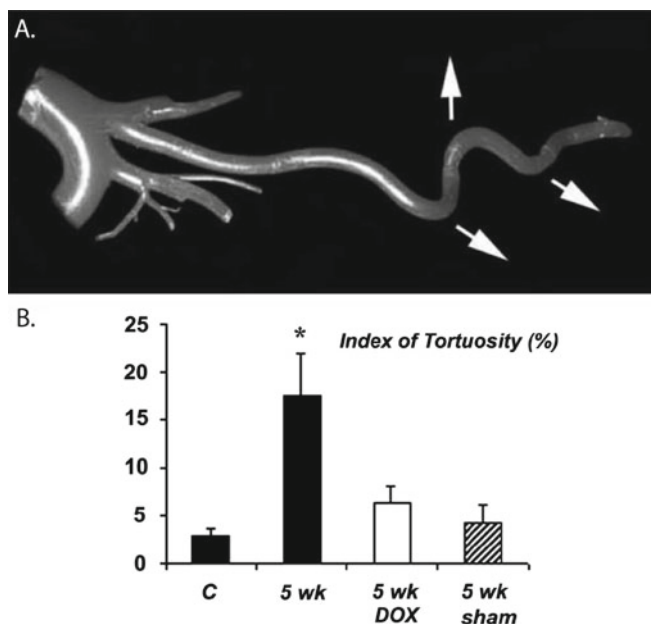


Figure 16.22 A. Buckling of the carotid artery of a rabbit following imposed axial shortening. B. Mean tortuosity index of unmanipulated left carotid arteries; of arteries five weeks after surgical off-loading of axial strain without and with doxycycline (DOX) treatment; and of arteries five weeks after sham manipulations [658].

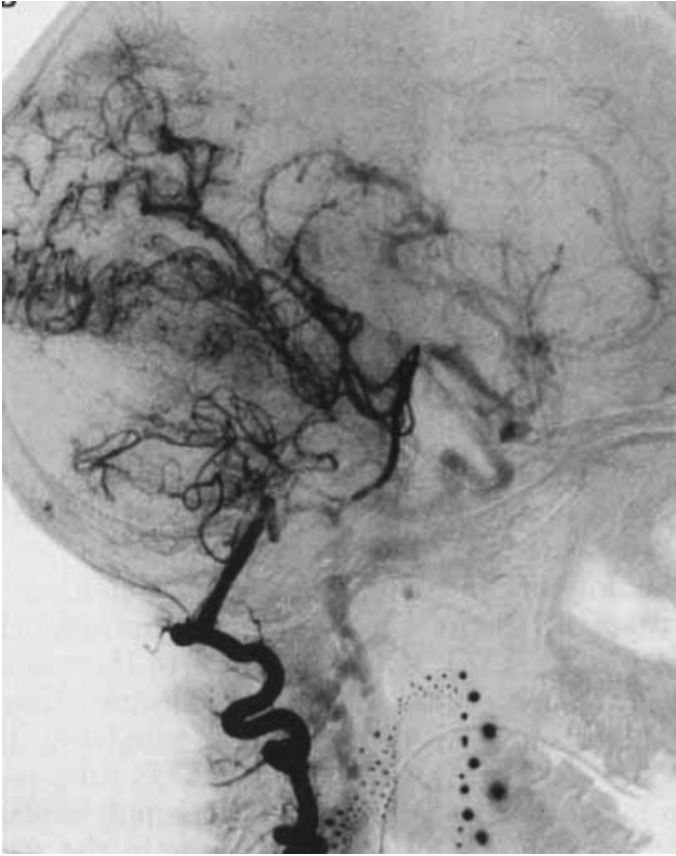


Figure 16.23 Angiogram of the right vertebral artery showing marked vessel tortuosity [7].

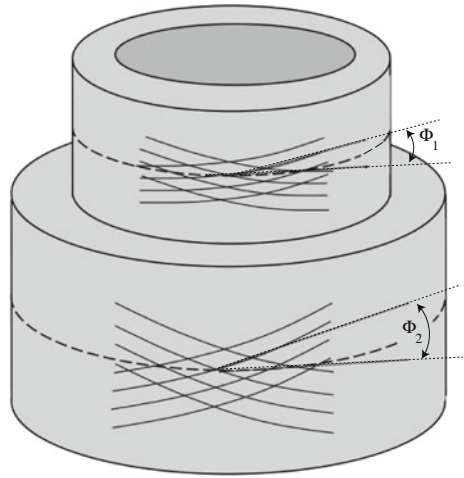
16.5.2 *The Model*

16.5.2.1 Elastic Response

The arterial wall consists of three layers, each containing specific histological features: the intima (the innermost layer), the media, and the adventitia (the outer layer). The intima is known to have negligible (solid) mechanical contributions [602] and therefore the arterial wall is approximated as a two-layer structure containing the media and adventitia.

Much is known about arteries and the simple toy model proposed in Section 11.8.3.1 is not sufficient to analyze the respective role of anisotropy and differential growth. Indeed, numerous constitutive models have been proposed for arteries (see review in [678]). Most models [208, 269, 1268] are formulated by fitting a given constitutive equations to experimental data. Here, we start with the multi-

Figure 16.24 A two-layer model representing the media and adventitia with a continuous family of fibers representing the effect of collagen fibers.



layer model for arteries introduced by Holzapfel, Gasser, and Ogden [601, 604] based on the theory of anisotropic materials with two fibers described in Section 11.11.2. This model has the advantage of being structural in the sense that it incorporates layer-specific histological features. Each layer is reinforced with collagen fibers with preferred directions that render the material anisotropic [66]. The model accounts for the orientations of the collagen fibers in each layer. The contribution of collagen fibers in the arterial wall is considered to be negligible at low pressures and therefore, the mechanical response is assumed to be isotropic. However, at higher pressures, the collagen fibers are stretched and the resulting mechanical response is anisotropic. For each layer Holzapfel et al. [601] suggest a strain-energy function of the form

$$W(I_1, I_4, I_6) = W_{\text{iso}}(I_1) + W_{\text{aniso}}(I_4, I_6), \quad (16.84)$$

where the invariants I_1, I_4, I_6 of the right Cauchy–Green tensor $\mathbf{C} = \mathbf{F}^T \mathbf{F}$ are given by

$$I_1 = \text{tr } \mathbf{C}, \quad I_4 = \mathbf{C} : \mathbf{M} \otimes \mathbf{M}, \quad I_6 = \mathbf{C} : \mathbf{M}' \otimes \mathbf{M}'. \quad (16.85)$$

As explained in Section 11.11.2, the invariants I_4 and I_6 are the squares of the stretches in the respective directions of the two families of collagen fibers. The unit vectors $\mathbf{M}$ and $\mathbf{M}'$ describe the orientations of these fibers and these vectors are defined for each layer in the reference configuration. In the usual cylindrical coordinate system, the components of the direction vectors are

$$\begin{bmatrix} M_r^{(j)} \\ M_\theta^{(j)} \\ M_z^{(j)} \end{bmatrix} = \begin{bmatrix} 0 \\ \cos \Phi_j \\ \sin \Phi_j \end{bmatrix}, \quad \begin{bmatrix} M_r'^{(j)} \\ M_\theta'^{(j)} \\ M_z'^{(j)} \end{bmatrix} = \begin{bmatrix} 0 \\ \cos \Phi_j \\ -\sin \Phi_j \end{bmatrix}, \quad j = 1, 2, \quad (16.86)$$

where the indices $j = 1$ and $j = 2$ refer to the inner layer (the media) and the outer layer (the adventitia), respectively. The fibers are assumed to lie in the tangent plane. The angle between the collagen fibers and the circumferential direction is denoted by Φ_j as shown in Figure 16.24. The isotropic and anisotropic strain-energy functions in (16.84) are then given by

$$W_{\text{iso}} = \frac{\mu}{2}(I_1 - 3), \quad (16.87)$$

$$W_{\text{aniso}}(I_4, I_6) = H(I_4 - 1)H(I_6 - 1) \frac{k}{2\nu} \sum_{n=4,6} \{e^{\nu(I_n - 1)^2} - 1\}, \quad (16.88)$$

where the material parameter k has the dimension of stress and ν is a dimensionless parameter. The Heaviside function, $H(\cdot)$, indicates that the anisotropic term contributes to the mechanical response only when the fibers are extended, in other words when either $I_4 > 1$ or $I_6 > 1$.

Typical material and geometric data used here are from a rabbit carotid artery [598] ($A_0 = 0.71$, $A_1 = 0.97$, $A_2 = 1.10$, $\mu_1 = 3.0000$ kPa, $k_1 = 2.3632$ kPa, $\nu_1 = 0.8393$, $\mu_2 = 0.3000$ kPa, $k_2 = 0.5620$ kPa, $\nu_2 = 0.7112$, $\Phi_1 = 29.0^\circ$, $\Phi_2 = 62.0^\circ$).

The cylinder is subjected to an internal pressure, P , and therefore the axial equilibrium and the boundary conditions at the inner and outer surfaces yield

$$2 \int_{a_0}^{a_2} 2r t_z dr = Pa^2, \quad (16.89)$$

$$t_r(a_0) = -P, \quad t_r(a_2) = 0, \quad (16.90)$$

where t_r and t_z are the Cauchy stresses in the radial and axial directions, respectively. Note that the cylindrical symmetry will be preserved in the finite deformation because the two families of fibers are mechanically equivalent and are arranged symmetrically.

16.5.2.2 Growth Response

We assume that the growth tensor is constant and diagonal in each layer so that

$$[\mathbf{G}] = \begin{cases} \text{diag}(\gamma_r, 1, \gamma_z), & A_0 \leq R_0 < A_1, \\ \text{diag}(\gamma_r, 1, 1), & A_1 \leq R_0 \leq A_2, \end{cases} \quad (16.91)$$

where we have assumed without loss of generality that $\gamma_z = 1$ in the inner layer. We also assume that the hoop residual stress in both layers results from the same radial growth γ_r . To estimate these constants from experimental data, we use the method of Taber and Humphrey [1213].

In our case, we use data on the opening angle from a radial cut on a thin ring of artery to determine the value of the constants appearing in the growth tensor. Within the framework of morphoelasticity, we assume that the current state of an unloaded artery is the result of a local growth step characterized by a growth tensor $\mathbf{G}$ followed by an elastic step characterized by an elastic tensor $\mathbf{A}$. In addition to the current configuration state $\mathcal{B}$, we also consider a configuration $\mathcal{B}_1$, which represents a single opened ring due to a radial cut as shown in Figure 16.25. The deformation $\mathbf{A}_a$ to configuration $\mathcal{B}_1$ will contain residual stress if the elements of $\mathcal{V}$ are geometrically locally incompatible. Finally, the deformation $\mathbf{A}_b$ bends the ring closed and the ring is subjected to an internal pressure P to produce the final configuration $\mathcal{B}$.

The cylindrical polar coordinates in $\mathcal{B}_1$ are given by (ρ, ϑ, ζ) . The elastic tensor $\mathbf{A}$ can be decomposed into the product of two tensors, $\mathbf{A} = \mathbf{A}_a \mathbf{A}_b$, where

$$[\mathbf{A}_a] = \text{diag}(\alpha_{a\rho}, \alpha_{a\vartheta}, \alpha_{a\zeta}), \quad (16.92)$$

and

$$[\mathbf{A}_b] = \text{diag}(\alpha_{b\rho}, \alpha_{b\vartheta}, \alpha_{b\zeta}). \quad (16.93)$$

The solution for the configuration $\mathcal{B}$ is given in Section 16.1 for $n = 2$ layers.

Once this solution is known, the geometry and corresponding stresses in the cut ring can be determined as follows. The total deformation in terms of the material coordinates in $\mathcal{B}_1$ is given by

$$r = r(\rho), \quad \theta = \pi\vartheta/\varphi_0, \quad z = \Lambda\zeta, \quad (16.94)$$

where Λ is the axial stretch and φ_0 is the angle related to the opening angle $\varphi = 2(\pi - \varphi_0)$ defined in Figure 16.26.

The kinematic relationships are given by

$$\alpha_{a\rho} = \lambda_r(\alpha_{b\rho}\gamma_r)^{-1}, \quad \alpha_{a\vartheta} = \lambda_\theta(\alpha_{b\vartheta}\gamma_\theta)^{-1}, \quad \alpha_{a\zeta} = \lambda_z(\alpha_{b\zeta}\gamma_z)^{-1}, \quad (16.95)$$

$$\alpha_{b\rho} = \partial r / \partial \rho, \quad \alpha_{b\vartheta} = \pi r / \varphi_0 \rho, \quad \alpha_{b\zeta} = \Lambda, \quad (16.96)$$

and the incompressibility conditions are given by

$$\alpha_{a\rho}\alpha_{a\vartheta}\alpha_{a\zeta} = \alpha_{b\rho}\alpha_{b\vartheta}\alpha_{b\zeta} = 1. \quad (16.97)$$

The equilibrium equation is

$$\frac{\partial t_\rho}{\partial \rho} + \frac{t_\rho - t_\vartheta}{\rho} = 0, \quad (16.98)$$

where the Cauchy stress components in $\mathcal{B}_1$ are given by

$$t_i = \alpha_{ai} \frac{\partial W}{\partial \alpha_{ai}} - \hat{p}, \quad i = \rho, \theta, z, \quad (16.99)$$

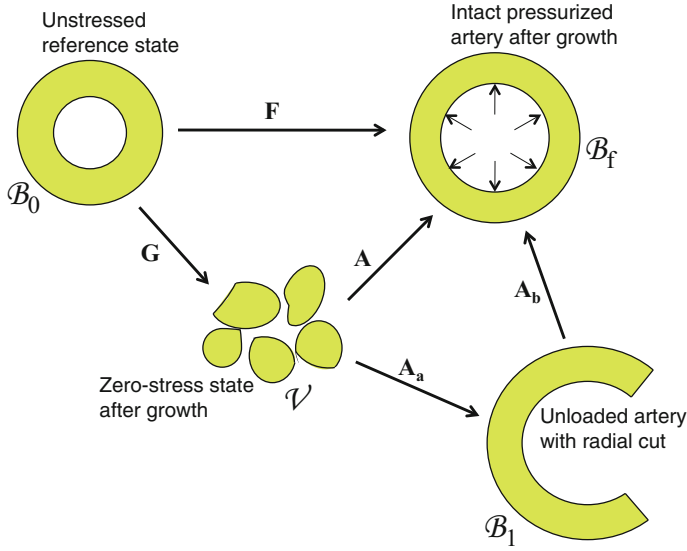


Figure 16.25 Decomposition into a single opened ring due to a radial cut. In addition to the standard multiplicative decomposition $\mathbf{F} = \mathbf{A}\mathbf{G}$, we consider an extra configuration where the cylinder is open. We can then relate the geometry of opening to the growth tensor.

where $\hat{p}$ is the Lagrange multiplier in $\mathcal{B}_1$, and the strain-energy function is $W = W(\alpha_{a\rho}, \alpha_{a\vartheta}, \alpha_\zeta)$. In the unloaded configuration $\mathcal{B}_1$, we assume zero net axial force and bending moment [1054] and zero normal traction on the inner and outer boundaries,

$$\int_{\rho(a_0)}^{\rho(a_2)} t_\zeta \rho \, d\rho = 0, \quad \int_{\rho(a_0)}^{\rho(a_2)} t_\vartheta \rho \, d\rho = 0, \quad (16.100)$$

$$t_\rho[\rho(a_0)] = t_\rho[\rho(a_2)] = 0, \quad (16.101)$$

where $\rho(a_0)$ and $\rho(a_2)$ are the inner and outer radii in $\mathcal{B}_1$.

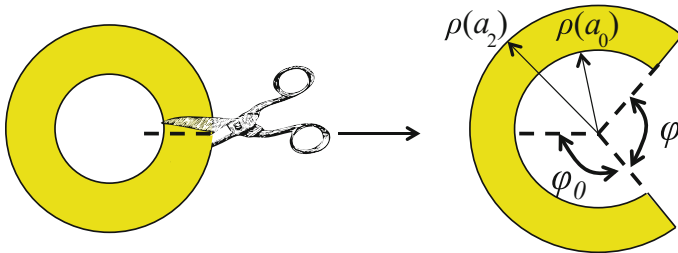


Figure 16.26 Schematic of a radial cut in an artery and the corresponding opening angle φ .

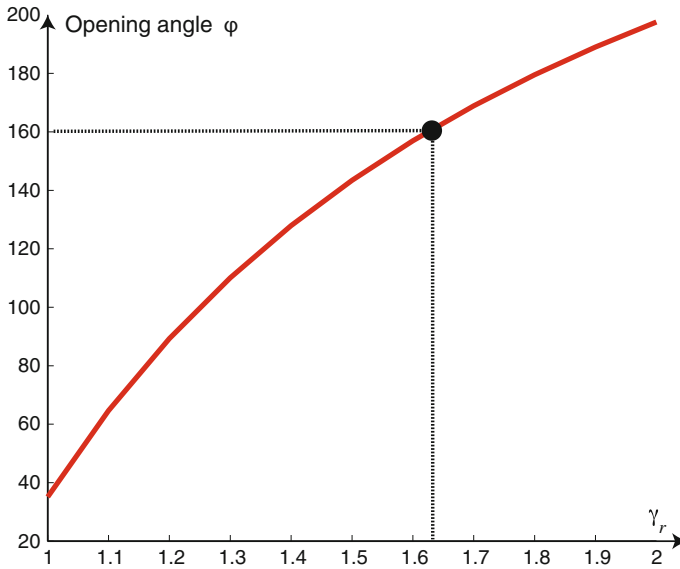


Figure 16.27 The opening angle of an artery as a function of the radial growth. The axial growth is assumed to be $\gamma_z = 1.2$.

Substituting the expressions from (16.95–16.96) into the incompressibility condition (16.97) yields

$$\frac{\pi \Lambda r}{\varphi_0 \rho} \frac{\partial r}{\partial \rho} = 1, \quad (16.102)$$

which can be integrated to obtain

$$\rho(r) = \left(\rho(a_0)^2 + \frac{\pi \Lambda}{\varphi_0} (r^2 - a_0^2) \right)^{1/2}. \quad (16.103)$$

Equations (16.100) can be written in terms of the material coordinate r using the relationship in (16.102),

$$\frac{\pi \Lambda}{\varphi_0} \int_{a_0}^{a_2} r t_\zeta(r) \, dr = 0, \quad \frac{\pi \Lambda}{\varphi_0} \int_{a_0}^{a_2} r t_\vartheta(r) \, dr = 0. \quad (16.104)$$

The equilibrium equation (16.98) is integrated to obtain an equation for the radial stress

$$t_\rho(r) = \frac{\pi \Lambda}{\varphi_0} \int_{a_0}^{a_2} \frac{r}{\rho(r)^2} (t_\vartheta(r) - t_\rho(r)) \, dr. \quad (16.105)$$

Substituting the boundary condition at the outer boundary ($t_\rho(a_2) = 0$) into the previous equation yields

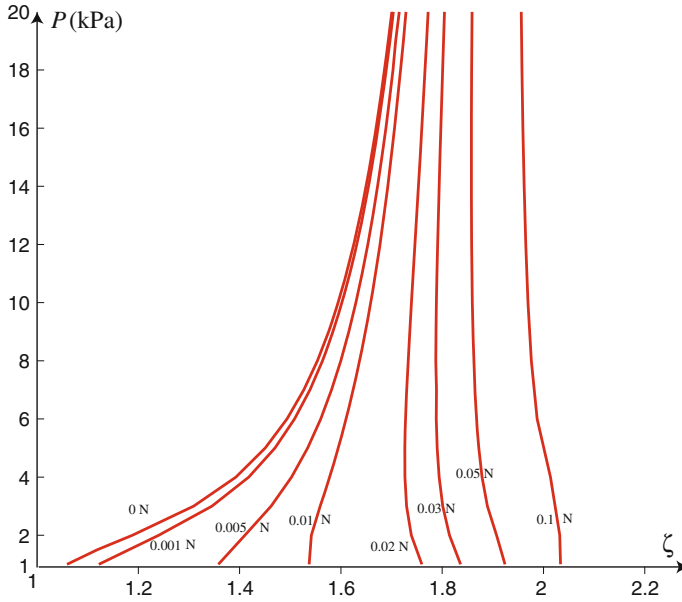


Figure 16.28 Pressure-axial stretch plot for a two-layer anisotropic cylinder without residual stress. Parameter values given in the main text.

$$\frac{\pi \Lambda}{\varphi_0} \int_{a_0}^{a_2} \left(\frac{r}{\rho(r)^2} (t_\psi(r) - t_\rho(r)) \right) dr = 0. \quad (16.106)$$

Equations (16.104) and (16.106) are solved to obtain the unknown parameters $\rho(a)$, Λ , and φ_0 and the solution for $\mathcal{B}_1$ is completely determined. For the set of parameter values given above for a rabbit carotid artery, the opening angle was found to be 160° . For an axial growth $\gamma_z = 1.2$, the opening angle is plotted with respect to varying values of the radial growth. The radial growth corresponding to an opening angle of 160° can then be determined as demonstrated in Figure 16.27.

16.5.3 Analysis

16.5.3.1 The Role of Nonlinearities

The solution to the cylindrical deformation problem is given by the method outlined in Section 16.1 for $n = 2$ layers with the parameters computed in the previous section. In order to study the mechanical factors responsible for the constancy of artery length in normal physiological regime, we reproduce the conditions leading to the pressure-axial stretch plot in Figure 16.20 with parameters from [598] and no

residual stress. An interesting trend is revealed in Figure 16.28. As the external load is increased, the length does not change as the pressure increases which agrees with the experimental findings where the end-to-end distance of major arteries remained mostly unchanged despite large variations of pressure [248, 1019]. This result is consistent with the inversion lines found in [1133] and can be obtained without residual stress. *Inversion lines* are regimes of axial stretch where the end-to-end distance remains constant as arterial pressure is varied. What is the origin of these inversion lines? Are they due to anisotropy, nonlinearity, or both?

In Figure 16.29, we compare an isotropic neo-Hookean model with an isotropic Fung model. The neo-Hookean model completely fails to account for the qualitative response of arteries as it does not exhibit inversion lines, but instead reveals a local maximum which is associated with the well-known limit-point instability discussed in Section 11.8.3.1. However, the isotropic Fung model is seen to capture the inversion lines of Figure 16.20. We conclude that the inversion lines are not due to the anisotropic property of the material or its residual stress. They are a direct consequence of the strong strain-stiffening behavior that can be modeled by a Fung strain-energy function (see also [979] for a discussion of these effects).

16.5.3.2 The Role of Radial Growth

Next, we study the effect of the radial residual stress by comparing the radial stress profile with and without residual stress. The computed stresses in the wall of both a pressurized artery with no residual stress and a pressurized artery with residual stress are shown in Figure 16.30. We observe that the transmural stress gradient is greatly reduced when residual stress is included in the model. We recover here the well-known effect of residual stress on the stress field across the arterial wall [208] discussed in Section 13.8.3.1.

16.5.3.3 The Role of Axial Growth

A bifurcation analysis can be used to determine the critical buckling pressure and to study the overall effect of axial stretch and residual stress on the critical pressure. The Holzapfel-Gasser-Ogden model is used with the parameter values found in the previous section. The grown cylinder with geometric parameters a_0, a_2, l_0 is subjected to an internal pressure and axial stretch, and the resulting cylinder has an inner radius a , outer radius c , and length l . The axial stretch ζ refers to the ratio l/l_0 .

The artery is first subjected to a constant axial stretch, and then the internal pressure is increased until the artery buckles. The critical internal buckling pressure for a given axial stretch is computed using a bifurcation analysis similar to the one developed in Section 16.3.2 with one major difference: The general relationships for the instantaneous elastic moduli given in Section 14.8 is only valid for the isotropic part of the strain-energy function. Here, the strain-energy function is of the form

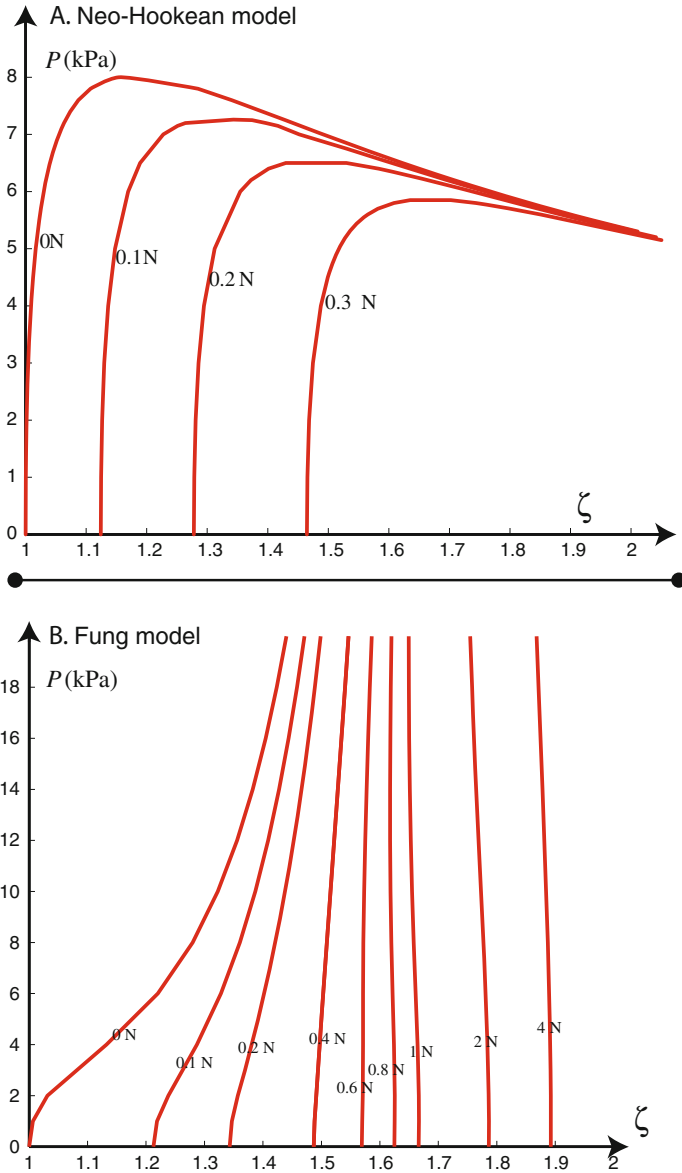


Figure 16.29 Pressure-axial stretch plot for a one-layer cylinder, $A_0 = 1.75$, $A_2 = 2.5$ without axial stress for *A*. A neo-Hookean material ($W = \frac{\mu}{2}(I_1 - 3)$ where $\mu = 30$). *B*. An isotropic Fung material ($\mu = 26.950$, $b_1 = 0.9925$, $b_2 = 0.418$, $b_3 = 0.0089$, $b_4 = 0.0749$, $b_5 = 0.0295$, $b_6 = 0.0193$) [602], where the Fung material is described by the strain-energy function $W = \frac{\mu}{2}(\exp(Q) - 1)$ where $Q = b_1 E_{\Theta\Theta}^2 + b_2 E_{ZZ}^2 + b_3 E_{RR}^2 + 2b_4 E_{\Theta\Theta} E_{ZZ} + 2b_5 E_{ZZ} E_{RR} + 2b_6 E_{RR} E_{\Theta\Theta}$.

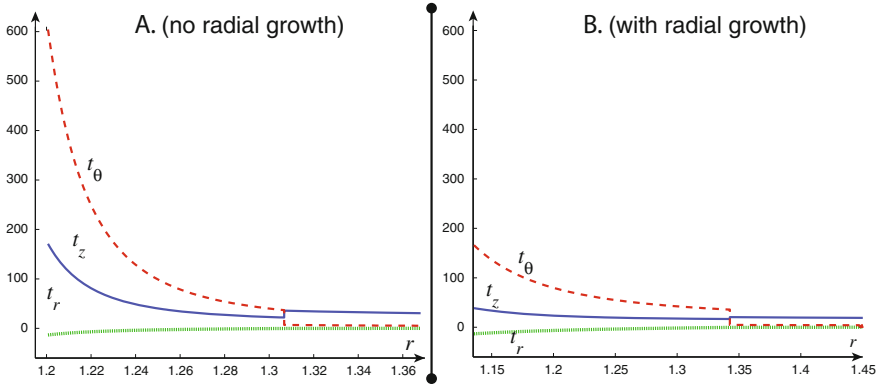


Figure 16.30 Stresses in the arterial wall A. without residual stress B. with residual stress. In both cases the artery is subjected to an internal pressure $P = 13.33$ kPa.

$$W(I_1, I_4, I_6) = W_{\text{iso}}(I_1) + W_{\text{aniso}}(I_4, I_6), \quad (16.107)$$

and the instantaneous elastic moduli are defined by

$$\mathcal{L} : \mathbf{F}^{(1)} = \mathbf{A}^{(0)} W_{\mathbf{AA}}^{(0)} : \mathbf{F}^{(1)} \mathbf{A}^{(0)}. \quad (16.108)$$

In components, the instantaneous elastic moduli are:

$$\mathcal{L}_{ijkl} = A_{im}^{(0)} \mathcal{A}_{mjkn} A_{nl}^{(0)}, \quad (16.109)$$

where $\mathcal{A}$ is the elastic moduli defined by

$$\mathcal{A} = \frac{\partial^2 W}{\partial \mathbf{A} \partial \mathbf{A}} (\mathbf{A}^{(0)}). \quad (16.110)$$

Since the strain-energy function is the sum of an isotropic and an anisotropic term, we decompose the elastic moduli in isotropic and anisotropic components

$$\mathcal{L}_{ijkl} = \mathcal{L}_{ijkl}^{\text{iso}} + \mathcal{L}_{ijkl}^{\text{aniso}}, \quad (16.111)$$

where the nonzero components of $\mathcal{L}^{\text{iso}}$ are given by the general relationships (14.122–14.127) with $W = W_{\text{iso}}$. The coefficients of $\mathcal{L}_{ijkl}^{\text{aniso}}$ must be given by other relationships [1044]. For our particular problem, due to the particular dependence of the anisotropic part on I_4 and I_6 only, we can directly compute the derivatives of W_{aniso} with respect to its invariants:

$$\begin{aligned} \mathcal{L}_{ijkl}^{\text{aniso}} = & 2 \left(\frac{\partial W_{\text{aniso}}}{\partial I_4} m_i m_k \delta_{jl} + \frac{\partial W_{\text{aniso}}}{\partial I_6} m'_i m'_k \delta_{jl} \right. \\ & \left. + 2 \frac{\partial^2 W_{\text{aniso}}}{\partial I_4^2} m_i m_j m_k m_l + 2 \frac{\partial^2 W_{\text{aniso}}}{\partial I_6^2} m'_i m'_j m'_k m'_l \right), \end{aligned} \quad (16.112)$$

where $m_i = \alpha_i M_i$, $m'_i = \alpha_i M'_i$ so explicitly $m_1 = m'_1 = 0$, $m_2 = m'_2 = \alpha_2 \cos \beta$, $m_3 = -m'_3 = \alpha_3 \sin \beta$. Note that there is no cross-derivatives with respect to I_4 and I_6 due to the fact that our particular strain-energy function does not contain terms that involve both invariants. We also have

$$\begin{aligned} \frac{\partial W_{\text{aniso}}}{\partial I_4} &= \frac{\partial W_{\text{aniso}}}{\partial I_6} \\ &= k_1 e^{\nu(-1 + \cos \beta^2 \alpha_2^2 + \sin \beta^2 \alpha_3^2)^2} (-1 + \cos \beta^2 \alpha_2^2 + \sin \beta^2 \alpha_3^2), \end{aligned} \quad (16.113)$$

and

$$\begin{aligned} \frac{\partial^2 W_{\text{aniso}}}{\partial I_4^2} &= \frac{\partial^2 W_{\text{aniso}}}{\partial I_6^2} \\ &= k_1 e^{\nu(-1 + \cos \beta^2 \alpha_2^2 + \sin \beta^2 \alpha_3^2)^2} [1 + 2\nu (-1 + \cos \beta^2 \alpha_2^2 + \sin \beta^2 \alpha_3^2)^2], \end{aligned} \quad (16.114)$$

due to the fact that $I_4 = I_6 = \alpha_2^2 \cos^2 \beta + \alpha_3^2 \sin^2 \beta$. Once the instantaneous elastic moduli are known, the procedure to identify bifurcations by solving the linearized boundary-value problem follows the same steps as before.

For our problem, in order to reproduce the condition of the experiments in Jackson et al. [658], we compute the critical pressure leading to buckling as a function of a prescribed axial stretch. The results are shown in Figure 16.31. The stability curve for a grown residually stressed cylinder is compared to a stress-free cylinder with the same geometric parameters. Axial *in situ* stretches of 1.5 have been reported for rabbit iliac arteries [410]. Note that in this regime the residually stressed cylinder can withstand a much greater internal pressure before it buckles. Furthermore, an artery under a typical physiological internal pressure $P = 13.33$ kPa is shown to withstand a greater reduced axial stretch if the artery is residually stressed.

Jackson et al. [658] performed a study that assessed the effect of reducing axial stretch in rabbit carotid arteries from $62 \pm 2\%$ to $33 \pm 2\%$ using interposition grafts. The arteries were held at an axial stretch of 30% for 12 weeks. The arteries displayed tissue growth and remodeling and all vessels became tortuous. Our analysis predicts that an artery subjected to an internal pressure of $P = 13.33$ kPa will buckle when the axial stretch is reduced to a value in the range between 1.25 and 1.33 for the given growth parameters. We conclude that the onset of axial tortuosity in arteries is consistent with a buckling instability triggered by variations of internal pressure.

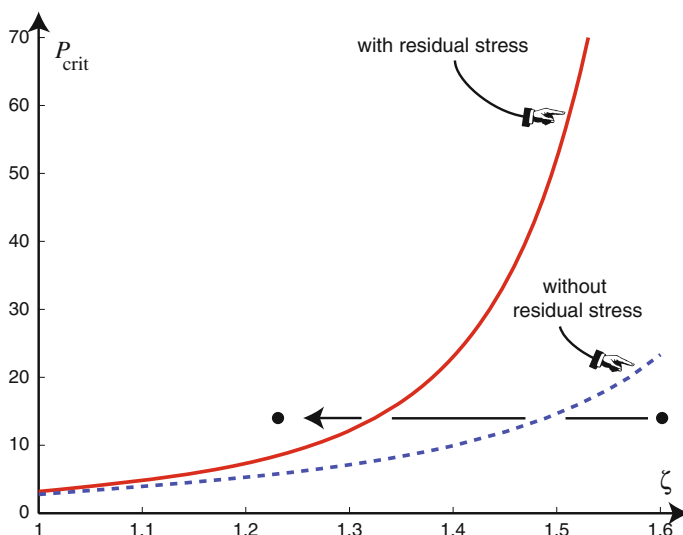


Figure 16.31 The critical internal pressure versus the axial stretch with and without axial residual stress (solid line: $\gamma_z = 1.2$, $\gamma_r = 1.6256$, dashed line: $\gamma_z = \gamma_r = 1$). The arrow represents the release of axial loading resulting in an axial stretch of about 1.25 for $P=13.3$ kPa. The artery becomes unstable.

16.5.4 Discussion

Our analysis of a two-layer morphoelastic model for the mechanical response of large arteries with differential axial and hoop growth reveals a number of interesting features.

First, material nonlinearities play an important role in capturing the correct behavior of arteries during a cardiac cycle. These nonlinearities are responsible for the inversion lines observed for arteries under axial tension.

Second, the hoop residual stress reduces hoop stress gradients, a well-known feature of differential growth in arteries that is recovered in the full model.

Third, the axial residual stress plays an important role in preventing buckling. This observation is consistent with our analysis of rigidification of plant stems which revealed the interplay between the nonlinear response of the material with the residual stress induced by differential growth. In the case where arteries become unstable under the internal pressure through a buckling instability, the mechanical analysis of arteries presented here is consistent with the onset of such an instability. However, this analysis cannot explain the remodeling of the structure after the instability that will eventually lead to permanent tortuosity. Such an analysis would require a post-buckling analysis for a model of arteries involving both growth and remodeling.

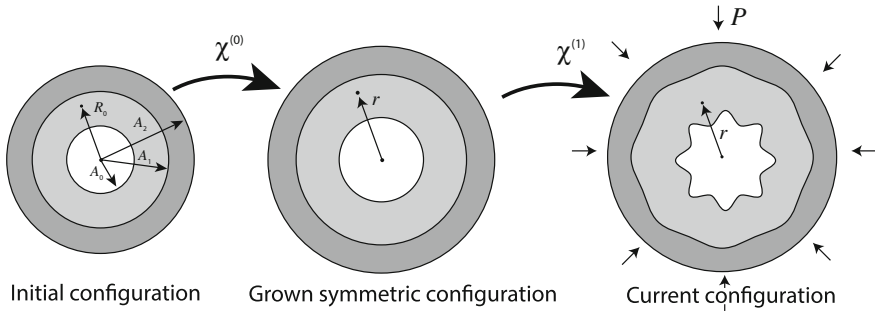


Figure 16.32 Radial instability in a two-layer cylinder can be induced through differential or incompatible growth.

16.6 Circumferential Buckling and Mucosal Folding

So far, we have considered axial instabilities, resulting in buckling or barreling. There is yet another interesting bifurcation that occurs in growing tubes. Consider a two-layer cylindrical shell and assume that each layer has constant radial and hoop growth but no axial growth as shown in Figure 16.32.

Depending on the geometry and stiffness of each layer, a number of interesting instabilities can arise with or without external pressure P . For instance, if the external cylinder is rigid and the inner tube grows isotropically, it will develop compressive stresses and the inner layer will buckle circumferentially. Similarly, if the inner layer is rigid and the outer layer grows isotropically, it will develop flower-like patterns as shown in Figure 16.33D. Depending on the relative stiffness of the two materials, their nonlinear responses, the geometry, and growth constants, various patterns can develop in the growth process.

We refer to these type of patterns as *circumferential buckling* or *mucosal folding* as they are observed in the oesophagus [790, 1349], blood vessels [778], and gastrointestinal tract [808]. Various examples are shown in Figure 16.33 and a detailed analysis of mucosal folding in airways is considered in the next section.

We can capture the onset of such patterns by looking for bifurcations around a grown configuration as shown in Figure 16.32. In the axial direction, one can either assume that no extension takes place by assuming no end displacement ($\zeta = 1$, in-plane strain) or, by assuming free-ends ($t_z = 0$, in-plane stress). Here, we will consider the simpler situation and restrict the deformation of cylinders to a two-dimensional cross-section by assuming no end displacement, so that $\zeta = 1$ is known from the onset. The general methods developed in this chapter are directly applicable to this setting. Before considering an application, we study the simple case of a single-layer cylinder growing under pressure.

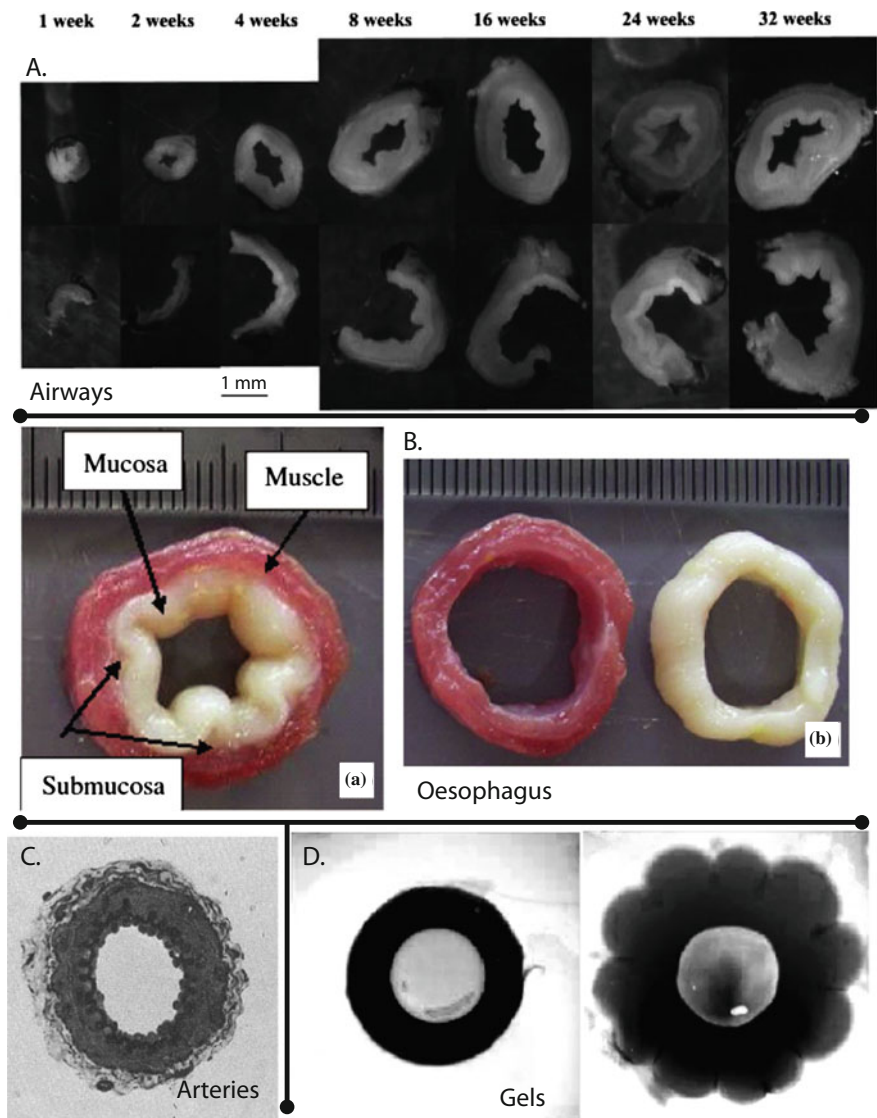


Figure 16.33 Examples of mucosal folding A. Airways from [512]. The top row shows tissue specimens in no-load state the bottom row shows the zero-stress state after a radial cut for rats aged 1–32 weeks. B. Oesophagus ring. (a) the mucosal folding in vitro and (b) the zero-stress state clearly showing that the folding pattern is due to the mismatch in length [1349]. C. Creasing in the inner wall of arteries [508]. D. Isotropic growth of a gel (black) attached to a hard core (adapted from [276]).

16.6.1 Example: Circumferential Buckling in a Cylinder

We consider a single-layer cylindrical shell under growth and external pressure and no end displacement. The cylinder has radii A_0, A_1 and a_0, a_1 in the initial and current configuration, respectively. Therefore, we have

$$[\mathbf{A}] = \text{diag}(\alpha^{-1}, \alpha, 1), \quad [\mathbf{G}] = \text{diag}(\gamma, 1, 1). \quad (16.115)$$

From our previous analyses, we known that the equilibrium solution is obtained by solving

$$-P = \int_{a_0}^{a_1} \frac{\alpha \hat{W}'(\alpha)}{r} dr, \quad (16.116)$$

where $\hat{W}(\alpha) = W(\alpha^{-1}, \alpha, 1)$. Here, P is the applied load on the cylindrical tube, such that $P > 0$ in the case of external pressure and $P < 0$ for internal pressure. For a given growth constant γ and fixed pressure P , (16.116) is an equation for the unknown parameter a_0 , since a_1 is related to a_0 through

$$a_1^2 = a_0^2 + \gamma(A_1^2 - A_0^2). \quad (16.117)$$

The stability analysis proceeds by considering incremental deformations restricted in the plane

$$\chi^{(1)} = u(r, \theta)\mathbf{e}_r + v(r, \theta)\mathbf{e}_\theta. \quad (16.118)$$

Then, in polar coordinates, we have

$$[\mathbf{F}^{(1)}] = [\mathbf{A}^{(1)}] = \begin{bmatrix} u_r & \frac{u_\theta - v}{r} \\ v_r & \frac{u + v_\theta}{r} \end{bmatrix}. \quad (16.119)$$

The incompressibility condition is

$$\text{tr}(\mathbf{A}^{(1)}) = u_r + \frac{u + v_\theta}{r} = 0. \quad (16.120)$$

Inserting (16.119) into the incremental equilibrium equation, $\text{div } \mathbf{T}^{(1)} = \mathbf{0}$, yields two differential equations involving the unknown functions u , v , and $p^{(1)}$. To simplify, these functions are assumed to be of the form

$$\begin{aligned} u(r, \theta) &= f(r) \sin(n\theta), \\ v(r, \theta) &= g(r) \cos(n\theta), \\ p^{(1)}(r, \theta) &= h(r) \sin(n\theta). \end{aligned} \quad (16.121)$$

The buckling mode n corresponds to the number of folds in the buckled state. Making these substitutions and using the incompressibility condition (16.120) to solve for $g(r)$ in terms of $f(r)$, the system can be simplified to a single fourth-order differential equation for $f(r)$:

$$B_4 f^{(4)}(r) + B_3 f'''(r) + B_2 f''(r) + B_1 f'(r) + B_0 f(r) = 0, \quad (16.122)$$

where

$$\begin{aligned} B_4 &= R_0^2, \quad B_3 = \frac{2(\gamma R_0^2 + 2r^2)}{r\gamma}, \\ B_2 &= -\frac{3R_0^4\gamma - 8R_0^2r^2 + n^2R_0^4\gamma + r^4n^2\gamma}{r^2R_0^2\gamma}, \\ B_1 &= \frac{-3r^4n^2\gamma R_0^2 + 2r^6n^2 + 3R_0^6\gamma - 4R_0^4r^2 + n^2R_0^6\gamma - 2R_0^4n^2r^2}{r^3\gamma R_0^4}, \\ B_0 &= \frac{-3R_0^4\gamma + 4R_0^2r^2 + 3n^2R_0^4\gamma - 4R_0^2n^2r^2 - r^4n^2\gamma + r^4n^4\gamma}{r^4R_0^2\gamma}. \end{aligned}$$

Note that $R_0 = R_0(r)$ is determined from the finite deformation via

$$r^2 = a_0^2 + \gamma(R_0^2 - A_0^2). \quad (16.123)$$

We solve this equation with the incremental boundary conditions by setting $\gamma \neq 1$, and choose the external pressure P as the bifurcation parameter. In Figure 16.34, the critical value of P is plotted as a function of the radial growth γ , for various modes n and for fixed tube thickness $A/B = 0.5$.

For a given γ , the smallest value of P_{cr} over all modes is the critical external pressure, denoted P_{cr}^* , at which the tube becomes unstable and buckles, and the corresponding mode n_{cr} is the critical buckling mode. For $P < P_{\text{cr}}^*$, the tube remains circular.

The value of P_{cr}^* for $\gamma = 1$ is the critical pressure without growth, which occurs for mode $n_{\text{cr}} = 2$. Growth can have both stabilizing and destabilizing effects. For this thickness, radial resorption ($\gamma < 1$) is destabilizing: P_{cr}^* is smaller for all values of $\gamma < 1$ than for $\gamma = 1$. Conversely, radial growth ($\gamma > 1$) has a stabilizing effect initially, but it is destabilizing for large γ . Observe that the strongest tube defined as the tube with the highest value of P_{cr}^* , is for $\gamma_r \approx 1.72$, the point marked b in Figure 16.34.

Along with the change in critical pressure, growth has a dramatic effect on the shape after bifurcation as well. Note that in Figure 16.34, the lower most deformation corresponds to buckling due solely to differential growth (since $P_{\text{cr}}^* = 0$). It should not be surprising that differential growth can cause instability without any external loading as it was demonstrated earlier that growth can induce sufficient residual stress to destabilize a structure even in the absence of external loads. Similarly, differential

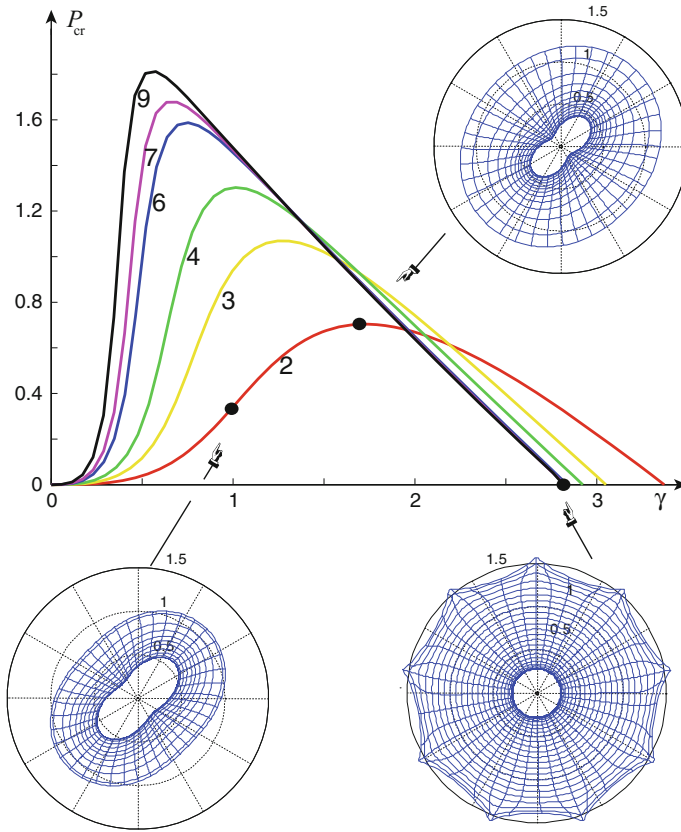


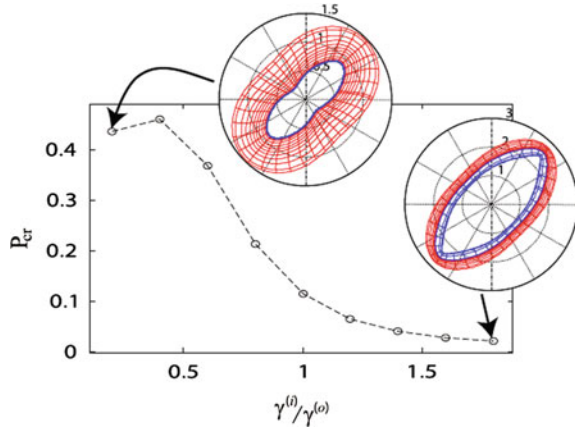
Figure 16.34 Critical buckling pressure as a function of radial growth γ for modes $n = 2, 3, 4, 6, 7, 9$, with the corresponding tube deformations. Note that the amplitude has been chosen to illustrate the structure - it has no physical significance since the shapes are produced in a linear stability analysis. Adapted from [912].

growth can have a stabilizing effect by changing the geometry of the body: A stubbier body is less likely to suffer buckling than a thin one. A greater range of possibilities opens up when considering a tube with two connected layers of material with different stiffness properties [912]. These ideas could be used in the design of biomaterials in which the fine tuning of critical pressure is desired.

16.6.2 Example: A Two-Layer Cylinder

Based on the previous analysis, it is now straightforward to look at the bifurcation of a two-layer cylinder, each layer with homogeneous properties. Here, we fix $A_0 = 1$,

Figure 16.35 Critical pressure as a function of the growth rate ratio between inner and outer layers for isotropic growth in each layer. The incremental boundary conditions are zero traction on both surfaces. The critical mode is $n_{cr} = 2$ at each point ($A_0 = 1$, $A_1 = 1.1$, $A_2 = 1.5$, $\mu_1 = 10$, $\mu_2 = 1$). Adapted from [912].



$A_2 = 1.5$ and the elastic moduli of the inner and outer neo-Hookean layers to be $\mu_1 = 10$, $\mu_2 = 1$. Under this fixed geometry, we investigate buckling for different isotropic growth in each layer. The critical pressure (smallest value over all modes) is plotted as a function of the ratio of growth rates γ_1/γ_2 in Figure 16.35. The critical pressure only depends on the ratio. Deformations with different values of the growth parameters with equal ratios are equivalent, up to an isotropic and equal growth of both layers, so that $\gamma_1/\gamma_2 = 1$ is equivalent to the case of no growth. Hence, higher growth in the inner layer is destabilizing, creating a compressive stress on the inner layer. Conversely, smaller growth in the inner layer creates a tensile, stabilizing effect on the inner layer.

The boundary conditions imply that both edges are unconstrained in the buckling deformation. If we forced the outer edges to remain circular during deformation by

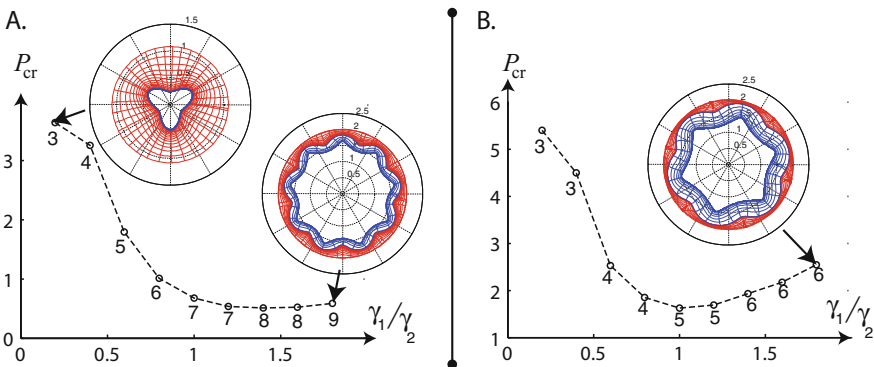
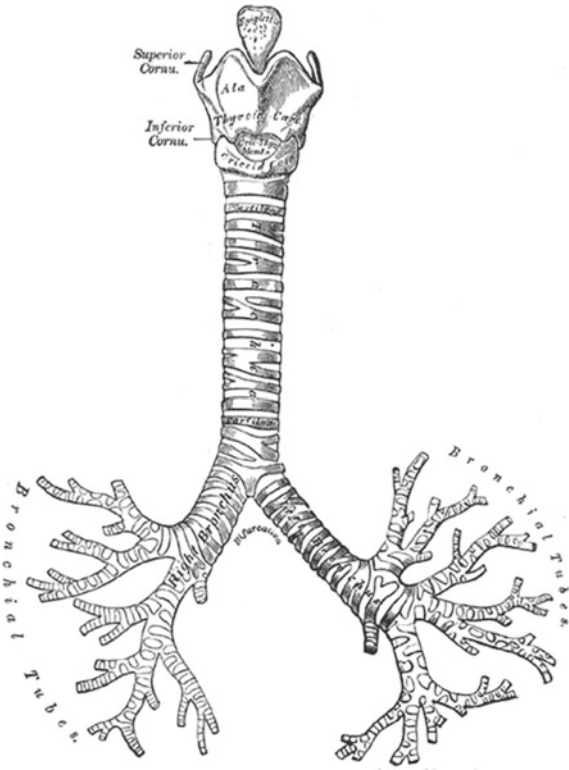


Figure 16.36 Critical pressure as a function of growth rate ratio between inner and outer layers for isotropic growth in each layer, for two different inner layers A. $B = 1.1$ and B. $B = 1.2$. The critical mode is labeled at each point, and select deformation patterns are included ($A_0 = 1$, $A_1 = 1.1$, $A_2 = 1.5$, $\mu_1 = 10$, $\mu_2 = 1$). Adapted from [912].

Figure 16.37 Cartilages structure of the lower airways. From Gray's *Anatomy of the Human Body* [498, plate 961].



requiring that the perturbation vanishes at the outer boundary, we obtain different buckling modes. Instead of exciting mode $n_{cr} = 2$, modes $n_{cr} = 3$ to $n_{cr} = 9$ are excited first as the growth ratio increases. We also notice that the buckling pressure is significantly higher, so that the tube is essentially stronger when the outer edge is kept circular. Furthermore, increasing the thickness of the inner layer results in an overall increase in the buckling pressure. It also has the effect of reducing the buckling mode. If the inner layer is thinner, there exists a growth ratio such that isotropic growth in each layer induces buckling without any external pressure (Figures 16.36 and 16.37).

16.7 Application: Asthma and Airway Remodeling

16.7.1 Background

Asthma is a complex disease characterized by a narrowing of the airway and reduced lung function. Chronic asthma is often accompanied by irreversible structural changes to the airway wall, collectively referred to as airway remodeling [1068].



Figure 16.38 Asthma is typically associated with an increase in wall thickness leading to a reduction of the air flow. Picture courtesy of Imtiaz Ibne Alam.

Airway remodeling is a complex process occurring at multiple time and length scales and involving many different chemical, biochemical, and physical stimuli. Despite a wealth of research, it is still not clear how each of the different structural changes individually affects airway function [1281], nor is it known whether these different changes are beneficial or detrimental to asthmatic patients [854]. A well-documented key feature of airway remodeling is an increase in airway wall thickness as shown in Figure 16.38, detected at all levels of the bronchial tree and all layers of the airway wall [631, 662, 745, 953].

In response to certain stimuli, the smooth muscle surrounding the airway wall contracts, and the luminal boundary folds or buckles. In normal physiological conditions, such an event is marked by only modest narrowing of the airway [903]. In asthmatic patients, however, this airway narrowing tends to occur for lower stimuli, and also leads to exaggerated narrowing [696] as seen in Figure 16.39. Viewed as a mechanical problem, this folding indicates an instability of the inner mucosal edge in response to an external pressure provided by the contraction of smooth-muscle cells.

Some of the key questions from a modeling perspective are

- What is the critical buckling pressure?
- What are the critical buckling modes (i.e., the number of folds in the buckled state)?
- What is the role of airway wall thickness on the instability?

Several authors have modeled mechanical and geometric aspects of mucosal folding. Lambert [753] modeled the basement membrane as a single-layer elastic tube and showed that the buckling mode can have a dramatic impact on airway narrowing; in particular an airway with fewer folds will have a greater degree of occlusion if the folds extend until epithelial cells come into contact.

This basic model was expanded upon in [754], in which a geometric constraint was included as a mechanism for selecting the number of folds, and was further expanded to include a thin layer of fluid on the inner edge of the airway allowing for possible surface tension effects [576]. Other geometry-based models have been proposed to take into account the inextensibility of the basement membrane: Seow et

al. [1136] showed that the number of folds was directly connected to tethers between the airway and smooth muscle; Donovan and Tawhai [293] studied effective airway radius given fixed folding geometry. A more sophisticated model for airways as a two-layer elastic tube was proposed by Wiggs et al. [1323]. By solving the buckling problem in a finite-elements analysis, these authors found that wall thickness has a significant effect on the buckling mode and degree of narrowing. Similar finite-elements models include the inertial effects of the basement membrane [56] and a comparison with buckling experiments on rubber tubes [626].

16.7.2 The Model

Here, following [913] we consider a model of asthma that includes both nonlinear material responses to large deformations, which are common in airway narrowing [961], and the relative change of geometry and residual stress due to growth [661]. We address whether growth significantly impacts the mechanical response of the airway to smooth-muscle contraction beyond the change in geometry, and thus be an important factor in airway remodeling.

We model the airway as a two-layer cylindrical morphoelastic structure. We only consider tissue interior to the smooth muscle. Following the model given by Wiggs et al. [1323], a stiff and thin inner layer corresponds to the mucosal region, consisting of the basement membrane, the lamina propria, and the epithelium [50]. Surrounding this region is a portion of the submucosa region, consisting of loose connective tissue. The inner layer is much thinner and stiffer than the outer layer as shown in Figure 16.40.

The airway smooth muscle surrounds the outer layer, with smooth muscle contraction providing a force that deforms and eventually induces buckling in the tube.

Figure 16.39 Cross section of a peripheral bronchus showing small folds at extremities of large folds [754]. Arrow points to submucosa. Smooth muscle (sm), lumen (L). Bar is 50 μm .

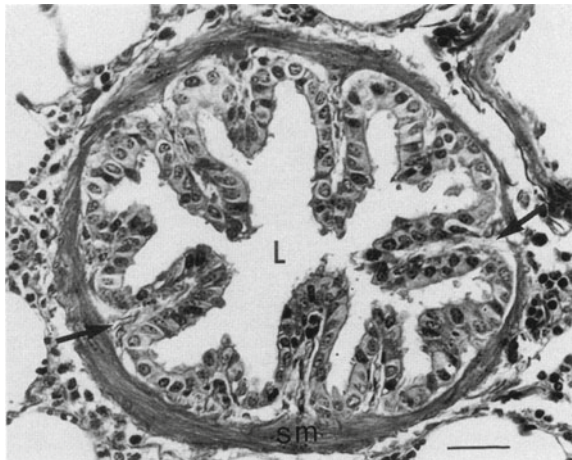
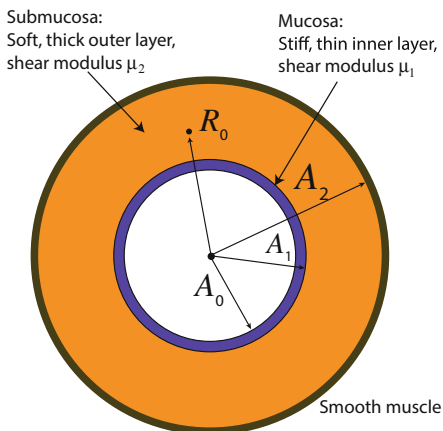


Figure 16.40 Bilayer model of airway wall, consisting of a stiff and thin inner layer, the mucosa, and a soft and thick outer layer, the submucosa. Surrounding the submucosa is smooth muscle, which applies a normal pressure when it contracts.



Smooth-muscle contraction is a fairly complex process, and several models have been formulated to couple the underlying chemical processes to mechanics [132, 1041, 1292]. The net mechanical effect of smooth muscle contraction is a normal force applied at the airway wall–smooth-muscle interface [1041].

Since our purpose here is to focus on growth and buckling, smooth-muscle contraction is taken into account as an applied normal pressure boundary condition at the outer edge. Also, since mucosal folding occurs at the mucosal region while the smooth muscle remains roughly circular [754], we impose the boundary condition that the outer edge remains circular in the deformed, buckled state.

Material dimensions for the airway in the initial configuration are the inner radius A_0 , the thickness of the inner layer, $A_1 - A_0$, and the thickness of the outer layer $A_2 - A_1$.

We assume that the tissue is an isotropic, incompressible hyperelastic material [119]. In the absence of detailed testing experiments on the different tissues, we model the two layers as either neo-Hookean with

$$W_i = \frac{\mu_i}{2}(I_1 - 3), \quad i = 1, 2, \quad (16.124)$$

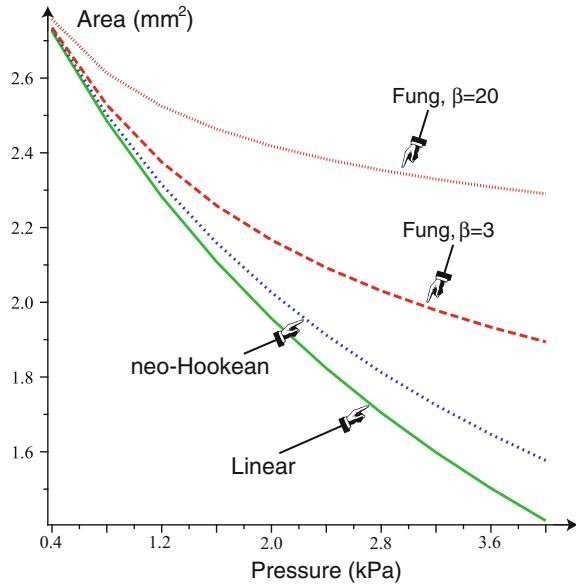
or a Fung model, to explore the possible role of strain-stiffening

$$W_i = \frac{\mu_i}{2\beta}[\exp \beta(I_1 - 3) - 1], \quad i = 1, 2, \quad (16.125)$$

where β is a measure of strain-stiffening with typical values between 3 and 20.

The model is three dimensional, but it assumes only plane-strain deformations, and the deformation is uniform along the tube axis and $\zeta = 1$ in all deformations. We can therefore focus our analysis on the two-dimensional problem and, as before, the elastic deformations are fully characterized by the hoop elastic stretch $\alpha = \alpha_\theta$, so that

Figure 16.41 A comparison of pressure vs area for the symmetric deformation of a two-layer tube for four different forms of model. Parameters are $A_0 = 0.98$, $A_1 = 1$, $A_2 = 1.5$, $\mu_1 = 40$, and $\mu_2 = 4$.



$$I_1 = \alpha^{-2} + \alpha^2 + 1. \quad (16.126)$$

The analysis of deformations and buckling proceeds as in the previous sections and details will be omitted.

16.7.2.1 The Role of Nonlinear Strain-Stiffening

In Figure 16.41, we plot pressure against area for the symmetric deformation of a two-layer tube for the neo-Hookean model, the Fung model with both $\beta = 3$ and $\beta = 20$, and also for a linear model. Each model gives qualitatively similar pressure area relationships as expected, but a significant quantitative difference exists between each curve. From this observation, we conclude that nonlinear effects may be important for quantitative predictions. However, most of the qualitative trends observed below remain unchanged when the neo-Hookean model is replaced by a Fung model. With the Fung model, effects are amplified, i.e., a more drastic change in buckling pressure and mode is observed. Therefore, the analysis will be restricted to neo-Hookean materials.

16.7.3 Analysis

The bilayer model for airways contains two growth parameters for each layer, two shear moduli, and three reference radii which makes for a very large parameter space. Our goal is to investigate the effect of growth on the buckling of a normal

versus a remodeled airway. Therefore, in our study we keep reference dimensions of the airway fixed and change the thickness of the airway by varying the growth parameters. Motivated by physiological measurements [626, 662, 1323], we use as reference for a normal airway, the base values $A_0 = 0.98$, $A_1 = 1$, $A_2 = 1.5$ (all measured in cm), and stiffness ratio $\mu_1/\mu_2 = 10$.

We assume that when the smooth muscle contracts, it creates a pressure normal to the circular cross section and the tube deforms in a symmetric fashion, maintaining its circular shape, until a bifurcation point is reached at a critical pressure, at which point the cylinder buckles to an asymmetric state. Physiologically, we are interested in the critical pressure at which folds form as it can be linked to the magnitude of the contractile force of the airway smooth muscle necessary to induce buckling of the airway. We assume here that the relationship between normal pressure and contractile force is monotonic. Thus, an increase in critical pressure corresponds to a greater contractile force for buckling. In terms of airway hyper-responsiveness, buckling pressure (or contractile force of airway smooth muscle for buckling) provides a measure of the “strength” of an airway.

16.7.3.1 The Role of Differential Growth

The first effect we consider is isotropic growth, but with different growth rates in each layer, that is, we assume $\gamma_r = \gamma_\theta = \gamma$ in each region, but $\gamma_1 \neq \gamma_2$. As an example, we fix $\gamma_2 = 1.2$ and vary $\gamma_1 > 1$. We show in Figure 16.42 the critical pressure and critical buckling mode as a function of γ_1 . In Figure 16.43 the same plots are shown with $\gamma_1 = 1.2$ fixed and γ_2 varying. The critical buckling pressure only depends on the ratio γ_1/γ_2 . Different values with the same ratio are equivalent up to an isotropic and equal growth multiple in each layer, with no change in the critical pressure (note that the airway dimensions will vary by the same scalar multiple).

Comparing the critical pressure to the reference case of no growth, it is interesting to note that when the ratio $\gamma_1/\gamma_2 > 1$, the airway is less stable, i.e., it buckles at a lower pressure. On the other hand, a greater pressure is required when this ratio is less than one. The airway is weaker with respect to buckling when the inner layer grows at faster rate than the outer layer, and likewise stronger when the outer layer grows faster. Observe that this effect is significant as the change in critical pressure increases by a factor of about 8 as γ_2 changes from 1 to 1.5.

We compare the size of the nonsymmetric deformation for different parameters. In this way we determine whether buckling at one set of parameters should result in more or less narrowing initially than buckling at another set of parameter values. At the lower value of γ_1 , the buckling pressure is much higher, but the airway narrows significantly more. At higher values, the airway narrowing is reduced, but the buckling pressure decreases. There is essentially a trade-off between the two growth rates. This trade-off does not occur in the case of fixed γ_1 as seen in Figure 16.43. The larger value of γ_2 has a higher resistance to buckling *and* comparable narrowing to the smaller value of γ_2 .

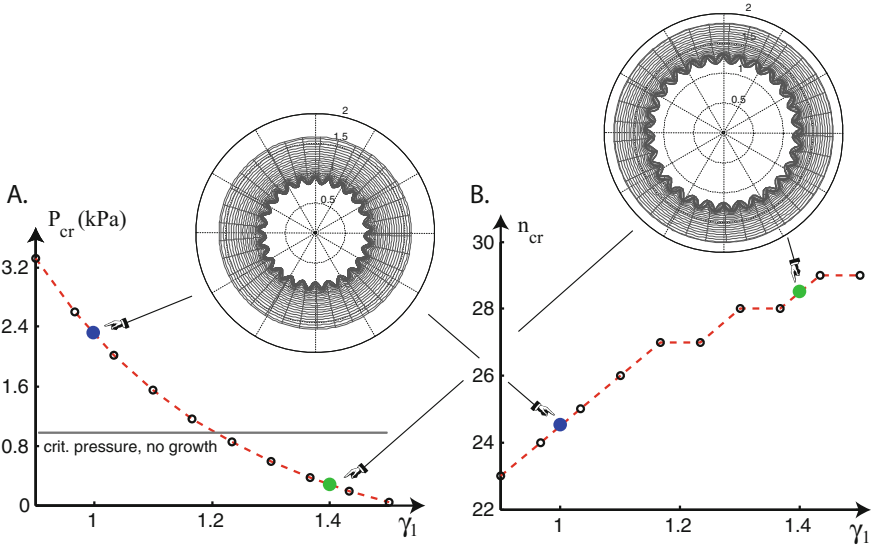


Figure 16.42 A. Critical buckling pressure and B. buckling mode as a function of isotropic growth of the inner layer, for fixed isotropic growth in the outer layer, $\gamma_2 = 1.2$.

It may seem counterintuitive that extra growth in the outer layer is required to strengthen the airway wall, since the inner layer is stiffer. In fact, a primary result of Wiggs et al. [1323] was that increasing the thickness in the inner layer has a greater impact on buckling than increasing the thickness of the outer layer. Indeed, differential growth creates residual stress, which induces a competition between mechanics

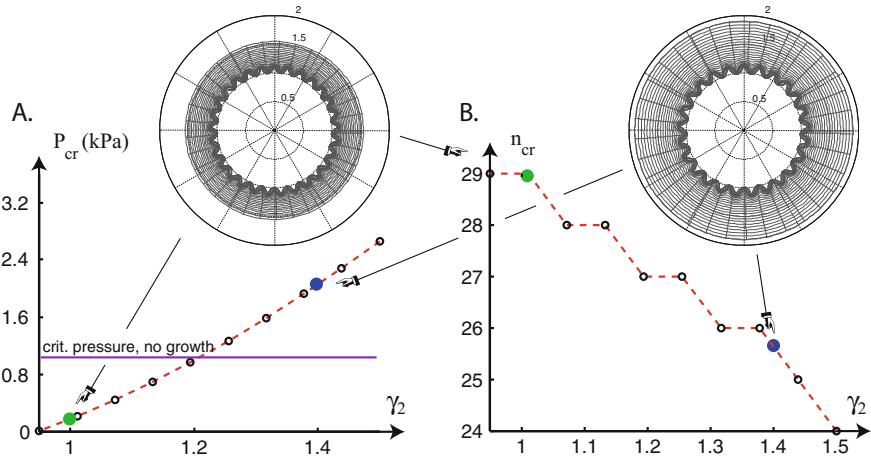


Figure 16.43 A. Critical buckling pressure and B. buckling mode as a function of isotropic growth of the outer layer, for fixed isotropic growth in the inner layer, $\gamma_1 = 1.2$.

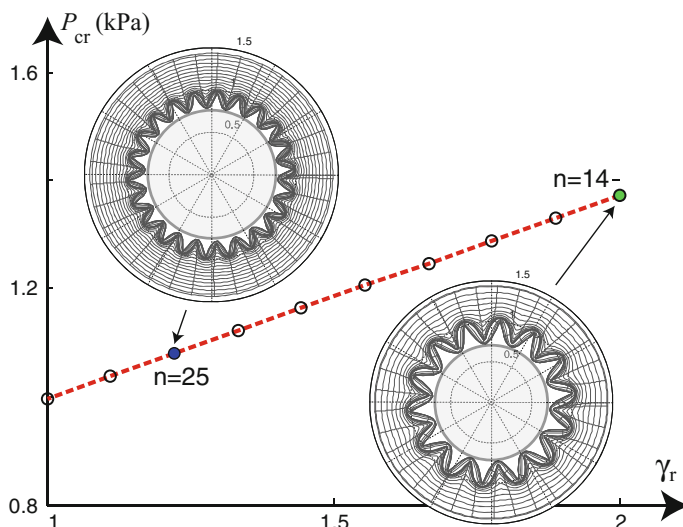


Figure 16.44 Critical pressure as a function of anisotropic growth of the inner layer. All other growth parameters are set to one.

and geometry. In particular, when the inner layer grows, it pushes against the outer layer, creating a compressive residual stress in each layer. This mechanical effect is destabilizing against external pressure. Conversely, when the outer layer grows faster, it pulls the inner layer, creating a stabilizing tensile stress. This counterintuitive result highlights the important mechanical role of differential growth.

16.7.3.2 Anisotropic Growth

Next, we consider the role of anisotropic growth. For simplicity, we assume that the outer layer does not grow and explore buckling as a function of anisotropic growth in the inner layer by varying the ratio γ_r/γ_θ . Thickening of the inner layer only occurs with radial growth.

In Figure 16.44, the critical pressure is plotted for $\gamma_\theta = 1$ fixed and γ_r varying from 1 to 2. As γ_r increases, the inner layer doubles in size from $\gamma = 1$ to 2. Correspondingly, the buckling pressure increases in a linear fashion. Again, there is a competition between mechanics and geometry: Radial growth causes the inner layer to be relatively thicker—a stabilizing geometric effect—but at the same time it creates a radial compressive stress, which is destabilizing mechanically. In this case, since the inner layer was very thin to begin with, the geometric effect is stronger, and the newly grown airway increases its stability.

In terms of the degree of narrowing, with increasing growth the buckling mode decreases monotonically and significantly, from $n = 27$ at $\gamma_r = 1$ to $n = 14$ at $\gamma_r = 2$. In Figure 16.44, the deformations at $\gamma_r = 1.2$ and $\gamma_r = 2$ show the effect of

the buckling mode. In both cases, the inner radius at the point of bifurcation is about 0.87. Both plots are produced using the same-sized perturbation in the incremental deformation, but the airway narrowing is exaggerated at the point where the lower mode, $\gamma_r = 2$.

16.7.4 Discussion

The morphoelastic model shows that differential growth can have a significant effect on airway buckling. Therefore, it may be an important contributing factor in understanding the mechanical behavior of airways which have undergone remodeling. Isotropic growth with differing rates in each layer leads to the somewhat surprising conclusion that if the stiff mucosa grows at a faster rate than the soft submucosa, the airway actually becomes less stable. Anisotropic growth of the inner layer leads to a strengthened airway, but it significantly decreases the buckling mode.

Differential growth provides a mechanism to explain otherwise contradictory structural changes, for instance an airway wall becoming thicker and at the same time less stable. However, airway remodeling involves more complex changes than just an increase of the mucosal and submucosal layers [200, 960]. The airway smooth-muscle layer also gains mass, and there is uncertainty as to whether the contractile potential changes [1015]. Thus, whether the airways are actually less stable after remodeling is not yet established.

The two-dimensional nature of the model and the plane-strain assumption are supported by the fact that folds in airways are observed as longitudinal ridges [1346]. The linear stability analysis has the drawback that it only provides information on the deformation up to the point of the buckling. Nevertheless, knowledge of the buckling pressure is a good measure of the “strength” of an airway, and previous studies have shown that a tube becomes much more compliant after buckling [1323], suggesting that narrowing occurs more rapidly after buckling. Thus, buckling pressure seems to be a valid measure for investigating the mechanical impact of growth on airway narrowing.

The study presented here is mostly qualitative as many physiological values are not available. Nevertheless, an estimate of the buckling pressure can be obtained. It relates the normal force induced at the interface due to smooth-muscle contraction. From a study on human airway walls [973], we estimate the shear modulus in the stiff mucosal layer, μ_1 , at around 120 kPa. Taking $P^* \approx 0.4$ as a typical value of buckling pressure leads to an estimate of 1.6 kPa as the amount of stress necessary to induce buckling, comparable to pressures that canine airways can generate of about 3 kPa [523].

16.8 Residual Stress Through Fiber Contraction

So far, we have studied the creation and effect of residual stress in cylindrical structures through inhomogeneous or anisotropic growth. Another possible mechanism for stress creation is the contraction or extension of fibers in an anisotropic material. Cylindrical geometry is particularly well suited to illustrate this process.

We recall that an anisotropic material with one family of fibers can be characterized by the theory of invariants as described in Section 11.11.1. A general anisotropic material with one fiber with reference direction $\mathbf{M}$ is fully characterized by a strain-energy function

$$W = W(I_1, I_2, I_3, I_4, I_5), \quad (16.127)$$

where I_k are the three isotropic and anisotropic pseudo-invariants

$$I_1 = \text{tr} \mathbf{B}, \quad I_2 = \frac{1}{2}[I_1^2 - \text{tr}(\mathbf{B}^2)], \quad I_3 = \det \mathbf{B} = J^2, \quad (16.128)$$

$$I_4 = \mathbf{M} \cdot (\mathbf{C}\mathbf{M}), \quad I_5 = \mathbf{M} \cdot (\mathbf{C}^2\mathbf{M}), \quad (16.129)$$

and $\mathbf{C} = \mathbf{F}^T \mathbf{F}$ and $\mathbf{B} = \mathbf{F}\mathbf{F}^T$.

Fiber contraction can be modeled by assuming that in the absence of an isotropic deformation, the strain-energy function does not vanish identically, that is, $W(3, 3, 1, 1, 1) \neq 0$.

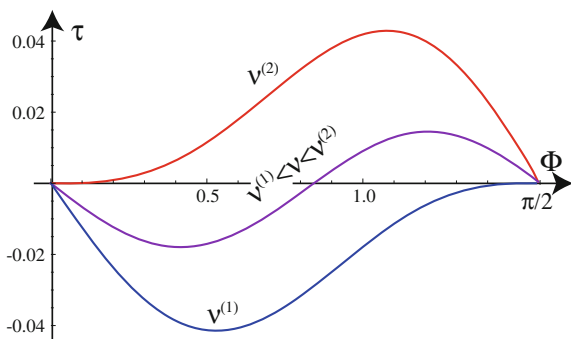
Rather than developing a general theory of fiber contraction, we illustrate the main idea by generalizing the standard fiber-reinforced model to include fiber contraction [272, 1025], that is, we consider materials described by the strain-energy function

$$W(I_1, I_4) = \frac{\mu_1}{2}(I_1 - 3) + \frac{\mu_4}{4}(I_4 - \nu^2)^2, \quad (16.130)$$

The parameters ν describes the effect of fiber compression in the matrix. Fibers can be inserted in the matrix while the matrix is under stress and, as we relax the matrix, the fibers may become compressed or stretched in the reference configuration. Thus the parameter ν is the stretch the fiber needs in order to attain its natural length in the reference configuration. For example, if an unstressed fiber is added to an elastic matrix in a state of tension, the fibers in the corresponding reference configuration will be compressed. Hence, the fiber needs to be stretched by a factor $\nu > 1$ to recover its natural length in that reference configuration. Note that for $\nu \neq 1$, $W(3, 1) \neq 0$ and the material is residually stressed; even in the absence of external loads, neither the matrix nor the fibers are stress-free.

Figure 16.45 The twist τ as a function of the fiber angle Φ for a capped cylinder under pressure with a single fiber in pre-compression.

The particular case $P = 0.2$, $\mu_4 = 10$ is used. In this case $\nu^{(1)} \approx 1.002082$ and $\nu^{(2)} \approx 1.05641$.



16.8.1 Rotation of a Pressurized Anisotropic Cylinder

As an example of the effect of fiber contraction, we consider the case of a capped pressurized thin tube with a single pre-compressed fiber helically wrapping around the tube so that, in the cylindrical basis $(\mathbf{E}_R, \mathbf{E}_\Theta, \mathbf{E}_Z)$, we have

$$\mathbf{M} = \cos \Phi \mathbf{E}_\Theta + \sin \Phi \mathbf{E}_Z. \quad (16.131)$$

Under pressure, the tube deforms to another tube so that the deformation reads, in the usual cylindrical coordinates $\{r, \theta, z\}$ and $\{R, \Theta, Z\}$,

$$r = \sqrt{a^2 + \frac{R^2 - A^2}{\zeta}}, \quad \theta = \Theta + \tau \zeta Z, \quad z = \zeta Z, \quad (16.132)$$

where, the axial stretch ζ , and the twist τ are constant, and as before, A and a are the inner radii of the tube in the reference and current configurations, respectively. In the thin tube limit, the axial stretch is simply $\lambda = a/A$.

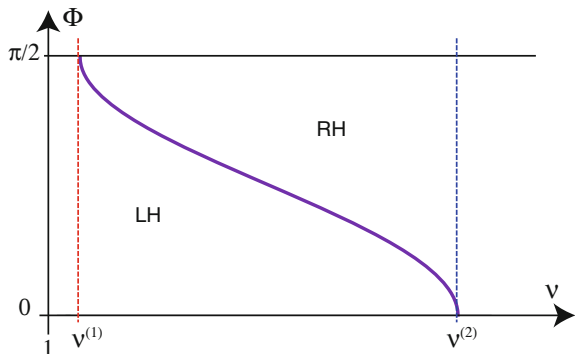
We take, without loss of generality, $\mu_1 = 1$ in (16.130) and we are left with three material parameters (Φ, ν, μ_4) and one load P . The problem is solved for the radial stretch λ , the axial stretch ζ and the twist τ by the method described in Section 11.11.4.

We now ask the following question: Does a capped tube with a right-handed single helical fiber $\Phi \in [0, \pi/2]$ under positive pressure P rotate clockwise ($\tau < 0$, left-handed) or counterclockwise ($\tau > 0$, right-handed)?

We start by considering the simple problem of twist for very small values of pre-compression as shown in Figure 16.45 (curve $\nu^{(1)}$). As expected, a tube with right-handed helical fiber under pressure creates a left-handed rotation. In the process, the tube unwinds. Note that the direction of rotation is opposite to the rotation of a spring in extension, discussed in Section 5.7.3.

Next, we consider the same system for increased values of the parameter ν . There, we observe that the rotation changes direction. Ultimately for larger values of ν , the rotation is completely inverted, i.e., entirely right-handed rotation for all values of the fiber angle (curve $\nu^{(2)}$).

Figure 16.46 Generic change of twist as a function of the angle and the pre-compression. For $\nu < \nu^{(1)}$, the rotation is left-handed (negative τ) and right-handed for $\nu > \nu^{(2)}$. For $\nu^{(2)} < \nu < \nu^{(1)}$, the rotation can be left-handed or right-handed depending on the fiber angle.



Based on these observations, we are interested in identifying the precise values of P , ν and Φ for which such an inversion of rotation occurs. To do so, we use the equations (11.345–11.347), obtained for the membrane limit of a pressurized cylinder, with $J_6 = 0$, J_4 replaced by $I_4 - \nu^2$, and an initial state with no load or rotation $M = F = \tau = 0$. These equations then read

$$\cos^2 \Phi = \frac{\zeta^2 + \lambda^2 - \nu^2}{\zeta^2 - \lambda^2}, \quad (16.133)$$

$$1 - 2\zeta^4\lambda^2 + \zeta^2\lambda^4 = 0, \quad (16.134)$$

$$\zeta^2\lambda^4 - 1 = P\zeta^3\lambda^4. \quad (16.135)$$

We can easily find the values of P , ν for which the inversion of rotation occurs at $\Phi = \pi/2$ and $\Phi = 0$, corresponding to the values $\nu^{(1)}$ and $\nu^{(2)}$ in Figure 16.45.

As shown in Figure 16.46, for $\nu < \nu^{(1)}$, the rotation is left-handed and right-handed for $\nu > \nu^{(2)}$. For a given P , the first critical value $\nu^{(1)}$ is the first real root larger than 1 of

$$\nu^{5/2} \left(\nu^3 + \sqrt{8 + \nu^6} \right) \left(P \left(\nu^3 + \sqrt{8 + \nu^6} \right)^{1/2} - 2\sqrt{\nu} \right) + 8 = 0. \quad (16.136)$$

Similarly, for a given P , the second critical value $\nu^{(2)}$ is the first real root larger than 1 of

$$\nu^2 P^2 + 4(\nu^6 - 1)(\nu P - 1) = 0. \quad (16.137)$$

Note that inversion only occurs for pressure values such that

$$P \leq \frac{\sqrt[6]{\frac{2}{13+3\sqrt{21}}} \left(2\sqrt{57+12\sqrt{21}} - 3 \left(1 + \sqrt{21} \right) \right)}{5^{5/6}} \approx 0.749868,$$

which corresponds to a maximal axial stretch of $\zeta \approx 1.17819$. Note also that none of these values depend on the fiber strength μ_4 .

The possibility of an inversion is a rather surprising result. Indeed it demonstrates that the chirality of the fibers does not necessarily determine the chirality of the cylindrical structure and its rotation, even for small values of pre-compression (less than 1%). In this range, the structure will exhibit macroscopic left-handed or right-handed rotation depending on the fiber angle, and small changes in the pre-compression and angle will change the rotation as observed in the rotation of *Phycomyces* described in the next section.

16.9 Application: The Spiral Growth of *Phycomyces*

16.9.1 Background

Phycomyces blakesleeanus is the most studied *Phycomyces*, a genus of fungi first reported by the Belgian biologist and cleric Jean-Baptiste Carnoy in 1870 [170]. After a complex reproductive cycle this fungus emerges as a strikingly large, single-celled, aerial hypha—known as the sporangiophore—reaching sizes of up to 10 cm long as shown in Figure 16.47. The organism, its rotating growth phases, and its remarkable tropic responses to various external stimuli has long been a source of fascination to biologists and biophysicists alike [90, 219, 375, 416, 670].

Helical growth is the rotation of a structure as it extends axially. It is observed in many different tubular structures across the plant kingdom [42]. However, it is not known whether this type of growth serves a biological function or provides some mechanical advantage, as hypothesized in the case of spiral grain of trees [66, 1132]. Nevertheless, elucidating the physical processes that lead to helical growth provides insights into the fundamental problem of relating cell wall structure to growth and form in plants. The physical explanation for helical growth is based on the intuitive notion that a cylinder with a helically structured (cell) wall, under axial stress due to turgor pressure, should unwind in the absence of an external axial moment. Hence, helical growth can be viewed as the macroscopic mechanical consequence of cell wall anisotropy. However, as we saw in the previous section, the direction of rotation of a fiber-reinforced pressurized cylinder is not only related to the orientation of the wall fibers, but also to its mechanical environment. We refer to right-handed growth (RH) when a point on top of the cylinder, viewed from above, turns counterclockwise during extension, and left-handed growth (LH) when the same point turns clockwise.

Similar to other systems exhibiting helical growth, the cell wall of the cylindrically structured sporangiophore of *Phycomyces blakesleeanus* is anisotropic, essentially composed of chitin microfibrils embedded in an elastic matrix of amorphous material made out of chitosan and chitin [886, 1095]. As illustrated in Figure 16.48, after an initial aerial growth phase (Stage I) and the development of the sporangium (Stages II and III), axial growth resumes in Stage IV. A remarkable behavior is then observed

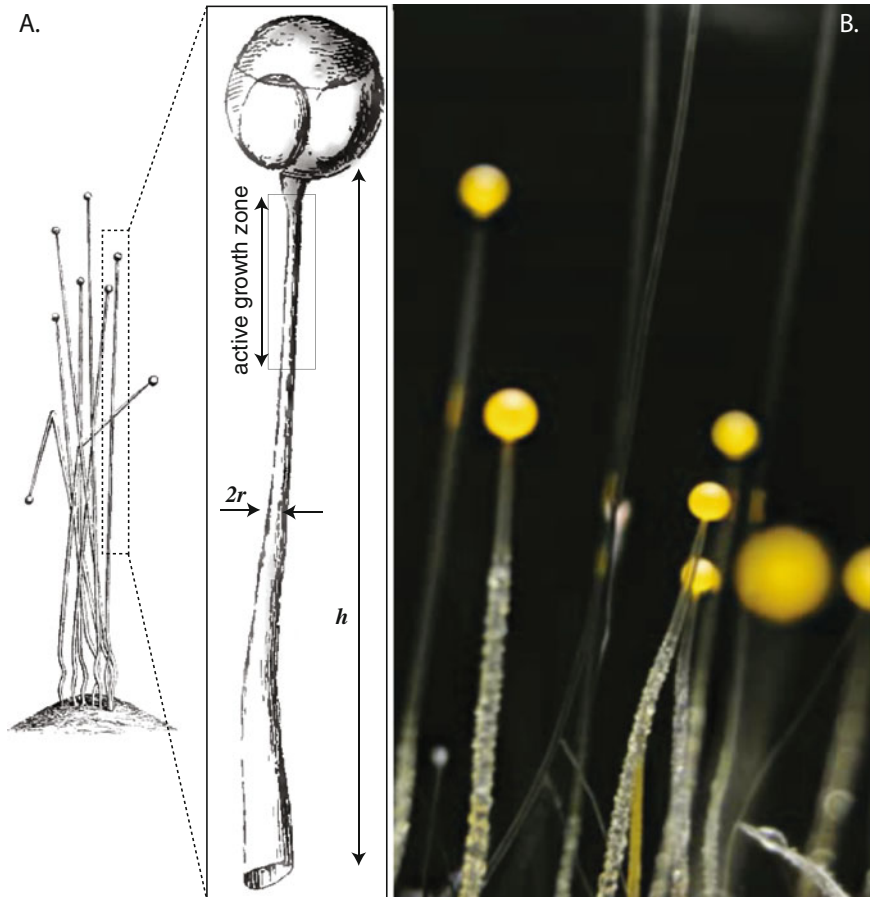


Figure 16.47 A. The fungus *Phycomyces blakesleeenanus* as drawn by Carnoy [170]. The spherical dome on top of the tube is the sporangium that contains the spores that are disseminated on completion of the life cycle. B. Optical microscopy of a colony of *Phycomyces* (courtesy of Michael Tabor and Robert Reinking).

[178]: in Stage IVa, RH growth takes place for approximately 1 hour; followed by Stage IVb in which LH growth is observed that can last up to 48 hours. A further rotational inversion (Stage IVc) has also been reported by some authors [993, 996, 1333].

The length and time scales in Stages IVa and IVb are as follows: A typical radius of the sporangiophore is $l = 50 \mu\text{m}$ and we will use this radius (assumed to be constant throughout these phases) as the length scale. The wall thickness is about $l/83$. The growth zone, which is the zone immediately below the sporangium where new cell wall material is added, extends to a size $h \approx 60l$. A typical sporangiophore length is $3 - 4 \times 10^3 l$.

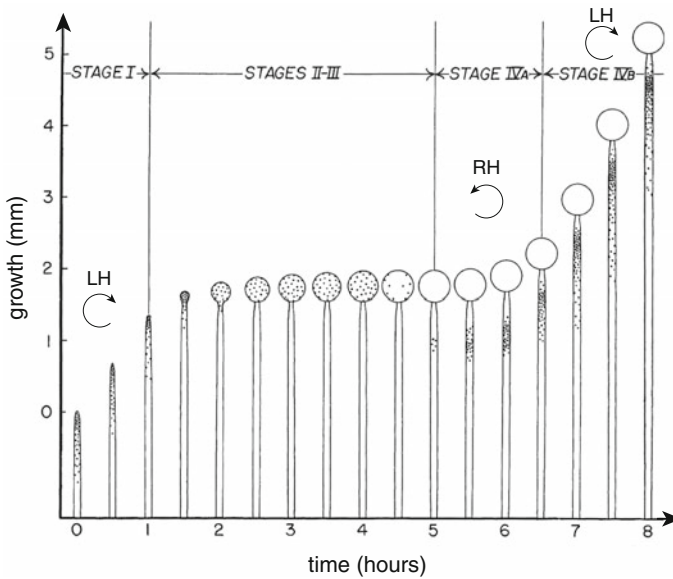


Figure 16.48 The four stages of growth for the aerial hypha. In Stage IV helical growth reversal is observed: Stage IVa exhibits right-handed growth and Stage IVb presents left-handed growth. Stage IVb continues for up to two days when the organisms can reach up to 10 cm in height. LH denotes left-handed (clockwise) rotation and RH denotes right-handed (counterclockwise) rotation (adapted from [178]).

In Stage IVb, the typical axial velocity is a constant $v_z = 60 \text{ l/hr}$ [1333]. This axial extension is accompanied by an angular rotation in Stage IVb of approximately $4\pi/\text{hr}$ for a duration of 24–48 hours. In contrast, Stage IVa lasts about 1 hour. A typical internal turgor pressure is about 0.4 MPa [234].

16.9.2 The Model

Here following [483], we present a mechanical model for the rotational reversals observed in Stages IVa, IVb, and IVc. We view the sporangiophore as a growing, fiber-reinforced, elastic structure, and include a dynamical remodeling and deposition of the fibers. Our basic assumption is that new fibers are deposited in a stress-free state along the direction of existing fibers.

We model the sporangiophore as an anisotropic, elastic, incompressible tube with two families of embedded fibers following the description of Section 11.11.4.

The first family of fibers is in the hoop direction and provides the cylinder with sufficiently strong radial reinforcement such that under pressure the radius can be considered to be constant and expansion is confined to a pure extension along the axis.

The second family of fibers winds helically (right-handed [1094]) around the axis and induces a rotation of the cylinder under extension. The presence of the hoop fibers together with the relative thinness of the wall compared to the radius are used to justify the membrane assumption, that is, we assume that there is no variation of strain or stress in the radial direction and that the tube radius is constant. Also, since the growth zone is much larger than the radius, we neglect gradient effects in the axial direction.

We consider finite deformations in which the cylinder is allowed to grow, rotate around its axis, and elongate axially while remaining cylindrical. Thus, using the notation of the previous section, in cylindrical coordinates with the z -axis corresponding to the vertical axis of growth, the deformation is

$$r = R, \quad \theta = \Theta + \tau \zeta Z, \quad z = \zeta Z, \quad (16.138)$$

where τ is the twist, and ζ is the axial stretch.

The material response is specified by the standard fiber-reinforcing model [272] with the simplest possible dependence for its isotropic and anisotropic parts

$$W(I_1, I_4) = \frac{\mu_1}{2}(I_1 - 3) + \frac{\mu_4}{4}(I_4 - \nu^2)^2, \quad (16.139)$$

where the Cauchy–Green deformation tensor invariants are given explicitly by

$$I_1 = \zeta^2 \tau^2 + \zeta^2 + 1/\zeta^2 + 1, \quad (16.140)$$

$$I_4 = \zeta \sin \Phi (\zeta (\tau^2 + 1) \sin \Phi + 2\tau \cos \Phi) + \cos^2 \Phi. \quad (16.141)$$

The angle Φ denotes the orientation of the fibers with respect to the horizontal plane in the reference configuration and ν is the pre-compression of the fibers in the initial configuration. The anisotropic contribution to the hoop stress is proportional to $(I_4 - \nu^2)$. Since $I_4 = 1$ in an unstressed configuration, the case $\nu > 1$ results in a negative, i.e., compressive stress. We recall from (11.323) that the fiber orientation, ϕ , in the current configuration is

$$\phi = \arctan \left(\frac{\zeta \sin \Phi}{\cos \Phi + \zeta \tau \sin \Phi} \right), \quad (16.142)$$

where we have assumed a thin-walled cylinder of constant (unit) radius.

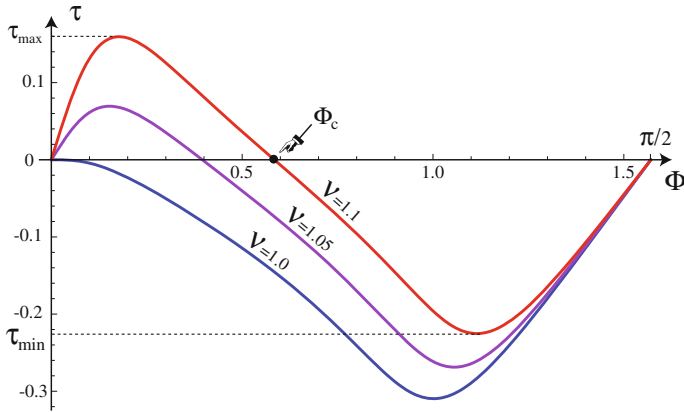


Figure 16.49 Effect of fiber pre-compression on the twist τ as a function of the fiber angle Φ ($\mu = 5$, $\zeta = 1.4$).

16.9.3 Analysis

We first consider a static model and assume that our tube is uniform with height H and a fixed fiber angle with a right-handed helical configuration $0 < \Phi < \pi/2$. We then subject it to an internal pressure leading to a given extension ζ that we use to parameterize the internal load. Note the difference with the example from the previous section where the pressure in a single fiber material was controlled rather than the extension. Here, the presence of hoop fibers guarantees that the axial stretch ζ is monotonic with the internal pressure.

16.9.3.1 Rotation of a Pressurized Sporangiphore

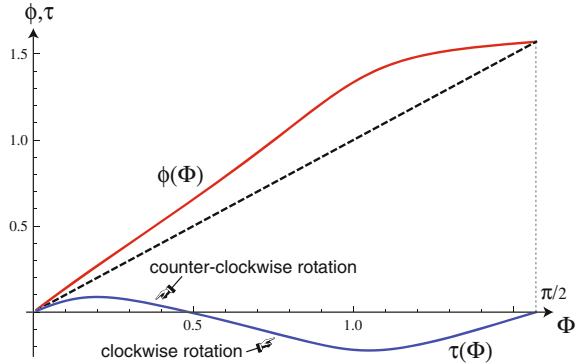
First, we consider the rotation of the tubular structure with uniform fiber direction and in the absence of remodeling and growth processes. From the strain-energy function, we compute the Cauchy stress tensor $\mathbf{T}$. Since no axial moment is applied on the surface of the tube, the boundary condition is simply $T_{\theta z} = 0$ where

$$T_{\theta z} = \mu_1 \zeta^2 \tau + \zeta \mu_4 \sin \Phi (\zeta \tau \sin \Phi + \cos \Phi) \times \\ (\zeta \sin \Phi (\zeta (\tau^2 + 1) \sin \Phi + 2\tau \cos \Phi) + \cos^2 \Phi - \nu^2), \quad (16.143)$$

which leads to a cubic equation for τ for given values of Φ , ν , ζ and ratio $\mu = \mu_4/\mu_1$. The first positive root is the twist needed to relax the torsional stress in the tube induced by the anisotropy. Some of these solutions are shown in Figure 16.49.

In the absence of pre-compressed fibers ($\nu = 1$) we see that the twist τ is always negative, i.e., the top of tube will rotate clockwise by an angle $\Theta = \tau h = \tau \zeta H$

Figure 16.50 Fiber orientation, ϕ , in the current configuration as a function of Φ , and the corresponding plot of $\tau(\Phi)$. The dashed diagonal line corresponds to $\phi = \Phi$.



leading to left-handed growth. The effect of pre-compression in the fibers is quite remarkable and nonintuitive. Even for small levels of pre-compression (e.g., $\nu = 1.05$), at small fiber angles, the cylinder will rotate counterclockwise as shown in Figure 16.49. The critical fiber angle Φ_c at which there is no rotation is given by

$$\Phi_c = \arccos \left(\sqrt{\frac{\zeta^2 - \nu^2}{\zeta^2 - 1}} \right), \quad (16.144)$$

and clearly requires $\zeta > \nu$. The inversion occurs when fibers go from compression to tension, since the critical angle corresponds to the point $I_4 = \nu^2$. In the absence of pre-compression, the cylinder rotates clockwise. We also note that despite the torsional inversion, the fiber orientation in the current configuration is always greater than the orientation in the reference configuration (see Figure 16.50).

From the expression for $T_{\theta z}$ it is possible to obtain a lower bound, $\tau_{\min}$, and an upper bound, $\tau_{\max}$, for the twist in the limit of stiff fibers $\mu \gg 1$, namely

$$\tau_{\min} = -\frac{\sqrt{\zeta^2 - \nu^2}}{\nu\zeta}, \quad \tau_{\max} = \frac{\nu}{\zeta}(\nu - 1)\sqrt{\mu}. \quad (16.145)$$

16.9.3.2 Growth and Remodeling of a Pressurized Sporangiophore

We have shown that a fiber-reinforced elastic tube with right-handed helical fibers can rotate clockwise or counterclockwise depending on the initial angle, axial extension, and initial stress in the fiber. We use this key result to develop a model of growing *Phycomyces* in which new fibers are continuously laid down in an evolving growth zone at the top of the sporangiophore.

Our key assumptions are:

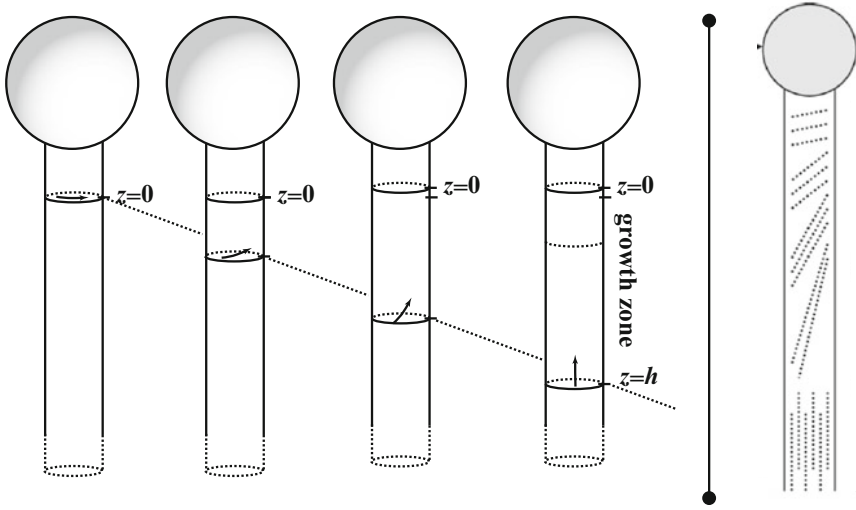


Figure 16.51 At the beginning of Stage IV, we assume that the growing zone extends linearly to a constant size h (drawing on the right adapted from [996]).

- New fibers are laid down stress-free along the direction of fibers in the current configuration;
- The growth zone extends linearly in time to a size h within the first two hours as shown in Figure 16.51.

A crucial concept is that the current configuration at a given time step becomes the reference configuration for the next time step. The overall growth process can now be explained as follows.

Consider a material point in the cell wall. Initially fibers are laid down at some small angle Φ_0 with $\nu_0 = 1$ at the top of the growth zone. The extension (due to the turgor pressure) and the rotation (due to the relaxation of the torsional stress) of the cylinder result in the fibers re-orienting to an angle $\phi_1 > \Phi_0$. As growth proceeds, the material point moves downward with respect to the top of the growth zone and new fibers at the same material point are laid down with angle $\Phi_1 = \phi_1$ and zero stress. This material point now has a mixture of fibers with angles Φ_0 and Φ_1 . The effective stress in the fibers in this new reference configuration (at this material point) is thus a combination of fibers with pre-compressions ν_0 and ν_1 .

A continuous model of this process is given by

$$\frac{\partial \Phi}{\partial t} = \kappa_1(\phi - \Phi), \quad (16.146)$$

$$\frac{\partial \nu}{\partial t} = \kappa_2(\zeta - \nu) \sin \Phi, \quad (16.147)$$

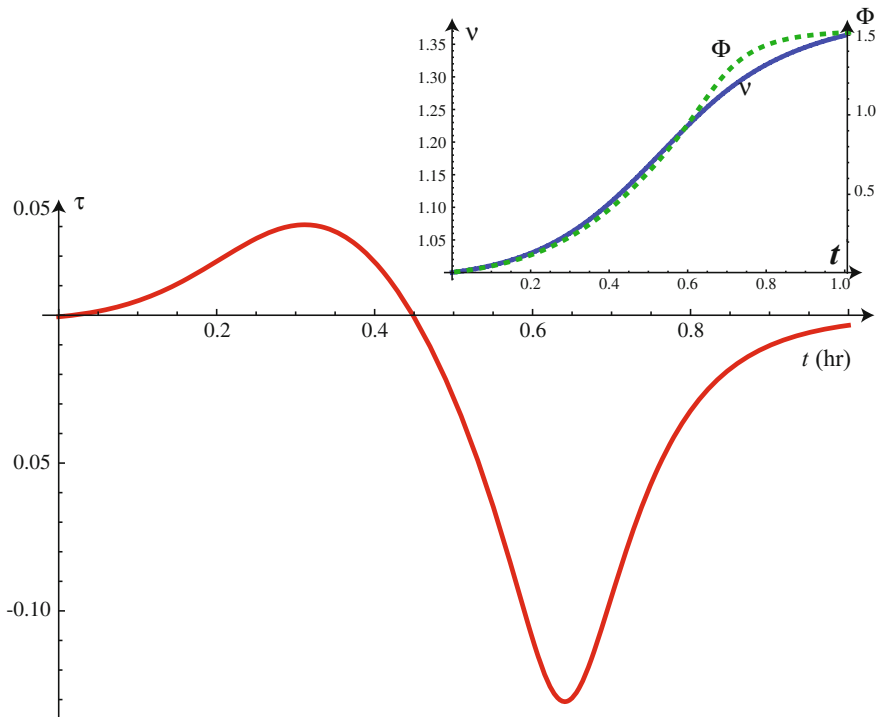


Figure 16.52 Dynamics of τ , ν , and Φ for a given material point as a function of time ($\kappa_1 = 16 \text{ hr}^{-1}$, $\kappa_2 = 4 \text{ hr}^{-1}$). While this process takes place, the material point at $t = 0$ starts on top of the growth zone and is convected downward with respect to a reference frame moving with the top of the growth zone.

where Φ , ϕ , ν , ζ are all evaluated at Z , the distance from the top of the sporangiophore of a material point in the reference configuration.

Following the property of the angle $\phi = \phi(\Phi)$ given above, we have

$$\lim_{t \rightarrow \infty} \Phi(Z, t) = \pi/2, \quad \text{and} \quad \lim_{t \rightarrow \infty} \nu(t) = \zeta \quad \forall Z. \quad (16.148)$$

The time constant $1/\kappa_1$ is fitted so that when a material point leaves the growth zone the associated fiber is oriented along the axis, i.e., $\Phi(1) \approx \pi/2$ and similarly $1/\kappa_2$ is fitted to match the time for rotational inversion. As an example of the dynamics generated by this system (coupled to the equations for ϕ and τ), we show in Figure 16.52 the evolution of τ , Φ , and ν as a function of time.

Each time the tube extends and twists as an elastic response to the extensional and torsional stresses, there is an evolution of the reference configuration due to the deposition of new fibers and other wall building materials. The net result is a continuous remodeling of the cell wall leading to an irreversible growth of the tube. The rotation of a small disk of height ΔZ at point Z measured from the top of the growth

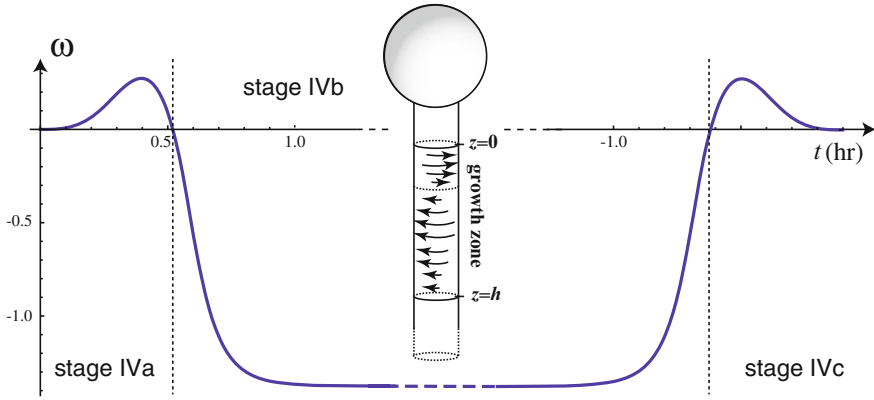


Figure 16.53 Rotational velocity (in units of radians per unit time, t_r) of the sporangiophore as a function of time. The time -1 on the right-side of the time axis refers to one hour before the end of growth, i.e., the time in this simulation at which the growth zone starts to retract.

zone with fiber angle Φ and pre-compression ν (in the reference configuration) is $\Delta\theta = \tau(\Phi(Z), \nu(Z))\Delta z = \tau\zeta\Delta Z$. Thus the total rotational velocity, ω , can be estimated as

$$\omega = t_r^{-1} \int_0^H \tau(\Phi(Z), \nu(Z))\zeta dZ, \quad (16.149)$$

where t_r is a characteristic time scale corresponding to the remodeling time of the reference configuration.

We can now use our model for the evolution of the fiber angle and the fiber pre-compression to compute the rotational dynamics of the growing cylinder. We assume that the growth zone extends linearly in time with a constant velocity v_z up to a length $h = H\zeta$ (corresponding to the end of Stage IVa). Subsequently, the length of the growth zone remains stationary (Stage IVb) and the tube extends, while rotating at a constant rate, until the growth zone retracts resulting in another inversion (Stage IVc) as shown in Figure 16.53.

Initially before the growth zone is fully established, only the fibers in the top part of the zone play a role and the net rotation is counterclockwise leading to right-handed growth (Stage IVa).

Once the growth zone is fully established, the observed rotation of the sporangium is determined by the integral over the entire zone, hence leading to a left-handed spiral (Stage IVb). Interestingly, the model predicts that at any given time there are individual material points in the growth zone turning both counterclockwise (top of the growth zone) and clockwise (bottom). The integrated effect of these rotations depends on the extent of the growth zone. This mechanism is entirely consistent with the detailed observations of Cohen and Delbrück [218] on the rotation of individual points in the growth zone of which they write: “The twist reaches negative values during the First few tenths of a millimeter. It then turns positive. The curious negative

values of the twist in the uppermost portion of the growth zone are undoubtedly real". Estimates of the rotational velocity depend on the choice of the time scale t_r . From Figure 5 we see that in Stage IVb $|\omega| \sim 1.5$, and for the range of t_r , $1/\kappa_1 \leq t_r \leq 1/\kappa_2$, one finds the corresponding range of 1 to 4 turns/hr. This result is qualitatively consistent with the observed 2 turns/hr.

16.9.4 Discussion

The model discussed here relies on two simple fundamental assumptions: First, new fibers are laid down along the direction of existing fibers; second, new fibers are laid down in a stress-free state. The rotational inversion is then a direct consequence of the response of a tubular, fiber-reinforced, morphoelastic material. The beauty of the inversion phenomenon is that it relies on the nonlinear anisotropic response of the system and leads to two apparent nonintuitive behaviors: First, the fibers tend to align with the axis, independently of the rotation; second, right-handed helical fibers can lead to both clockwise and counterclockwise rotation depending on the angle and level of pre-compression.

At a smaller scale, a fundamental problem of plant physiology is to understand the regulation of expansive growth in organisms with walled cells (plant, algal, and fungal cells). The sporangiophore of *Phycomyces blakesleeanus* has been used as a model organism for investigating the relationship between the rate of growth regulation and the mechanical properties of the cell walls [995, 997].

Part V

Conclusion: Where It Does Not End

*Last scene of all,
That ends this strange eventful history,
Is second childishness and mere oblivion,
Sans teeth, sans eyes, sans taste, sans everything.*

Chapter 17

Ten Challenges



The theory of growth presented so far is still in infancy. A number of key challenges need to be addressed thoroughly before it stands as a complete mechanical theory that can be readily accepted and used universally. Below, I outline briefly some of these challenges in the hope that they will motivate further studies.

17.1 The Rheology of Growth

We discussed in Chapter 13.1, the problem of varying time scales appearing in the growth and remodeling of materials. In standard rheology, it is appreciated that depending on the time scale at which a system is being observed, it may be described by different theories. The classic example is the evolution of a mountain: A mountain is a solid on human time scales but would appear to flow on geological time scales. In 1928, this example was used by Markus Reiner and Eugene Bingham to introduce the notion of a Deborah number, a term inspired by a biblical passage. Reiner famously said: “In her famous song after the victory over the Philistines, [the prophetess Deborah] sang *The mountains flowed before the lord*” [268, 1072]. The Deborah number De is defined as

$$De = \frac{\text{Time of stress relaxation}}{\text{Time of observation}}. \quad (17.1)$$

It combines a material parameter and an observation parameter. At low value of the Deborah number, corresponding to high stress relaxation or long observation time, the material behaves mostly as a Newtonian viscous fluid. For high Deborah numbers, corresponding to a very long time of relaxation or a very short observation time, the material is dominated by a solid-like behavior.

Closely associated with the Deborah number is the Weissenberg number Wi [1309, 1322] describing the relative contribution of viscous forces with respect to elastic forces

$$Wi = \frac{\text{Viscous forces}}{\text{Elastic forces}}. \quad (17.2)$$

Depending on the relative values of these two numbers, different regimes can be obtained, as classified by Pipkin [1039]. Materials with small Weissenberg and Deborah numbers can be studied within the framework of linear viscoelasticity. Very large Deborah numbers correspond to either linear elastic-like materials (small Wi) or nonlinear elastic materials (larger Wi) as the Weissenberg number in that regime gives a relative measure of the strain amplitude. Intermediate values of Wi and De correspond to nonlinear viscoelastic materials, which are still poorly understood [651].

The problem with growing biological systems is that, in addition to the material and observation time scales used to characterize the rheology of polymers, it involves new time scales associated with mass addition, remodeling, and other active processes. It also involves new length scales associated with cellular processes. Therefore, it cannot be simply modeled as an inert viscoelastic material. New dimensionless numbers must be introduced to keep track of these new time and length scales and to classify possible material behaviors associated with development, growth, remodeling, and homeostasis.

Nevertheless the study of complex fluids gives us the understanding that the type of theories to be used to model a particular phenomenon depends crucially on the period of observation. For instance, in the study of axon growth in Section 4.4.4, we observed that the elastic properties of axons can be obtained on very short time scales by plucking the axon and observing its deformation. On longer time scales, the growth of the axon can be described either as a viscous fluid [1002] or by the evolution of the reference configuration [1067].

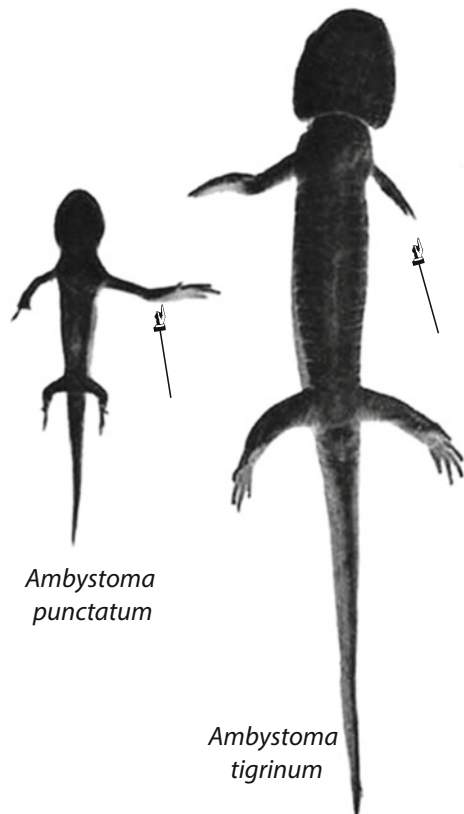
More generally, the evolution of the reference configuration can be used to capture many processes such as plasticity and viscosity. Therefore, the central idea of an evolving reference configuration offers a unifying framework to understand the rheology of growing biological systems. Within this framework, the description of particular asymptotic regimes based on the type of biological, materials, and observational time scales should provide systematic methods to obtain simple models for specific systems and guide new experiments.

● **Challenge #1:** Within a general theory of evolving reference configurations for anelastic systems, classify different rheological regimes corresponding to different realizations of growth in biological systems.

17.2 The Regulation of Growth and Growth Size

During development and regular life time in many plants and animals, the body and most of the organs are actively regulated to maintain size and shape. This regulation mechanism occurs through growth and appropriate shrinking. One of the fundamental questions of both development biology and of physiology is to uncover how the size of an organism or an organ is determined and controlled [1289]: Why do arms have the same size? Why do elephants grow larger than mice? How do eye balls fit snugly in the eye socket and match the focal length of their optics? How do clownfish change their body size according to their social status? How does the size of a snake heart change by a factor two to three before and after a meal is digested?

Figure 17.1 In two salamander species of different sizes, the amputation and reattachment of a limb (arrows) early in development lead, in mature animals, to the original limb size (adapted from [1264]).



The size of an organism or an organ depends both on the number and size of cells and on fluid and extracellular material. As a first approximation, it is the number of cells that decide the overall size of an organism. For instance, a 70 kg human contains about 10^{13} cells whereas a 25 g mouse (*Mus musculus*) has about 3×10^9 cells. The weight ratio $70,000/25 = 2,800$ is roughly equivalent to the cell number ratio of 3,333 [223]. It is therefore natural to consider cell proliferation and death as the main driver for size control. However, a closer examination and the experimental manipulation of either cell proliferation or cell size in various organs have revealed that some organs manage to retain their size by modulating cell size. These organs may have fewer but larger cells, or more cells of smaller size [265, 1308].

A central dogma of developmental biology is that apart from an overall effect of extrinsic factors on the entire organism, such as nutrition, organ size, proportion, and patterning are mostly controlled intrinsically. This dogma is illustrated by the celebrated experiments of Twitty and Schwind [1264] who exchanged limbs and eyes in species of salamanders of different sizes. As shown in Figure 17.1, the transplanted organ reached the size dictated by its own species, suggesting that growth follows internal positional and size information. The proposed theoretical mechanism for such an internal programming is that growth is controlled by *morphogens*. Morphogens are molecules produced by cells at discrete sources of an organ that create extracellular concentration gradients over some distance from the source. Therefore, morphogens provide cues for the position of different cell types, limiting cell proliferation, or initiating the production of secondary morphogens [1338]. These elusive morphogens were eventually identified in the wing imaginal disk of *Drosophila* (fruit fly), a model organ of a model organism of developmental biology. Proteins encoded by the *decapentaplegic* (Dpp) and *wingless* (Wg) genes were shown to pattern the fly's disk wing [776, 1364] and control cell proliferation as illustrated in Figure 17.2. The wing blade develops over 4 days starting from approximately 50 cells to about 50,000 in 10 cycles [1017]. Remarkably, all cells divide homogeneously in space until proliferation stops.

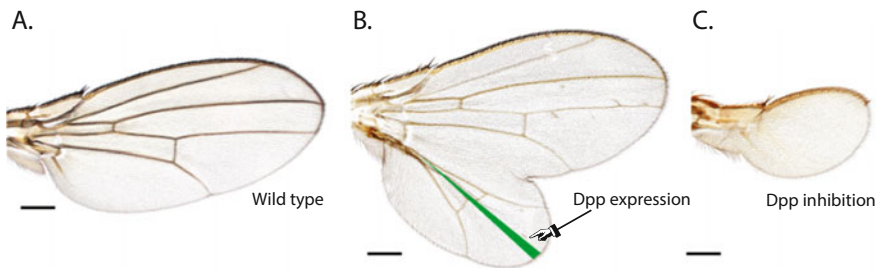


Figure 17.2 The role of morphogens in the regulation of size is revealed in experiments on *Drosophila*'s disk wing. Compared to the wild type (A), an over-expression of Dpp (shown by the arrow in B) induces proliferation in surrounding cells and leads to an enlarged wing. C. Conversely, inhibiting Dpp creates a smaller wing (adapted from [1017, 1363]).

Despite the well-accepted fact that morphogens play a crucial part in organizing growth, patterning, and controlling size, the mechanisms by which cells interpret these gradients and possibly other spatial and physical clues remain elusive despite growing evidence of the role of mechanotransduction [355, 361]. In particular, wing size cannot be simply explained by the length scale associated with Dpp gradient [10]. A possible mechanism for size control is that there exist extra morphogens produced at the differentiation stage that are diluted as mass increases [1299]. However, these chemicals have not yet been identified. Another possible mechanism is that physical forces acting on the cells are used to carry global information [11, 632, 952]. These models assume that proliferation depends on the concentration of morphogens. Stronger gradients in the central region of the disc create differential growth and, accordingly, regions of tensile hoop stress in the periphery. At the center of the disc, compressive forces increase with disk size up to a critical value, where growth stops. More sophisticated models [27] rely on anisotropic growth response and active actin contraction to explain the scaling of the wing disc.

Another striking example of global organization is found in plants. Wild type leaves of snapdragon (*Antirrhinum*) are naturally flat [937]. The *cin* mutant of *Antirrhinum* has excess growth in the marginal regions and has a crinkly and folded shape. Flatness is not only a local notion associated with zero curvature, it is a global property that is carried through the entire organ through local regulation. If some parts of the leaf grow much faster, it will develop stresses that will naturally lead to buckling. The fine balance between stresses, geometry, genetics, and diffusion seems to be key in many other plant systems to control size and shape [217, 502, 1097].

● **Challenge #2:** Determine the respective roles of mechanics and genetics in determining the size of animals and organs. Understand how morphogen gradients, chemical clues and pathways, physical inputs, and mechanical transduction combine to obtain organism size information and conspire to control global size through local growth.

17.3 The Elusive Growth Law

In the theory of continuum mechanics, the fundamental equations are obtained from a consideration of kinematics for the type of deformations allowed, physical arguments for the balance of forces acting in a material; and constitutive laws describing the material properties of a material. For the case of elastic materials, the proper choice of a constitutive law, based either on fundamental statistical and thermodynamical principles [40] or purely phenomenological considerations, is still an active field of research. Nevertheless, there is a large body of the literature describing these laws and how they should be used when modeling a given system [119, 597, 978]. There is an excellent agreement between the three approaches necessary to put a physical theory on firm grounds: A theoretical physical description of the material at the micro- and macro-scales, detailed experiments measuring the response of these systems

under loads, and reliable computer simulations. Each links theory to experiments and allows for the exploration of more complex systems. This physical theory of elastic materials is further established by various mathematical treatments providing a rigorous foundation for the theory as well as insight into its mathematical structure.

The situation is not as pristine for the theory of growing solids. Indeed, the kinematics of growth for continuum solids introduces a new object, the growth tensor $\mathbf{G}$. Therefore, an appropriate constitutive equation, namely the growth law, must be postulated for this new object. Following the discussion of Chapter 14, this constitutive law takes the form of an evolution law describing the rate of change of the growth tensor as a function of possible growth stimuli, be it chemical, genetics, or physical. However, the precise form that these laws should take is still not correctly understood and it is perhaps one of the most challenging problems in establishing a mechanical theory of growth.

For the present discussion, we restrict our attention here to the coupling of growth to mechanics by neglecting all other stimuli. These effects will be discussed as another challenge. We know that the overall change of mass is given by $(\det \mathbf{G})$. Yet, even if we assume that growth is isotropic, that is $\mathbf{G} = g\mathbf{1}$, the functional form of g is still an unsolved issue. Worst, the choice of dependent variables, of stresses, strains, tractions, or forces is not agreed upon. Whereas some of these formulations may be mathematically equivalent, it is not clear whether growth processes in biological tissues are primarily governed by stress or strain [634].

In the theory of elastic solids, the use of the second law of thermodynamics and the absence of entropy sinks at the microscale can be used to find constraints on possible constitutive laws. It is therefore natural to expect that it could be similarly useful in giving us insight into the growth law. However, we have seen that growth fulfills many different roles in living systems. In normal conditions, it is used in the early development of an organism to reach an adult size as well as the regular maintenance of an organism by homeostasis. It is also found in pathology, through abnormal growth response and tumor growth. It is therefore unreasonable to expect that all these different processes be described by a universal law for growth based on simple physical principles. Indeed, we do not expect that pressure applied to a growing embryo, a healthy artery, or a growing tumor would result in the same growth process or even that it would result in a systematic mass addition or mass resorption.

The different biological processes related to growth are governed by biological pathways and typically require external sources of energy. The existence of these pathways indicate that there is information at the cell level that is processed through cellular mechanisms so that the cells are able to react to external stimuli. This cellular information and energy input create at the tissue level possible sinks of entropy. In the presence of these sinks, the thermodynamic argument breaks down since no strict inequality can be established among the various fields appearing in the theory. Yet, thermodynamics allows us to distinguish between purely physical passive processes and biological active processes. It also helps us to identify particular combinations of mechanical quantities, such as Mandel's and Eshelby's stress tensors, that are likely to play a fundamental role in a growth law.

In the absence of a well-established theory for a growth law, a phenomenological approach can be used to formulate evolution laws based on both experiments and general observations. For instance, the notion of homeostasis can be used to postulate the existence of a special homeostatic stress that a given system maintains through mass addition and removal. In such cases, it is assumed that the rate of change of the growth tensor vanishes identically when the system reaches the homeostatic stress and is such that the system tends to this stress for small enough perturbations. However, even in this simple case, the specific form that the growth law must take to ensure the stability of the homeostatic state is not well understood as observed in the simple case of homogeneous deformations discussed in Section 14.6. Yet, the theory of morphoelasticity constitutes a powerful framework in which new experiments can be systematically formulated.

Another approach consists in using the theory of mixtures for which the exchange between different components is easier to model based on fundamental principles and out-of-equilibrium thermodynamics. The response of the different active constituents to different mechanical stimuli would require specific modeling based on their cellular properties. If the promises of these theories are fulfilled, it would then be possible to coarse-grain these models to obtain the homogenized response at the tissue level. We consider the challenges at the cellular level in the next Section.

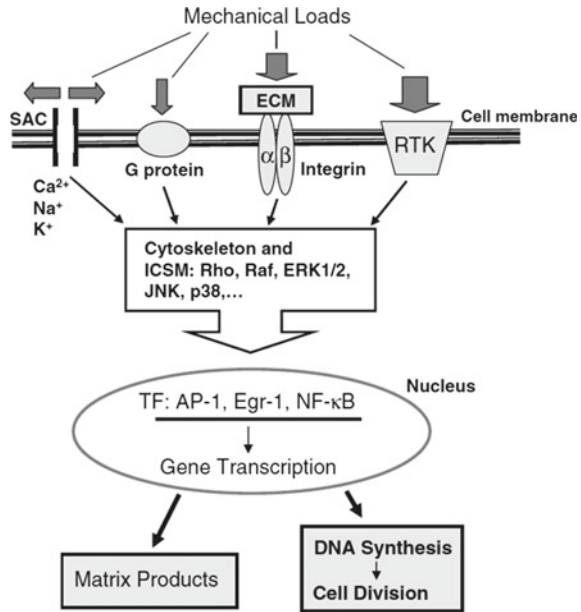
• **Challenge #3:** Use the theory of morphoelasticity as a general constitutive framework to identify possible functional forms of growth laws and to design new experimental protocols. Test these protocols theoretically and computationally in order to classify families of growth laws. Following the established protocols, run experiments on different classes of biological systems to obtain specific constitutive laws within these families.

17.4 Multiscale: From Discrete to Continuous and Back

Closely related to the previous challenge is the problem of connecting our accumulated knowledge of growth at the tissue level to our understanding of cellular mechanics. In particular, we know that mechanical signals at the tissue level are transmitted into a cascade of cellular and molecular events [629, 664], as illustrated in Figure 17.3. These *mechanotransduction* processes have been abundantly documented in various biophysical experiments where different cells lines were loaded statically or cyclically while their proliferation or increase in various components are recorded [1294].

These experiments demonstrate the great complexity and diversity of cellular responses to mechanical stimuli and, in particular, how the extracellular matrix and cell adhesion play an equally important role in dictating overall tissue properties. So far, most of these studies are disconnected from similar considerations at the tissue or organ levels and one of the key challenges of biophysics is to connect this microscopic response to macroscopic scales [1198].

Figure 17.3 Illustration of various known cellular mechanotransduction mechanisms (from [1294]).



The starting point to connect multiple scales is to reconcile the discrete cell-level models described in Section 3 with the continuum theory of morphoelasticity. This connection can be established by the methods of homogenization. Homogenization denotes the set of mathematical techniques for the study of physical media with a well-defined microstructure with typical length scales much smaller than the system size [1115]. The basic idea behind homogenization is to average the properties of the microstructure to obtain the effective properties of the body, seen as an homogeneous system, at larger scales [86, 438, 884]. Homogenization is easier to achieve when the heterogeneous material has a periodic, or nearly periodic, microstructure. Then, the process amounts to approximate asymptotically, as $\varepsilon \rightarrow 0$, the solutions of partial differential equations with coefficients oscillating with a period ε [19].

In biomechanics, since many materials often have a regular structure [439] these methods have been successful in modeling the response of bones [594], the effective properties of soft-tissues [160, 359], the design of scaffold in tissue engineering [593, 1149], and fluid transport in tumors [1148].

If a tissue does not have the required periodicity, the traditional methods of homogenization cannot be directly applied but bounds on the effective properties can be obtained by comparing the material with another material that has well-defined structure, and that shares some of the statistical properties of the original system [801, 802, 892, 1042].

So far, applications of homogenization in biomechanics have mostly focused on either obtaining effective strain-energy density functions for elastic materials or averaged equations for fluid transport in poroelastic materials. Assuming that we have suitable models to describe the mechanical response of a tissue under loads at any

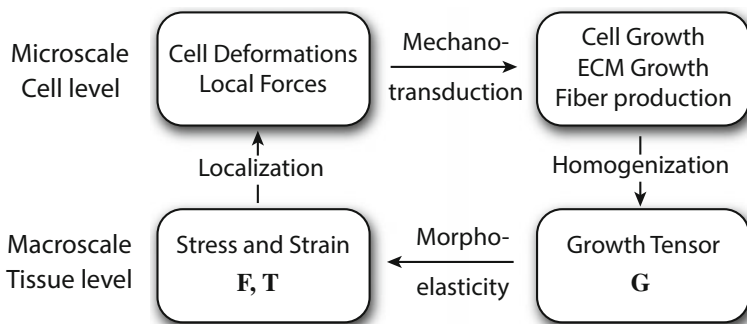


Figure 17.4 The required steps to include microscopic properties in a continuum model for growth (adapted from [672]).

given time, we can try to use homogenization on longer time scales in order to obtain a growth law based on a simple rule of evolution for a microscopic lattice [199]. Ideas and methods from homogenization in plasticity theory may be particularly relevant for this task. However, in plasticity problems there is a well-defined lattice structure and the anelastic part of the deformation can be directly linked to slip lines and other microscopic defects [1070, 1071]. These approaches seem particularly promising in establishing a rigorous framework linking microstructure to tissue evolution. To obtain the feedback between mechanics and growth, the deformation at the cell level must be known. This is the problem of *localization*. If stresses and strains are known at the macroscale, the forces or deformations experienced by the cell level are not simply given by the pointwise value of the corresponding fields. Localization provides a method to obtain microscale information from both the macroscale and the microscopic structure. The different steps in a true multiscale approach are sketched in Figure 17.4. We emphasize that this cartoon is a highly idealized picture of a multiscale process and that much thought must be given in defining the different concepts.

A real theory of growth will only emerge when there is a clear bridge between microscopic response and macroscopic behavior. The development of the theory of elastomers by Flory, Rivlin, and others in the 1940s relied on simple observations of the microscopic structures of polymers that resulted in the derivation of the neo-Hookean strain-energy density function using proper statistical averaging. This, in turn, served as a basis for further refinement and development. It is hoped that a similar development will take place in the mechanical theory of biological growth.

• **Challenge #4:** Starting from a simple representation of tissues, with given elastic properties and rules for growth based on microscopic biophysical laws, systematically obtain average laws for growth in terms of macroscopic quantities such as the growth and stress tensors. Localize these effective models to check independently the local behavior of cells when the tissue is loaded.

17.5 Growth Versus Diffusion

Our discussion of a possible growth law has been restricted so far to mechanical stimuli. Clearly, the growth of most biological systems is not just driven by mechanics but is typically the result of coupling with other physical or chemical fields. In particular, the traditional view of morphogenesis is that patterns appearing during development are driven by spatiotemporal variations of various chemical concentrations competing with each other and creating Turing-type instabilities [819, 927]. The equations modeling these phenomena typically take the form of nonlinear reaction–diffusion equations, which in the simplest cases read

$$\frac{\partial c_i}{\partial t} = D_i \Delta c_i + f_i(c_1, \dots, c_n), \quad i = 1, \dots, n, \quad \mathbf{x} \in \Omega \subset \mathbb{R}^N, \quad (17.3)$$

where $(c_1, \dots, c_n)$ is a vector of concentrations Δ is the N -dimensional Laplacian and $(D_1, \dots, D_n)$ are the diffusivities, assuming no cross-diffusion. The functions $(f_1, \dots, f_n)$ describes the reaction kinetics between the different species.

In his celebrated article of 1952, Turing showed that by choosing $n = 2$ and (f_1, f_2) linear in (c_1, c_2) , these equations are sufficient to generate spontaneously spatial patterns from uniform solutions [1259]. He further suggested that pattern formation in morphogenesis could be modeled by the evolution of *morphogens*, dictating the time and place at which cells would grow and remodel. These ideas are the starting point of a large body of work on biological pattern formation [440, 820, 860].

Even in the absence of any mechanical feedback, there is an interesting coupling between growth and Turing-type patterns [52, 252, 253]. If we assume that the domain on which a pattern is established Ω_t grows slowly, it will affect the pattern as the growth of the domain induces a flow in the current configuration so that, we have now

$$\frac{\partial c_i}{\partial t} + \operatorname{div}(\mathbf{u}c_i) = D_i \Delta c_i + f_i(c_1, \dots, c_n), \quad i = 1, \dots, n, \quad \mathbf{x} \in \Omega_t \subset \mathbb{R}^N. \quad (17.4)$$

The term $\operatorname{div}(\mathbf{u}c_i)$ can be decomposed into an advection term $\mathbf{u} \cdot \operatorname{grad}(c_i)$ due to the motion of material points during growth and a dilution term $c_i \operatorname{div}(\mathbf{u})$ due to local volume change. The flow $\mathbf{u}$ is determined by the deformation of the domain due to growth. Since, we assume that we have no elastic response, we have simply

$$\mathbf{x} = \chi(\mathbf{X}, t) \quad \mathbf{X} \in \Omega_0, \quad (17.5)$$

where Ω_0 is the initial domain. This growth function is related to the growth tensor $\mathbf{G}$ through its gradient: $\mathbf{G} = \operatorname{Grad}\chi$. Then, the local flow is determined by

$$\mathbf{u}(\mathbf{x}, t) = \frac{\partial \mathbf{x}}{\partial t} = \frac{\partial \chi}{\partial t}. \quad (17.6)$$

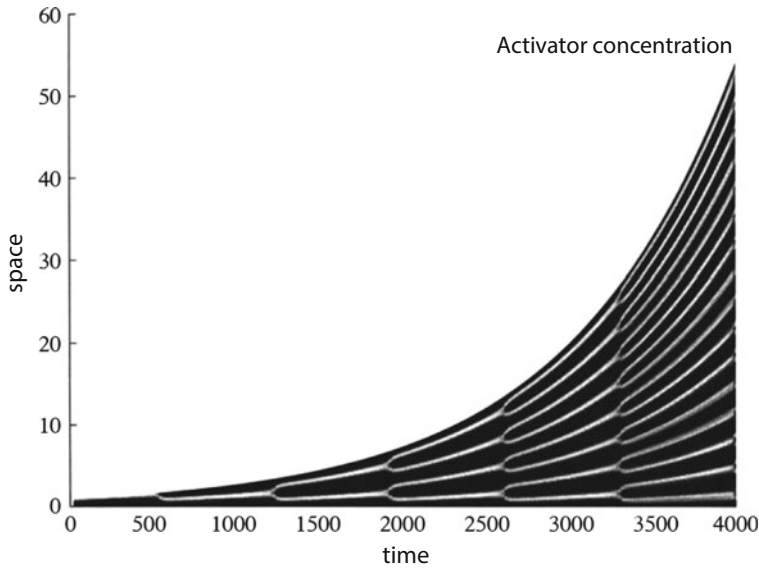


Figure 17.5 Space–time evolution of activator concentration profile on an exponentially growing domain. Light and dark shading represent high and low concentrations, respectively (adapted from [252]).

The slow evolution of the domain creates an interesting variation of patterns. For instance, in one dimension ($N = 1$) with two species ($n = 2$), a simple activator–inhibitor system shows frequency-doubling of patterns as seen in Figures 17.5 and 17.6

The coupling between chemical fields and mechanical fields has long been suspected to play an important role in biological pattern formation [671, 928, 929, 1244], but the relative importance of each effect and of their coupling remain poorly understood. An interesting case in point is the problem of *phyllotaxis*, the arrangement of leaves on a plant stem. These patterns also appear in the arrangement of seeds on sunflower heads, bracts on pine cones, and spines on cacti, shown in Figure 17.7. These initial elements, appearing originally as small bumps on leaves or homologues, are collectively referred to as *primordia*. Understanding and modeling phyllotaxis has been an active field of research for centuries, going back to Leonardo da Vinci and Kepler (see [1026]). The geometry of such patterns can be modeled from a purely geometric point of view as the sequential optimal packing of new primordia in a given geometry [43] .

Phyllotaxis can also be explained as a developmental process, related to purely biochemical effects, by following the transport and localization of the growth hormone auxin. In this scenario, phyllotaxis emerges from the chemical interaction between existing and incipient primordia in a growing structure, mediated by actively transported auxin. High auxin concentration triggers the formation of new primordia

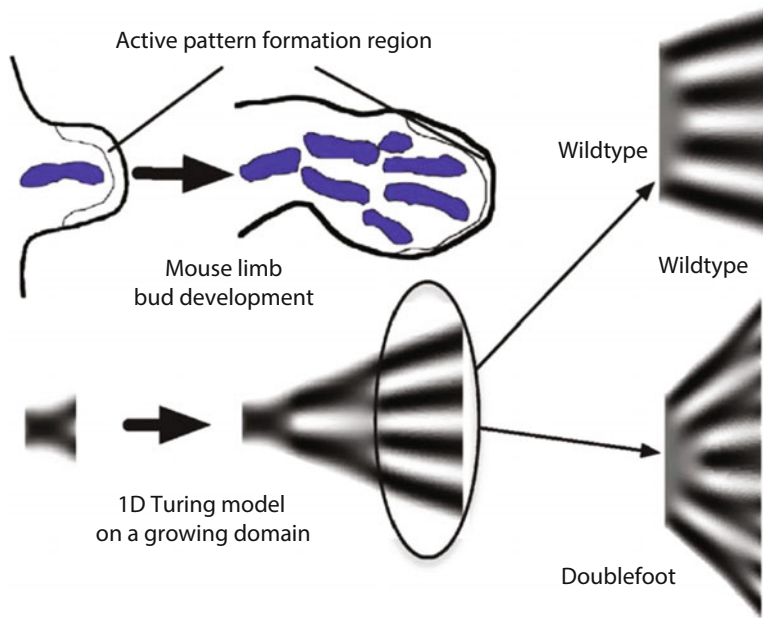


Figure 17.6 Digit formation in the development of a mouse limb (*Mus musculus*). Top: traditional self-organization model where pattern formation only occurs at the distalmost part of the limb bud. Bottom: 1 D-turing model in a growing domain reproducing both the wild type and the supernumerary digit mutant when growth speed is increased (adapted from [893]).

which are separated from each other by the local depletion of auxin around them as verified in computer simulations [674, 1178] (Figure 17.8A).

Yet another approach is to explain the apparition of new primordia as a mechanical buckling instability due to differential growth [312, 315, 507, 1187]. Modeling the soft outer layer where cell division and growth occurs as an overdamped, curved,

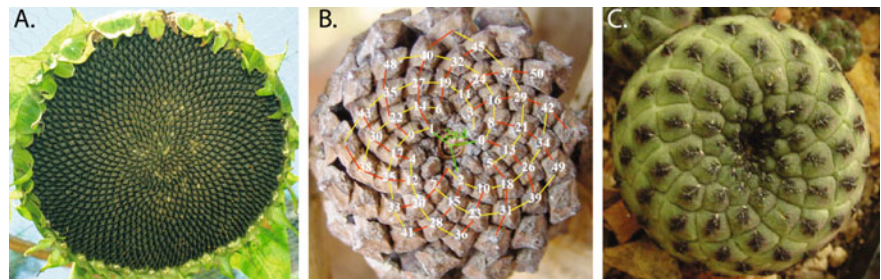


Figure 17.7 Phyllotaxis is the particular spiral arrangement of markers found in plants. A. Seeds on sunflower heads. B. Bracts on pine cones with 8 counterclockwise and 13 clockwise spirals. C. Spines on cacti [1026]. Pictures courtesy of Patrick Shipman.

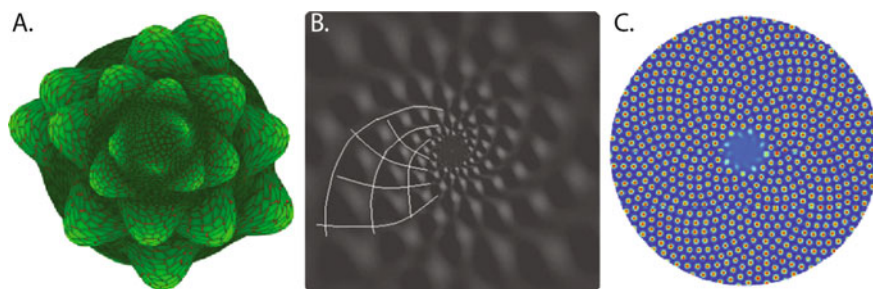


Figure 17.8 Simulation of phyllotaxis for a biochemical model (A. courtesy of Richard Smith), a mechanical model (B. from [1152] courtesy of Patrick Shipman) and a coupled mechanical/biochemical model (C. courtesy of Matt Pennybacker [1026]).

elastic shell with circumferential and radial stresses leads to buckling patterns with many phyllotactic features, such as the whorls and Fibonacci progressions [947, 1151, 1152], as shown in Figure 17.8B. At the cellular level, experimental evidence and simulation further showed that mechanical stress plays an important role in the organization of the microtubule cytoskeleton, which in turn leads to morphogenetic patterns by setting anisotropic direction for cell division [528].

The biochemical and mechanical approaches can be combined by assuming that there is a coupling between the local concentrations of key molecules, the local stress field, and the growth field [948]. These different feedback mechanisms provide a complete picture of the different patterns and allow to recover almost all features of phyllotaxis [1026], as illustrated in Figure 17.8C.

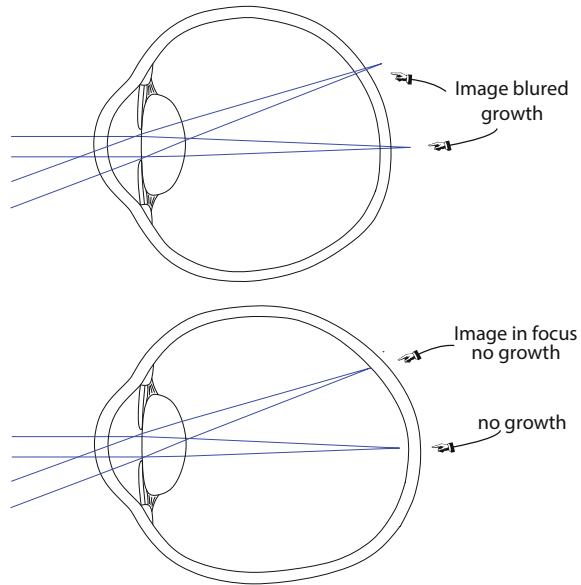
Despite the fact that both chemical diffusion and mechanical stresses play an important role in growth and remodeling [145], their coupling is usually weak in the sense that the coefficients appearing in the equations governing either process only depend weakly on the coupling. Therefore, it is mostly through changes in geometry that the two processes are coupled.

• **Challenge # 5:** Determine the respective role of diffusion and mechanics in establishing biological patterns. In particular, identify systems dominated by one or the other effect and systems where the coupling between both is necessary to obtain generic and robust patterns.

17.6 Multiphysics: Coupling Growth with Other Fields

Biochemical diffusion and mechanics are not the only stimuli affecting growth. An example of a physical stimulus is found in the growth of the eye and the process of *emmetropization* which describes how, in health, the human eye grows during childhood to adopt the right shape and size for focussed vision. The goal of emmetropiza-

Figure 17.9 An illustration of differing focal lengths for blue light. In this example, local growth of the sclera is possible only where the retina is in front of the best focus point for blue light. Top: There is growth in the peripheral sclera and at the posterior pole. Bottom: growth ceases when the retina is either at the best focus point or behind it (adapted from [695]).



tion is to position the retina at the correct axial distance behind the lens for the optical power of the anterior eye. When this process fails, the individual is either myopic, with excessive axial length, or hyperopic, with insufficient axial length. Animal studies have revealed that emmetropization is sensitive to the wavelength of light [858] and that the application of negative powered lenses induces myopia [1289]. These studies suggest that apart from possible genetic and environmental factors, the signal controlling emmetropization is locally interpreted at the retina [1312] and is produced through the optic of the eye lens. A possible hypothesis, shown in Figure 17.9, is that the retina can separately detect blur in red and blue light and that it uses the differing amount of blur at these wavelengths to determine not only how blurred an image is but also whether that blur is due to hyperopia or myopia. This signal is used to drive growth according to the assumption that the posterior sclera is capable of local growth to relieve the stress due to intraocular pressure whenever that region of the sclera is in front of the position of best focus for blue light. As the eye elongates to reach a focussed vision, it changes the overall geometry of the eye, hence the focus of the lens. Hence, there is a two-way coupling between optics and growth.

Another example of physical coupling is found in the swelling in the brain following trauma. Swelling is the volume increase due to fluid intake from the capillaries. As a first step, it can therefore be modeled as a growth process where swelling is directly induced by a change of mass. This approach can be used to understand the stress created during swelling and the release of stresses following decompressive craniectomy, a surgical procedure used to reduce stresses in swollen brains [1305, 1306]. An example of such computations, based on the theory of morphoelasticity, is shown in Figure 17.10.

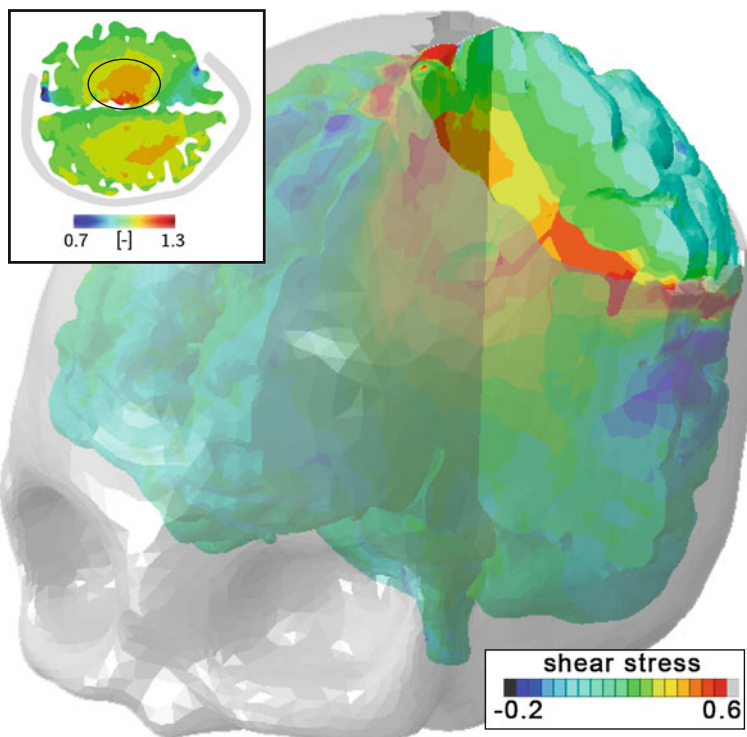


Figure 17.10 Finite-element simulation for 10% brain swelling showing regions of high shear stress close to the opening. Insert: Transverse section showing radial fiber stretch and possible axonal damage (adapted from [487]).

However, at the tissue level, the water intake is tightly controlled by difference in turgor pressure due to electrochemical imbalance [762]. In this case, the change of volume can only be properly understood by coupling the solid deformations with both fluid and ions transport. Again, the coupling acts both ways since the increase in volume reduces the concentration of fixed charge densities. This coupling can be achieved close to equilibrium using the methods of irreversible thermodynamics that provide a systematic way to derive generic transport equations for coupled fields.

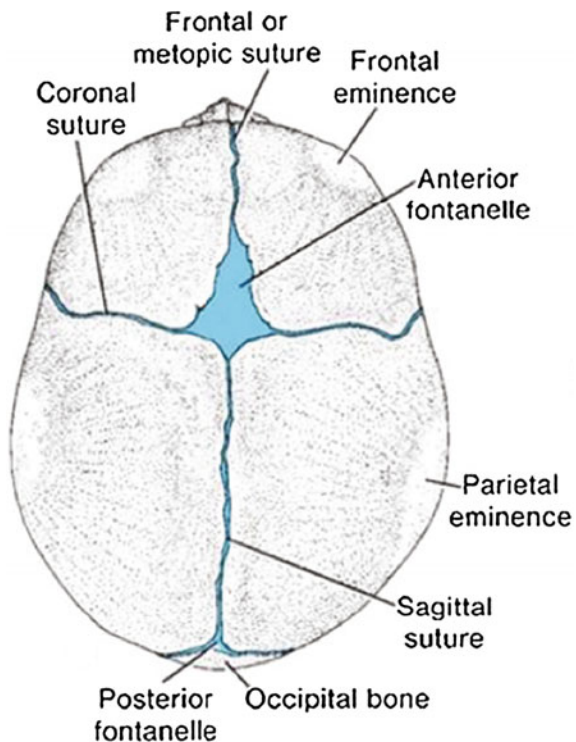
The theory of coupled fields is a well-developed theory of continuum mechanics even though some fundamental physical and mathematical issues remain [340]. It combines aspects of solid mechanics, mixture theory, and the thermodynamics of irreversible processes. However, this theory has not yet been adapted to the specificity of biological systems and needs to be reformulated to include evolving microstructures and mass addition. The theory needs to be both generalized to include such key aspects of biological systems but it also needs to be adapted and simplified, in a pragmatic way, to address the reality of experimental biology which often does not give the luxury of experimental control or access to microscopic parameters.

• **Challenge #6:** Understand the intrinsic coupling between different physical theories in tissues, organs, and organisms with evolving microstructures. Develop a general theory of out-of-equilibrium nonlinear thermodynamics coupling multiple fields for growing biological systems. Couple this theory to gene regulatory networks and biochemical pathways.

17.7 A Theory of Accretive Growth

Most of the work on growth focuses on volumetric, surface, and tip growth. In these cases, growth is expressed as a change of the volume element attached to a material point. In the case of surface growth or tip growth, only points close to the boundary experience growth, but no new material points are added to the system. In accretive growth, new layers of materials are added at the boundary through a process of deposition, as found in the problem of crystal growth [154, 1319] or protoplanetary disks fusion [105, 1318]. Examples of biological systems evolving by accretive growth include seashells [202, 1265], horns [1173], coral [676, 875], and, to some extent, bone growth.

Figure 17.11 Cranial skull in the newborn. The calvaria is composed of the bones that can be seen from the top. Large sutures and fontanelles are present in the newborn (adapted from [1112]).



An important example of accretive growth is found in the early growth and development of the skull and in particular, the bones of the cranial vault composed of the superior portions of the frontal bone, the occipital bone, and the parietal bones (see Figure 17.11). At birth, these different bones are joined by soft fibrous cartilaginous tissues referred to as *sutures* and *fontanelles*. Bones of the cranial vault form primarily by intramembranous ossification, a mode of ossification where bone forms directly from undifferentiated mesenchymal cells without first forming a cartilaginous scaffold.

There are two principal modes of growth and remodeling to increase intracranial volume and shape the skull after birth, both related to accretive growth: sutural growth and plate growth. *Sutural growth* takes place at the suture and results in the deposition of new bone at the margin of the bone plates. Sutural growth is the primary mode of intracranial volumetric expansion for the skull as approximately 90% of intracranial volume growth occurs within the first two years after birth in humans. The leading theory is that the differentiation of osteoblasts and the ossification at the sutural edge is regulated by signaling interactions between the mesenchyme, the osteogenic fronts, and the dura mater. The main signaling is believed to be of mechanical origin: As the brain grows, it generates tensile strain across the sutures that influences bone deposition [333, 909] at the suture edge and inhibits ossification within the suture itself [989] (Figure 17.12).

Plate growth takes place on both surfaces of the bone plates and results in remodeling and thickness increase. Typically, it happens by mass removal at the inner surface and mass deposition at both the inner and outer surface. Mechanically, the pressure exerted by the growing brain stimulates bone resorption by osteoclasts. On the outer surface, a layer of osteoblasts continuously produces new bone growth and is believed to be controlled by the tension in the periosteum [567].

While there seems to be broad agreement in the literature about the basic physical mechanisms at play during growth, the detailed signaling processes that lead to this overall behavior is extremely intricate as it relies on different cell lines as well as on many different biochemical pathways [1081]. From a mechanical point of view,

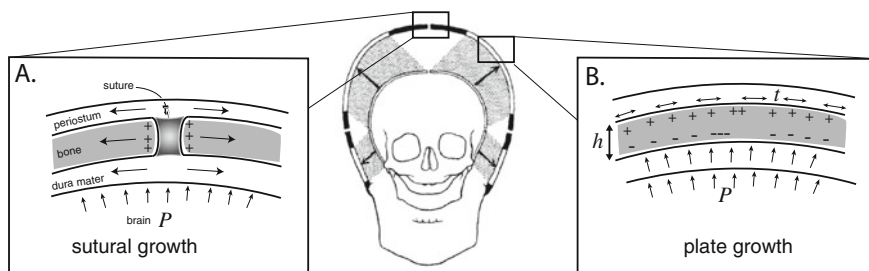


Figure 17.12 Cranial growth and remodeling occur primarily through A. sutural growth in the suture and is remodeled by B. resorption and addition of material on the upper and lower surfaces of the bone plates (middle sketch adapted from [909]).

explicit forms for the two growth processes have yet to be proposed. For instance, assuming that edge growth depends on the mechanical forces applied at the suture level, does it depend on force, stress, tension, or strains? These different mechanical quantities are related but since the thickness of the calvarial bones change (by a factor of about 3) and the stiffness of the suture changes (by a factor of about 50), the different measures of force change drastically during the growth process. Furthermore, what reasonable law for this process could explain some of the basic observations, both in healthy and pathological skull growth? In particular, detailed simultaneous studies of skulls and brains in mice and humans indicate that the brain and skull fit tightly together even in the case of premature closure or different genotypes [951, 1079, 1080]. How does this synchrony take place? And how does it fail, in craniosynostosis, when sutures fuse early [1326]?

This important example underlines some of the difficulties related to accretive growth. From a theoretical point of view the main problem stems from the fact that the body changes by adding new material points. This change of boundary can easily be described by an accretion field that describes the motion of the boundary in time [914, 1173]. This approach was used in the modeling of seashells described in Chapter 7. However, this description is purely geometric and the material properties and mechanical state of these new points must also be described. Therefore, unlike the problem of volumetric growth where a reference material manifold is postulated such that all mechanical quantities can be defined, in accretive growth, the boundaries of the reference manifold are also changing [579, 630]. This evolution is quite different to the local expansion of a volume element and is particularly difficult to model from a continuum perspective even for a rigid body [987]. For a deformable solid, tracking the evolution of the boundary becomes a challenge. It can easily be performed as a discrete iterative process but its continuous version remains difficult even in the simplest cases [338, 1358].

● **Challenge #7:** Unify the theory of volumetric and accretive growth within a single framework. Establish a constitutive theory for accreted materials. Develop computational and mathematical tools to properly handle boundary accretion. Apply these ideas to explain the morphological patterns found in seashells and the pathological shape of skulls observed in craniosynostosis.

17.8 Dynamics and Post-bifurcation Behavior

Volumetric growth creates residual stress. These stresses can be used to regulate a physiological system, to maintain homeostasis, or to develop instabilities that will evolve into morphological patterns. The theory presented so far can be used to detect these instabilities and to understand how a system remains close to a dynamic equilibrium. After an instability sets in, the system enters a regime that is mostly controlled by nonlinearities. The question is then to understand how the system behaves post-bifurcation.

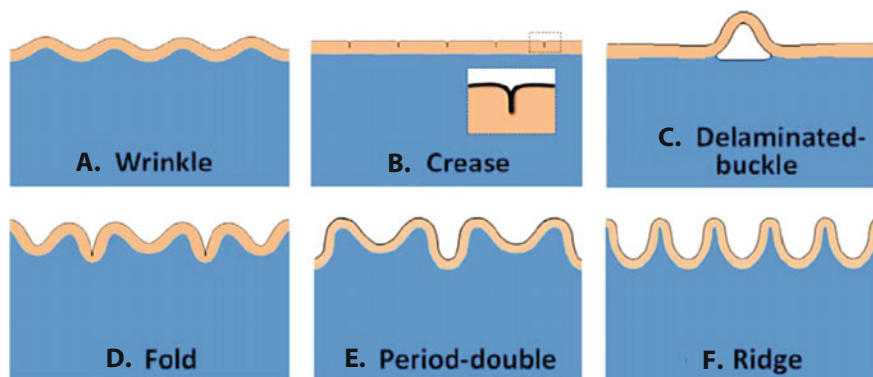


Figure 17.13 Post-bifurcation patterns for the growth of a thin layer on an elastic foundation (adapted from [1295]).

An interesting system to study post-bifurcation instabilities is the growth of a thin elastic layer attached to an elastic foundation [436]. As the thin elastic layer grows, it develops residual stresses that eventually trigger a *wrinkling instability*. Physically, this pattern reduces the overall energy of the system by relaxing stresses in the stiffer layer. Theoretically, this initial wrinkling instability can be easily captured by a linear instability. However, the development of this wrinkling pattern beyond the onset of instability is surprisingly intricate and depends on the various parameters of the systems. Phenomenologically, the wrinkles can evolve into creases, ridges, buckles, folds, or period-doubling wrinkles as sketched in Figure 17.13.

The pattern adopted by the system depends on the relative stiffnesses of the two layers [139], the thickness of the thin layer, the growth of the top layer [789], the curvature of the foundation [141], the adhesion energy between the layers [185, 1277], the imperfection of the substrate [166], the anisotropic response [592, 1194] and the nonlinear elastic response of the materials [645]. For small ratios of layer μ_l to foundation μ_s stiffnesses, $\mu_l/\mu_s \lesssim 10$, the system localizes the deformation and a fold or crease develops as observed in many biological systems. For example, the deep folding patterns that are formed during the growth of brains are believed to be partially caused by this instability [70, 142, 362]. The analysis of this instability is particularly difficult due to the existence of multiple unstable linear modes and possible contact. Surprisingly, a complete theoretical description is still lacking.

For large ratios of $\mu_l/\mu_s \gtrsim 10$ and sufficient growth, a period-doubling instability occurs due to nonlinearities in the substrate response [125, 167] as shown in Figure 17.14. Whereas period-doubling is well understood in dynamical systems, understanding the development of a spatial period-doubling pattern is more challenging even in the absence of growth [401].

The wrinkling of a growing layer on a substrate is usually studied as a quasi-static problem in which the system relaxes between different growth steps. This is well justified by the difference in time scales and the fact that growth is imposed as an

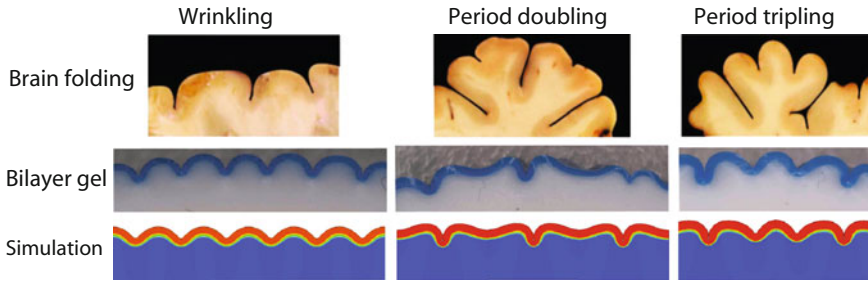


Figure 17.14 Period doubling and tripling in the mammalian cortex, swelling polymeric gels, and numerical simulations of a growing thin layer on an elastic foundation (courtesy of Ellen Kuhl and adapted from [138, 143]).

external field. However, for many biological systems the evolution of the growth field depends intimately on the mechanical field itself. When an instability takes place, this coupling and dynamics over the long time scales of growth should be taken into account. A natural question is then to understand the dynamics of growing systems. We saw in Section 14.6 that for homogeneous deformations, the coupling between the growth dynamics and the nonlinear response of the material is such that the resulting dynamics may be quite complex even in one and two dimensions.

When the deformation is nonhomogeneous, the problem becomes challenging. Consider for instance a system with a growth law driven by stress, such that there is no growth when the Cauchy stress reaches a given homeostatic value. A natural question is then to determine under which conditions this state of stress is stable. Surprisingly, this simple question is far from trivial in the presence of residual stress. The analysis of a system of two growing cylindrical shells with constant growth reveals that the dynamics in these systems depends not only on the growth law but also on the geometry and nonlinear response of the material.

• **Challenge #8:** Develop theoretical and computational methods to analyze the behavior of morphoelastic systems beyond initial bifurcations. Identify and classify generic post-bifurcation patterns. Describe the long-term dynamics of growth and determine generic criteria for the stability of homeostatic states based on the growth law. Find conditions under which growth dynamics produces oscillatory growth.

17.9 Active Forces, Actives Stresses, and Active Strains

An important mechanical effect found in living systems is the presence of *active forces* such as muscular fiber contraction [1060] or the traction exerted by neuronal growth cones [1067]. These active forces are essential for all aspects of life [656] from motility [493] and cell division [515] at the cellular scale to muscular motion at the organ level [366]. They are developed actively within the material by expanding energy. At the cellular level, the term *active material* mostly refers

to filament networks containing molecular motors such as myosin [1144]. These force-generating units are attached to filaments and consume adenosine triphosphate (ATP) to change their molecular configurations which result in the relative sliding and tensioning of these filaments. In an active fluid system, such as bacterial suspension responding to chemotactic stimuli, these forces create a bath of interacting self-propelled microorganisms which are known to undergo complex dynamics and pattern formation as a result of the interplay between active force generation and hydrodynamic interactions [1113].

Mechanically, these forces are not due to the action of external loads or external body forces and are not present in a typical engineered material. From a modeling perspective, they can be introduced in the governing equations at different levels. Here, we consider the effect of active forces on an elastic solid. Assuming that active forces do not generate torques, their presence does not alter the basic governing equation expressing the balance of linear and angular momenta, that can be expressed in the current configuration as

$$\operatorname{div} \mathbf{T} + \rho \mathbf{b} = \rho \dot{\mathbf{v}}, \quad \mathbf{T}^T = \mathbf{T}, \quad (17.7)$$

where, as detailed in Section 11.2.2, ρ is the density, $\mathbf{v}$ the velocity of a material point, $\mathbf{T}$ is the Cauchy stress tensor and $\mathbf{b}$ a body force density.

Active forces: At the microscale, the forces developed by a cell due to division, apoptosis, or motion act locally at the points of contact with the elastic medium [1058]. Assuming that there are N such discrete points in the medium, these forces can be represented as local force dipoles and included within the body force as

$$\mathbf{b} = \mathbf{b}^e + \mathbf{b}^a, \quad (17.8)$$

where $\mathbf{b}^e$ represents the external body forces and the active body force term is

$$\mathbf{b}^a = \operatorname{div} \mathbf{Q}, \quad (17.9)$$

where

$$\mathbf{Q} = \sum_{i=1}^N \mathbf{D}^{(i)} \delta(\mathbf{x} - \mathbf{x}^{(i)}), \quad (17.10)$$

represents the body force stress due to the force dipoles. Here, $\mathbf{D}^{(i)}$ is a symmetric tensor and $\delta(\mathbf{x} - \mathbf{x}^{(i)})$ is Dirac's distribution centred at the point of contact $\mathbf{x}^{(i)}$. By analogy, the effects of these force dipoles can be treated in the same way as electric charges in a polarizable medium, defects in solids, or interacting active molecules in nematic liquid crystals [829].

In linear elasticity, a suitable Green's function can be introduced to represent the effects of highly localized forcing terms for the Cauchy equation (17.7). However, in nonlinear elasticity, the presence of distributions as forcing terms cannot be easily

handled unless a weak form of the equations is used within a computational framework [1297]. It may therefore be more suitable to directly introduce an active stress tensor.

Active stresses: Rather than postulating the existence of active forces, the presence of active mechanisms within a continuum tissue can be modeled by an active stress. In this approach, the Cauchy stress tensor $\mathbf{T}$ is split into two components

$$\mathbf{T} = \mathbf{T}^e + \mathbf{T}^a, \quad (17.11)$$

where $\mathbf{T}^e$ represents the stress produced by the elastic response of the material in the absence of active mechanisms. The choice of an additive decomposition between active and elastic components is made out of convenience. Following the description of Section 11.3, for a hyperelastic incompressible material with a strain-energy density $W = W(\mathbf{F})$, the elastic stress is given constitutively by

$$\mathbf{T}^e = \mathbf{F} \frac{\partial W}{\partial \mathbf{F}} - p \mathbf{1}. \quad (17.12)$$

The *active stress* $\mathbf{T}^a$ is a symmetric tensor postulated phenomenologically to represent the effect of local contractions. Since contraction is typically localized and directed it will be both inhomogeneous and anisotropic. The stress generated depends also on the deformation itself, therefore, we expect the active stress to be a function of the deformation tensor $\mathbf{T}^a = \mathbf{T}^a(\mathbf{F})$. Along these lines, different models have been proposed in connection with heart muscle contraction [112, 1012, 1177]. It follows immediately from this description and (17.8) that this active stress tensor defines an active body force through the relationship

$$\rho \mathbf{b}^a = \text{div } \mathbf{T}^a. \quad (17.13)$$

Active strains: Muscular contraction or relative sliding of actin filaments can be interpreted as an internal remodeling of the continuum. This remodeling can be modeled by the methods used in the theory of growth as a change in the reference configuration. In this approach [201, 936], the deformation gradient is decomposed multiplicatively similar to the one used in morphoelasticity

$$\mathbf{F} = \mathbf{F}^e \mathbf{F}^a, \quad (17.14)$$

where $\mathbf{F}^e$ and $\mathbf{F}^a$ are the elastic and active deformation tensors, respectively. Since, typically we do not expect a change in volume during an active response, we restrict the choice of *active strains* so that $\det \mathbf{F}^a = 1$. The advantage of this representation is that it can be linked directly to the relative displacement of materials taking place during contraction.

From a theoretical point of view, this decomposition is exactly the one used in morphoelasticity and the entire machinery developed to understand growth problems

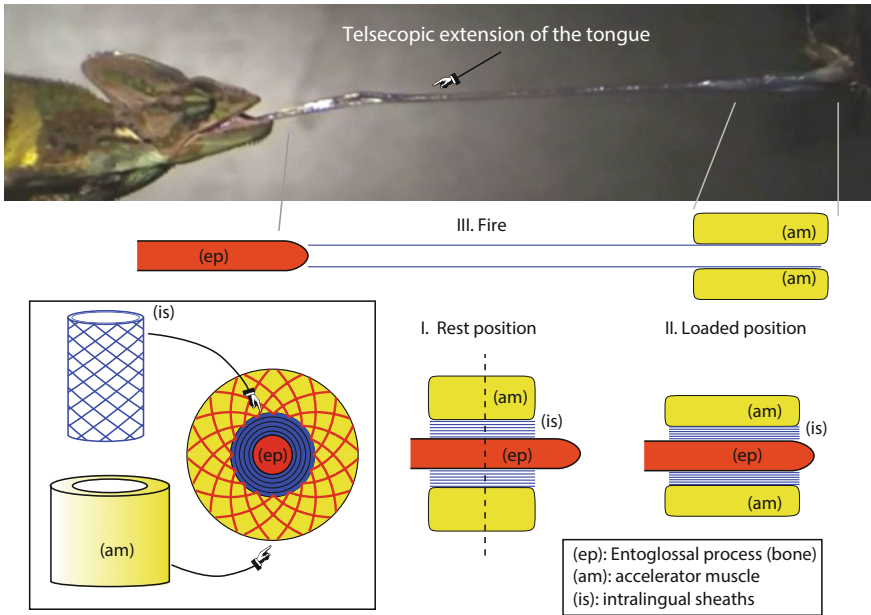


Figure 17.15 The ballistic projection of the chameleon tongue relies on an active mechanism of elastic energy build-up by muscular contraction in the tongue complex. Muscle fibers are wound spirally around collagenous sheaths that expand telescopically (adapted from [918], photograph of *Chamaeleo calytratus* courtesy of Stephen Deban).

can be used directly to understand the active stresses generated by active strains with the appropriate change of terminology. It has also been argued that it presents several advantages from a theoretical and computational point of view [28, 1034].

Active fibers: Yet another way to model active growth is at the level of the strain-energy density, either by using pseudo-elasticity [1004] or by assuming that the zero-strain-energy along contracting fibers differs from the zero-strain state for the rest of the tissue [918]. As an example, following the theory of invariants for anisotropic materials from Section 11.11, we assume that the strain-energy density only depends on the invariants I_1 , I_2 for the isotropic part and I_4 for the anisotropic part, so that

$$W = W(I_1 - 3, I_2 - 3, I_4 - \nu). \quad (17.15)$$

We recall that I_4 represents the stretch along fibers. When $\nu = 1$, the strain-energy has a global minimum in the absence of deformations given by $I_1 = I_2 = 3$ and $I_4 = 1$. However, the elastic energy increases when $\nu \neq 1$ describing the rest state of the fiber (with $0 < \nu < 1$ describing active fiber contraction). This approach was used to model the active contraction of muscle fibers in the chameleon tongue resulting in ballistic extension, as shown in Figure 17.15.

• **Challenge #9:** Understand the links between different methods to model active processes within a unifying framework. Connect active processes at the tissue level to specific mechanisms and energy expenditure at the microscale.

17.10 The Mathematical Foundations

The framework described in this monograph is a first step in building a general mechanical theory of growing and evolving biological systems. In building such a theory, one seeks to harmonize experiments, theory, and simulations so that each discipline can inform the other. A general theoretical framework where ideas and concepts are clearly discussed is of fundamental importance but is not sufficient. Another crucial aspect of such a construction is to build rigorous mathematical foundations for the theory so that it stands on solid ground. Very little is known about the mathematical aspects of this theory and most of the outstanding mathematical problems lingering in classical nonlinear elasticity [54] are completely open when it comes to the more general theory of morphoelasticity. In particular there are two important mathematical aspects of the theory that need further discussion.

Geometry: An important aspect of morphoelasticity is the distinction between growth deformations and elastic deformations modeled through the decomposition of the deformation gradient $\mathbf{F} = \mathbf{A}\mathbf{G}$. Being able to separate the two processes allows us to use a material constitutive law for the instantaneous response of the material and an evolution law for the remodeling and growth dynamics. Both processes can be clearly identified and the consequences of a change in geometry can be directly obtained by the proper kinematics. The traditional view is that the growth process is described by a local map, mapping vectors in the tangent space of the initial configuration at a point to vectors in the tangent space of the virtual configuration. This decomposition is perfectly suitable to define all kinematic and mechanical quantities as well as to obtain the governing equations of morphoelasticity. However, the mathematical status of this so-called intermediate or virtual state is not clear. The usual picture of a dislocated configuration viewed as a collection of sub-bodies is unsatisfactory as there could be infinitely many of these pieces and their connections must be somehow specified. What is the mathematical nature of such an object?

In Section 12.5.1, we showed that differential geometry provides a natural way to justify the multiplicative decomposition. In this framework, the reference configuration is seen as a material manifold with vanishing curvature tensor and a torsion tensor $\mathcal{T}$ directly determined by the growth tensor $\mathbf{G}$ through

$$\mathcal{T}(\mathbf{G}) = \mathbf{G}^{-1} \text{Skw}(\text{Grad } \mathbf{G}). \quad (17.16)$$

Therefore, the virtual configuration can be formally defined as a Weitzenböck manifold with torsion tensor $\mathcal{T}(\mathbf{G})$ and its tangent bundle is the natural space on which all kinematic quantities appearing in morphoelasticity can be defined. This *a posteriori*

justification of the morphoelasticity approach provides a rigorous way to answer fundamental questions on the mathematical nature of growth processes. Borrowing ideas from the geometric theory of defects in solids, the theory can then be further generalized to introduce new effects associated with growth and remodeling such as localized point or line growth. These effects are known to require a generalization of the Weitzenböck manifold to include nonvanishing curvature and nonmetricity [1352, 1353, 1355].

An interesting difficulty arises when considering the dynamic evolution of growth. If we assume that the growth tensor depends on the stress, the torsion is determined by a set of partial differential equations involving torsion itself. The evolution of the geometry and topology of manifolds through differential equations, such as Ricci flows [206], is an important topic of differential geometry that is of direct relevance to the mathematical description of growth. The use of differential geometry also opens the door to the development of new numerical schemes taking advantage of the underlying geometric structure [31, 32].

Analysis: Independent of the geometric nature of the governing equations, the problem of growth can be formulated as either a variational problem with respect to the modified strain-energy density function or as a set of nonlinear partial differential equations. Viewed as a problem in partial differential equations, several results on well-posedness and local existence of solution of morphoelasticity can be established [419] giving hope that general global results will follow. A natural question is to see how the classical problems of elasticity extend to morphoelasticity. For instance, as discussed in Section 11.9, Ericksen's problem states that there exist several classes of universal solutions for isotropic materials [677, 833]. For simple enough growth tensors, such as dilations, these universal solutions persist but the general conditions on the growth tensor where the universal solutions persist are not known. Similarly, the general conditions on both the strain-energy functions and the growth tensor under which there exist local or global energy minimizers for problems in morphoelastostatics are largely unknown. The smoothness of these minimizers if they exist is also unknown. Once the existence of such solutions can be established, general bifurcation and stability problems can be studied for problems that involved both mixed boundary conditions and varying growth parameters.

● **Challenge #10:** Provide a full mathematical description of growth using the tools of differential geometry. Describe the evolution of these geometric quantities and link them, in a practical way to physically and biologically relevant objects. Study the evolution of manifolds under generic flows relevant to growth processes. Generalize Ericksen's problem for systems with residual stress. Prove the existence of static solutions for morphoelasticity under generic conditions on both the growth tensor and the strain-energy functions.



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