Treadmilling stability of a one-dimensional actin growth model

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Abstract

Actin growth is a fundamental biophysical process and it is, at the same time, a prototypical example of diffusion-mediated surface growth. We formulate a coupled chemo-mechanical, one-dimensional growth model encompassing both material accretion and ablation. A rod-like element composed of actin monomers is fixed at one end and connected to an elastic device at the other. The mechanical behaviour of the rod, the diffusion of free actin monomers in a surrounding solvent and the kinetic growth laws at the accreting/ablating ends are accounted for. The constitutive behaviour of actin is prescribed in fairly general terms by mainly requiring that the elastic strain energy density of the material be convex. The existence of treadmilling solutions, characterized by a constant length of the continuously evolving body, is investigated. It is shown that the present model admits at most one such solution and that it is always stable.

Keywords: actin, treadmilling, stability, surface growth

sec:intro

1. Introduction

It is well known that growth in living systems is not only promoted by biological and chemical signals but results as well from mechanical stimuli (Goriely, 2017).

Modelling growth, intended as variation of mass, poses a number of challenges in mechanics which are still being actively investigated. Among them is surface growth or accretion which, following the work of Skalak and others (Skalak et al., 1982, 1997), requires to define and track in time an ever changing, usually stress-free, reference configuration, i.e. collection of material points. The

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phenomenon of accretion of a solid on its boundary, occurs in several contexts of physical, technological, and biological interest. One of the most common examples of surface growth is the solidification of water at the ice-water interface near the freezing temperature; other examples include technological processes such as chemical vapor deposition and 3D printing, layered building (Bacigalupo and Gambarotta, 2012; Zurlo and Truskinovsky, 2017, 2018); in biology, the growth of hard tissues like bones and teeth (Ciarletta et al., 2013; Ganghoffer and Goda, 2018).

A second delicate issue regards the prescription of a growth law. One may simply assume that as given. Conversely, growth speed could be obtained as a result of mechanical and biochemical local conditions. These in turn may be expressed by a suitable kinetic law once the thermodynamical force driving growth is consistently defined (Abeyaratne and Knowles, 1990; Tomassetti et al., 2016).

Third, one may also describe the transport of free particles providing the material constituents for growth. In this way essential features of growth may emerge from the balance of tied mechanical and biochemical responses.

In this work we precisely analyze a one-dimensional model featuring the three aforementioned characteristics, albeit in a simplified manner. We consider an elastic bar fixed at one end and connected to an elastic device at the other. The bar can grow by attaching or detaching its constituting particles (or monomers), at either end. The diffusion of free particles in a surrounding or permeating solvent and the kinetic condition for growth are accounted for. The first objective of this model is to investigate a basic reference template of chemo-mechanical growth which allows to discuss more easily modelling choices, notions and solutions.

The second motivation for this study is provided by a specific biological example, namely the growth of actin filaments. Actin in its polymerized network-forming state is an essential constituent of the cytoskeleton and is involved in cell contraction, division, motility. It is intensely studied in the bio-physical literature. See e.g. Prost et al. (2015) for a review on the physics of active gels like actin, the Ph.D. thesis of Zimmermann (2014) for a review of quantitative models of actin-based motility, and Bindschadler et al. (2004) and Cardamone et al. (2011) for just two of the many examples of different biophysical and computational models of the properties of actin networks. Pertinent to this study, but not including mechanical aspects, is a one-dimensional mathematical model of actin polymerization kinetics by Edelstein-Keshet and Ermentrout (2000).

There are interesting experimental studies (Parekh et al., 2005; Chaudhuri et al., 2007; Bieling et al., 2016) which have a setup similar to the one considered herein: an actin network is grown on a surface below the cantilever tip of an atomic force microscope (AFM) thus realizing a rod-like structure fixed at one end and restrained by an elastic device at the other. Among other things, these experiments consistently suggest that the actin network adapts to higher values of applied compressive force by correspondingly increasing its density and stiffness. This is a feature that is currently not included in our model, but it constitutes a possible refinement for future work.

Actin filaments exhibit a peculiar growth mode called treadmilling in which the length of the filament remains constant while accreting (i.e. adding) actin monomers at one end and ablating (i.e. shedding) them at the other at equal rates (see e.g. Theriot, 2000). This energy dissipating state is made possible by the hydrolysis of ATP (adenosine triphosphate) bound to actin monomers into an ADP (adenosine diphosphate) molecule and a phosphate. Despite its peculiarity, treadmilling may also be seen as a specific instance of a more common biological paradigm by which systems, tissues or organisms continuously substitute their constituents or cells at specific rates even when their overall size is no longer changing.

This work has two main results. First, under general assumptions on the behaviour of the material constituting the bar, it is possible to prove the existence of at most one treadmilling state.

Secondly the stability of such solution is discussed. Herein stability is not addressed geometrically in classical structural mechanics terms (i.e. buckling), but it is instead asked whether perturbations of the treadmilling state may cause the bar to abandon indefinitely its stationary length. It is found that in the latter sense the treadmilling solution is always stable whenever it exists.

These results may hopefully constitute a useful term of comparison and interpretative tool for other more complex models and experiments. For instance, the latter one concerning stability of treadmilling solutions may provide clarification or further evidence in support of the "emergence of a universal growth path" observed in a similar context by Abi-Akl et al. (2018) in a forthcoming paper.

The discussion on stability of the solution has also been motivated by experiments studying the growth and relative stability of an annulus of actin accreting on the surface of a spherical bead (Cameron et al., 1999; Noireaux et al., 2000; van der Gucht et al., 2005). These experiments where in turn inspired by bacterium Listeria monocytogenes which exploits cytoplasmic actin to form a polymerized tail and move out of the cell membrane and spread (Prost et al., 2008). Existing numerical and modelling efforts on this subject can be found in (John et al., 2008; de Buyl et al., 2013).

A model for a spherical annulus of actin growing on the surface of a sphere was formulated by Tomassetti et al. (2016). Therein the treadmilling solutions were characterized as well. A planned continuation of the above study and of the present one is the analysis of stability of the treadmilling solutions of that system.

The article is structured as follows. Section 2 describes the one-dimensional model in its mechanical, chemical and growth aspects. Section 3 provides the material constitutive description of the bar while the derivation of the kinetic laws is given in Section 4. The system is reduced to a differential algebraic equation in Section 5, a form suitable for the discussion concerning the existence and stability of treadmilling solutions carried out in Section 6. Conclusive remarks are made in Section 7.

To finish the introduction I need to add some discussion of the literature. I also want to properly cite the previous work by Tomassetti et al. To be done

after the introduction:

- Derive the kinetic relationships
- Compute the force velocity relationship and see whether it is possible to perform any comparison with experiments (should we also discuss the constant force case in this regard as done by a number of authors?)
- See if we can claim global stability of the treadmilling solution and connect it with Cohen and Abi Akl's result.
- Plan the figures for each section
- Write section together with accompanying figures

sec:model

2. One-dimensional model

subsec:set

2.1. Problem setting

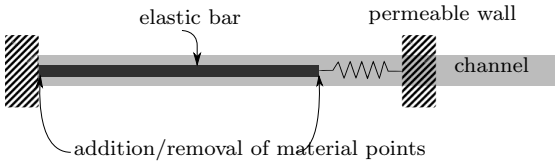

Figure 1: Label left box as "impermeable wall". I don't think we need the permeable wall on the RHS. An elastic bar clamped between a hard and a soft device, immersed in a semi-infinite channel. to be redrawn

fig:01

We consider a one-dimensional body, represented by a bar in Figure 1, which grows and deforms in a one-dimensional physical space.

The bar has a natural reference configuration that occupies the segment $(x_0(t), x_1(t))$ and whose generic point is denoted by x . Here and in the following subscripts 0 and 1 refer to the left and right end sections of the bar respectively, both in the reference and in the current configurations.

As represented in Figure 2, the body is mapped into (?) the physical one-dimensional space through the function $y(x,t)$ where it occupies the segment $(y_0(t), y_1(t))$. Here and in what follows the shorthand notation

$$f_\alpha(t) = f(x_\alpha(t), t) \qquad \text{with } \alpha = 0, 1\ , \tag{1}$$

eq:fam

denotes in general the value of a material quantity $f(x,t)$ at the end sections of the bar at time t. In particular $y_0(t)$ and $y_1(t)$ simply indicate the position of the end sections of the bar in the current configuration.

In regard to constraints, the terminal side x_0 of the bar is attached to the point Y_0 in the physical space, so that $y_0 = y(x_0(t), t) = Y_0$. Likewsie, the terminal side x_1 is attached to one end of a linear spring of stiffness K. The

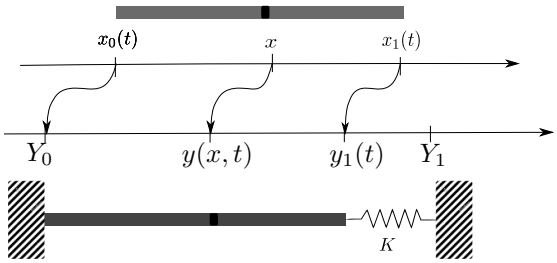

Figure 2: The way the figure is currently drawn, the reader might think the permeable wall is at Y_1. As before, I suggest deleting the permeable wall, and making sure Y_1 does not appear to be any special point of the figure. Reference (top) and current (bottom) configuration of the elastic bar. to be redrawn

fig:02

rest position of this end of the spring is Y_1 , i.e. the spring is unstretched with zero force when this end is at Y_1. Its other end is fixed. It is worth noting that while the left-hand end of the bar is always located at Y_0 in physical space, the right-hand end is located at Y_1 only when the spring force vanishes.

The bar is made of "material units", hereafter referred to as monomers, which are in a bound, polymerized state. The same monomers in a free, unbound state are in solution in the solvent which fills a one-dimensional semi-infinite channel, depicted with a gray-shaded rectangle in Figure 1. Free monomers flow in the interval $(y_0(t), y_1(t)) = (Y_0, y_1(t))$ according to Fick's law. We can think of them as either flowing only through the bar or flowing as well through the portion of the channel not occupied by the bar. They can freely cross the point y_1, where the body is in contact with a reservoir of monomers, but cannot flow past the left support $y_0 = Y_0$ which is assumed to be impermeable. The chemical potential of free monomers at $y_1(t)$ is held fixed and equal to [see margin comment] μ_1, and there is an infinite supply of monomers at y_1.

The symbol μ_1 and M_1 are both used in the manuscript to denote the same quantity $\mu(y_1(t), t)$. I suggest using the symbol M_α for the bound monomers and keeping μ_α for the free monomers.

Finally, under suitable growth conditions to be later specified, free monomers may accrete, i.e. attach, at either end of the bar and conversely, bound monomers occupying the end positions x_0 and x_1 of the bar may ablate, i.e. detach, and return to their free state. When accretion or ablation occurs, the referential points x_0 and x_1, and hence the reference length of the bar, can change. Specifically, at the left-hand end x_0, accretion occurs when $\dot{x}_0 < 0$ while ablation occurs when $\dot{x}_0 > 0$. Similarly accretion and ablation at the right-hand end x_1 correspond to $\dot{x}_1 > 0$ and $\dot{x}_1 < 0$ respectively.

We now specify the equations governing the system just described.

subsec:mech

2.2. Mechanics

We require the deformation mapping $y(x,t) : x \to y$ to be one to one by prescribing that the stretch $\lambda = y' = \partial y/\partial x$ be positive:

$$\lambda(x,t) = y'(x,t) > 0 \,.$$

Here and in the following we use a prime to denote the derivative with respect to a variable other than time ~~for functions of one variable other than time or for functions of time and of an additional variable~~. That is $f' = \partial f/\partial \bullet$ with $f = f(\bullet)$ or $f = f(\bullet, t)$ with t indicating time and $\bullet \neq t$. A superior dot is used, as customary, to indicate the partial derivative with respect to time, i.e. $\dot{f} = \partial f/\partial t$.

~~We do not specify a constitutive law for the bar. We simply~~ We assume the material to be hyperelastic and therefore characterized by a strain energy density $W(\lambda)$ from which we can compute the axial force σ in the bar as

$$\sigma(x,t) = W'(\lambda(x,t)) \ .$$

A number of additional assumptions on the strain energy density are detailed in Section 3.1. Given that W does not depend explicitly on x, ~~it is anyway already evident that~~ the material constituting the bar is taken to be homogeneous.

The mechanical model for the bar is summarized in the set of equations (2) below.

eq:mech

$$\begin{cases} \dfrac{\partial \sigma}{\partial x} = 0 & \text{in } (x_0(t), x_1(t)), \quad (2a) \\ \sigma = W'(\lambda), \quad \lambda = y' & \text{in } (x_0(t), x_1(t)), \quad (2b) \\ y_0(t) = y(x_0(t), t) = Y_0 & \text{in } x_0(t), \quad (2c) \\ \sigma_1(t) + K(y_1(t) - Y_1) = 0 & \text{in } x_1(t) \ . \quad (2d) \end{cases}$$

eq:mech1 eq:mech2 eq:mech3 eq:mech4

Equation (2a) represents ~~the~~ local equilibrium in the reference configuration and ~~it~~ implies that the axial force is constant in x. In eq. (2b) we state again the constitutive law and the definition of the stretch λ. Since σ is constant in x, it follows that λ is constant ~~as well~~ in x and that y is linear in x.

The boundary condition prescribing that the leftmost section of the bar is fixed in $y = Y_0$ is expressed in eq. (2c). The axial force $\sigma_1(t) = \sigma(x_1(t), t)$ in in the bar at $x = x_1(t)$ is prescribed by the force in the spring of stiffness K in eq. (2d). Since σ is independent of x, (2d) actually prescribes the value of the axial force in the whole bar.

We call σ force here and stress later see text below eqn (5). Need to be consistent.

The conclusion that λ is constant assumes $W'(\lambda)$ to be ~~monotonic~~, something we haven't yet said. I suggest we state it in word near the equation above (2) so we can retain the conclusion here as is.

I changed Y_0 to y_0 in (3) since its is then more similar to the solution form in (29). We certainly want to use x_0 in

subsec:diff

2.3. *Diffusion*

eq:diff

The following system Should we use a prime instead of $\partial h/\partial y$ below?

$$\begin{cases} \dfrac{\partial h}{\partial y} = 0 & \text{in } (y_0, y_1(t)), \quad (3a) \\ h + m\mu' = 0 & \text{in } (y_0, y_1(t)), \quad (3b) \\ h(y_0, t) = \varrho \dot{x}_0(t) & \text{in } y_0, \quad (3c) \\ \mu(y_1(t), t) = M_1 & \text{in } y_1(t) \ . \quad (3d) \end{cases}$$

eq:diff1 eq:diff2 eq:diff3 eq:diff4

governs the flux of free monomers in the solvent. Here $h(y,t)$ in the monomer flux in the positive y direction, $\mu(y,t)$ is the associated chemical potential and m is the mobility. The first equation (3a) expresses the conservation of mass. In

it we have omitted a term $\partial h/\partial t$ by assuming that diffusion is much faster than growth. Flux has the dimension of moles per unit time. The second equation (3b) represents Fick's law. The third equation (3c), a boundary balance of mass, states that the flux of monomers at the impermeable wall is equal to the amount of monomers that detach from the left endpoint of the bar per unit time, which in turn is proportional to the ablation velocity $\dot{x}_0$ through a constant ϱ. We think of ϱ as the number of moles of bound actin monomer per unit length in the reference configuration. The fourth equation (3d) expresses the condition of chemical equilibrium at y_1 by equating $\mu(y_1(t), t)$ to the chemical potential μ_1 of the monomers in the semi-infinite monomer pool to the right of y_1. Rohan comment: it was confusing to refer to the bar in this paragraph since this is the flux of free monomers and not bound monomers. So I changed wording. ~~the rightmost point of the bar through a constant, assigned value M_1 of the chemical potential $\mu(y_1(t), t)$~~. Note that $\mu_0 = \mu(y_0, t)$ is as yet unknown and to be determined.

See earlier comment about μ_1 and M_1.

subsec:accr

2.4. Accretion

As anticipated in the Introduction, a key ingredient of this model is the growth law governing the evolution of the referential configuration of the bar. We assume a simple, linear kinetic law of the form

$$B_\alpha V_\alpha = F_\alpha \qquad \text{with } \alpha = 0, 1 \tag{4}$$

eq:kinshort

Rohan comment: moved text from here. In eq. (4), $\alpha = 0, 1$ refer to the ends of the bar, V_α is the accretion velocity, B_α is a positive kinetic coefficient and F_α is the thermodynamical force driving accretion. Note that $V_0 = -\dot{x}_0$ and $V_1 = \dot{x}_1$. Realistically (4) is most suitable for small deviations from thermodynamic equilibrium. The expression for F_α, derived afterwards in section 4, is

$$F_\alpha = \varrho(\mu_\alpha - M_{B,\alpha}) + W^*(\sigma_\alpha), \tag{5}$$

eq:Fa

where σ_α and μ_α are material descriptions of the fields μ, σ evaluated at x_α ~~and~~ following the notation introduced in (1). Parameter $M_{B,\alpha}$ is a material constant interpreted as the chemical potential of bound monomers at x_α and $W^*(\sigma)$ is the complementary strain energy density whose definition and properties are given in Section 3.2. In particular in there we will see that a tensile stress $\sigma > 0$ corresponds to positive $W^*(\sigma)$ thus promoting growth according to (4)-(5). This is consistent with the layman's notion of stress induced growth popularized by images of abnormal growth of earlobes, necks and other body parts subject to sustained tension, especially observed in some indigenous tribes (see e.g. Goriely, 2017, Chapter 2.1).

Motivated by the behaviour of actin filaments, see e.g. Theriot (2000), Add another reference to panel 16-2 in Chapter 16 of Bruce Alberts, Alexander Johnson, Julian Lewis, Martin Raff, Keith Roberts and Peter Walter, Molecular Biology of the Cell, Garland Science, 2002. Suggest another reference.we admit two distinct values $M_{B,0}$ and $M_{B,1}$ for the chemical potential of monomers in

the bound state. Actin monomers are bound to ATP (Adenosine TriPhosphate) when they first polymerize, i.e. accrete, but after some time a hydrolysis reaction ensues by which the ATP releases a phosphate group and the polymerized actin monomer is now tied to an ADP (Adenosine DiPhosphate) molecule. The hydrolysis reaction releases energy, part of which remains stored in the polymerized actin Rohen comment: I don't understand this. On one hand it is released, on the other it is stored?. Therefore ADP-actin is at a higher energy level, i.e. chemical potential, than ATP-actin:

$$M_{B,1} > M_{B,0}. \tag{6}$$

eq:M1M0-order

I don't think introducing the terms barbed and pointed adds anything and is only another set of terms we don't really need. Perhaps put it in the introduction. ~~Due to differences in the properties of opposite ends of actin filaments, respectively called "barbed" and "pointed", the former is usually occupied by a lower-energy ATP-actin monomer and the latter by a higher energy ADP bound actin monomer.~~ Rohan comment: next sentence not needed gives preceding inequality added. ~~Hence the distinction between values of the chemical potential of polymerized actin $M_{B,0}$ and $M_{B,1}$ at the two ends of the bar.~~

As noted previously, a positive accretion velocity corresponds to a negative rate $\dot{x}_0$ and to a positive rate $\dot{x}_1$ whence $V_0 = -\dot{x}_0$ and $V_1 = \dot{x}_1$, and recalling that we are using the notation of equation (1), the specialization of (4) and (5) to the two ends of the bar can be written as

eq:accr

$$\begin{cases} -B_0\dot{x}_0(t) = \varrho(\mu_0 - M_{B,0}) + W^*(\sigma_0(t)), & \text{in } x_0(t), \quad (7a) \\ B_1\dot{x}_1(t) = \varrho(\mu_1 - M_{B,1}) + W^*(\sigma_1(t)) & \text{in } x_1(t). \quad (7b) \end{cases}$$

eq:accr1 eq:accr2

I think we should delete the "in $x_0(t)$" and "in $x_1(t)$" in eqn (7).

Despite the simplicity of the one-dimensional model, the above equations close the feedback loop between stress and growth. On the one hand ~~in fact,~~ the presence of the spring in (2) allows growth to affect stress, while on the other hand, growth rates in (7) are influenced by stress.

The evolution equations (7) also provide closure for the boundary-value problem (2) and (3). In fact, the solution of (2)–(3) depends only on the instantaneous values of $x_0(t)$, $x_1(t)$ and of the rate $\dot{x}_0(t)$. This means, in particular, that the right-hand sides of the equations (7) ultimately depend only on $x_0(t)$, $x_1(t)$ and $\dot{x}_0(t)$. We therefore conclude that the combination of (2), (3), and (7) is equivalent to a first-order system in the unknowns $x_0(t)$ and $x_1(t)$. As such, this system must be complemented by initial conditions

$$x_0(0) = x_{00}, \qquad x_1(0) = x_{10} \quad \text{and} \quad y_1(0) = Y_{10}. \tag{8}$$

eq:xyinit

Reader might expect to see only 2 initial conditions for the system comprised of two 1st order equations. I guess there is another equation hidden away somewhere. Can we help reader understand the need for 3 initial conditions in

sec:const

3. Constitutive behaviour

We assume the bar to be made of a homogeneous, hyperelastic material and we define its constitutive behaviour through the strain energy density function $W(\lambda)$. As seen in equation (2b), the stress σ is given by $W'(\lambda)$ while $W''(\lambda)$ represents the tangent stiffness.

subsec:W

3.1. *Strain energy density*

eq:Wass

A specific expression for $W(\lambda)$ is not prescribed. Instead, we merely assume that the strain energy density has the following characteristics:

$$\begin{cases} W(1) = 0 & & \text{(9a)} \quad \texttt{eq:Wass1} \\ W'(1) = 0 & & \text{(9b)} \quad \texttt{eq:Wass2} \\ W(\lambda) \to +\infty & \text{as } \lambda \to 0^+ & \text{(9c)} \quad \texttt{eq:Wass3} \\ W(\lambda) \to +\infty & \text{as } \lambda \to +\infty & \text{(9d)} \quad \texttt{eq:Wass4} \\ W'(\lambda) \to +\infty & \text{as } \lambda \to +\infty & \text{(9e)} \quad \texttt{eq:Wass5} \\ W''(\lambda) > 0 & \forall \lambda > 0 & \text{(9f)} \quad \texttt{eq:Wass6} \end{cases}$$

~~and~~ discussed in the following.

The strain energy density is defined but for an arbitrary constant which is conveniently set in (9a) by assigning zero energy to the undeformed state in which the stretch λ is equal to 1. In this latter case the stress σ is also zero according to eq. (9b). Equations (9c) and (9d) express the requirement that infinite strain energy is necessary to, respectively, infinitely compress and infinitely extend the material ~~the bar is made of~~. Probably the strongest condition on $W(\lambda)$ is given by eq. (9f) which enforces convexity of the strain energy which in turn implies that the stress is a monotonic function of the stretch, and the tangent stiffness is positive everywhere, i.e. there are no stress softening branches under increasing stretch. Note that $\sigma > 0$ for $\lambda > 1$ and $\sigma < 0$ for $0 < \lambda < 1$. Assuming sufficient regularity of $W(\lambda)$, equations (9c) and (9f) can be used to prove that, when the stretch tends to zero, the stress tends to infinity, that is $\sigma \to -\infty$ when $\lambda \to 0^+$. It is easy to see that conditions (9d) and (9f) are not sufficient to obtain an analogous result for the case in which the stretch tends to infinity. The condition that $\sigma \to +\infty$ when $\lambda \to +\infty$ is therefore explicitly given in (9e). We note in passing that the set of assumptions (9) is introduced in a constructive way and is not minimal since (9d) follows from (9e) and (9f).

From the properties of $W(\lambda)$ ensue those of the stress σ. Let

$$\widehat{\sigma}(\lambda) := W'(\lambda) \quad , \quad \widehat{\sigma}(\lambda) : \mathbb{R}^+ \longrightarrow \mathbb{R} \, . \qquad \text{(10)} \quad \texttt{eq:shat}$$

Rohan comment: inserted period in eqn above. Then from (9f) we know that $\widehat{\sigma}$ is monotonically increasing and, taking into account (9c)-(9e) as well, that it spans the whole real line.

The stress $\widehat{\sigma}$ as a function of the stretch is therefore invertible and function

$$\widehat{\lambda}(\sigma) : \mathbb{R} \longrightarrow \mathbb{R}^+ \, , \quad \widehat{\lambda}(\sigma) \text{ such that } W'(\widehat{\lambda}) = \sigma \qquad \text{(11)} \quad \texttt{eq:lhat}$$

is uniquely defined. It can be easily seen that $\widehat{\lambda}(\sigma)$ is monotonically increasing

$$\widehat{\lambda}'(\sigma) = \frac{1}{W''(\lambda)} > 0 \qquad \text{(12)} \quad \texttt{eq:lhat'}$$

and that it possesses the following properties:

$$\widehat{\lambda}(\sigma) \to 0^+ \text{ as } \sigma \to -\infty, \qquad \widehat{\lambda}(0) = 1, \qquad \widehat{\lambda}(\sigma) \to +\infty \text{ as } \sigma \to +\infty. \qquad \text{(13)} \quad \texttt{eq:lhatprop}$$

subsec:W*

3.2. Complementary strain energy density

The complementary strain energy density $W^*(\sigma)$ is the Legendre transform of $W(\lambda)$. It defined as

$$W^*(\sigma) = \sigma\widehat{\lambda}(\sigma) - W(\widehat{\lambda}(\sigma)) \,, \tag{14}$$

eq:W*def

eq:W*

and has the properties

$$\begin{cases} W^{*\,\prime}(\sigma) = \lambda > 0 & \text{with } \lambda = \widehat{\lambda}(\sigma) \quad (15a) \quad \texttt{eq:W*1} \\ W^{*\,\prime\prime}(\sigma) = \widehat{\lambda}'(\sigma) > 0 & \forall \sigma \in \mathbb{R} \quad (15b) \quad \texttt{eq:W*2} \\ W^{*\,\prime}(\sigma) \to 0^+ & \text{as } \sigma \to -\infty \quad (15c) \quad \texttt{eq:W*3} \\ W^{*\,\prime}(\sigma) \to +\infty & \text{as } \sigma \to +\infty \quad (15d) \quad \texttt{eq:W*4} \\ W^*(0) = 0 & \quad (15e) \quad \texttt{eq:W*5} \\ W^*(\sigma) \to \pm\infty & \text{as } \sigma \to \pm\infty \quad (15f) \quad \texttt{eq:W*6} \end{cases}$$

all of which follow from assumptions we have made previously. The key property of $W^*(\sigma)$ for our purposes is (15a). It ensues from the definition (14) since

$$W^{*\,\prime}(\sigma) = \widehat{\lambda}(\sigma) + \sigma\widehat{\lambda}'(\sigma) - W'(\lambda)\widehat{\lambda}'(\sigma) = \widehat{\lambda}(\sigma) \,.$$

Given that λ is always positive, we have that $W^*(\sigma)$ is a monotonically increasing function. Moreover, (15b) follows from (12) whence $W^*(\sigma)$ is also strictly convex. Properties (15c) and (15d) are simply restatements of (13). Property (15e) follows from the definition of $W^*(\sigma)$ and, together with monotonicity, implies that $W^*(\sigma) > 0$ when $\sigma > 0$ and $W^*(\sigma) < 0$ when $\sigma < 0$. The last property (15f) follows as well from the definition and the preceding properties. It is important because it implies that $W^*(\sigma) : \mathbb{R} \longrightarrow \mathbb{R}$ is surjective, and given the injectivity implied by (15a), also invertible. We will use this result in what follows so it is worth noticing that it is a consequence of the assumptions (9c) and (9e).

sec:kinder

4. Derivation of the driving force

Accretion is a non-equilibrium process involving dissipation. The latter can be computed as the product of a flux, accretion rates in our case, and of a conjugate driving force which quantifies the departure from thermodynamic equilibrium.

In this section we provide the derivation of the expression of the driving force in eq. (5). We follow Tomassetti et al. (2016) and Abeyaratne and Knowles (1990, 1997).

We start from the expression of the dissipation rate associated with the bar, change = to ≔ below

$$\text{dissipation rate} = \sigma \frac{dy}{dt}\Big|_{x_0}^{x_1} + \varrho(\mu - M_B)\dot{x}\Big|_{x_0}^{x_1} - \frac{d}{dt}\int_{x_0}^{x_1} W(\lambda)dx \,, \tag{16}$$

eq:dissdef

which is given by the sum of three terms. The first represents the mechanical power of external loads, the second the inflow of chemical energy per unit time and the third the energy flow per unit time elastically stored in the material and therefore not dissipated.

We observe that the velocity of a point on the boundary is given by Rohan comment: I have edited eqn below.

$$\dot{y}_\alpha(t) = \frac{d}{dt} y(x_\alpha(t), t) = v_\alpha + y' \dot{x}_\alpha = v_\alpha + \lambda_\alpha \dot{x}_\alpha, \tag{17}$$

eq:vel

from which we see that it is distinct from the velocity v_α of a material point sitting at the boundary at the current instant; here $v_\alpha(t) = v(x_\alpha(t), t)$ where $v(x,t) = \partial y(x,t)/\partial t$ ~~and of the velocity of the boundary~~.

Recall earlier comment about μ_1 and M_1. Nice to know (??) the way you have it meaning use μ_1 not M_1.

We rewrite the third term in (16) using Leibnitz's rule (the divergence theorem in one-dimension), transport theorems and equations (2a) and (2b),

$$\begin{aligned} \frac{d}{dt} \int_{x_0}^{x_1} W(\lambda) dx &= \int_{x_0}^{x_1} W'(\lambda)(\dot{y})' dx + W(\lambda)\dot{x}\Big|_{x_0}^{x_1} \\ &= (\sigma \dot{y} + W(\lambda))\dot{x}\Big|_{x_0}^{x_1} . \end{aligned} \tag{18}$$

eq:Wdiv

On substituting equations (17) and (18) into the expression (16) of the dissipation rate we obtain

$$\begin{aligned} \text{dissipation rate} &= (\sigma\dot{y} + \sigma\lambda\dot{x} + \varrho(\mu - M_B)\dot{x} - (\sigma\dot{y} + W(\lambda))\dot{x})\Big|_{x_0}^{x_1} \\ &= (\varrho(\mu - M_B) + (\sigma\lambda - W(\lambda)))\, \dot{x}\Big|_{x_0}^{x_1} \\ &= \Big(\varrho(\mu - M_B) + W^*(\sigma)\Big)\dot{x}\Big|_{x_0}^{x_1} , \end{aligned} \tag{19}$$

eq:diss2

I changed (to (in last line in which the multiplier of the accretive flux $\dot{x}$ is precisely the driving force of growth introduced in equation (5).

sec:DAE

5. Reduction to a differential algebraic equation

Here the system of equations presented in Section 2 is reduced to a differential algebraic equation and new notation is introduced, suitable for the ensuing discussion on the existence and stability of treadmilling solutions.

subsec:DAEmech

5.1. *Mechanics*

Let

$$\ell(t) = x_1(t) - x_0(t) > 0 , \tag{20}$$

eq:ell

be the length of the bar in the reference configuration. The integration of the mechanical system of equations (2) yields

eq:msol

$$\begin{cases} y(x,t) = \lambda(t)(x - x_0(t)) + Y_0, & \forall\ x_0(t) \le x \le x_1(t) \quad (21a) \\ \sigma(t) = W'(\lambda(t)) & (21b) \\ K\lambda(t)\ell(t) = \sigma_{\max} - \sigma(t) & (21c) \end{cases}$$

eq:msol1 eq:msol2 eq:msol3

where we have termed

$$\sigma_{\max} = K(Y_1 - Y_0) \tag{22}$$

eq:smaxdef

the maximum force attainable in the bar and in the spring. Since both $\lambda > 0$ and $\ell > 0$, it follows from (21c) that

$$\sigma < \sigma_{\max}. \tag{23}$$

eq:s<smax

We consider $\sigma_{\max}$ to be an arbitrarily tunable parameter since we can imagine being able to vary the rest position Y_1 of the spring, to the right or to the left of Y_0, to attain any desired value of $\sigma_{\max}$.

From (21a) we have

$$\lambda = (y_1 - y_0)/(x_1 - x_0) = (y_1 - y_0)/\ell \qquad \Rightarrow \qquad (y_1 - y_0) = \lambda\ell \tag{24}$$

eq:lamell

and so, as expected, $\lambda\ell$ denotes the length of the body in physical space.

Equations (21) describe a unique motion $y(x,t)$ and stress $\sigma(t)$ in terms of x_0, x_1. To see it, combine (21b) and (21c) to give Added period below.

$$W'(\lambda) = \sigma_{\max} - K\ell\lambda. \tag{25}$$

eq:lamsol

In light of the assumed properties (9) of $W(\lambda)$, it is readily shown that there exists a unique root $\lambda > 0$ of this equation corresponding to any given $\ell > 0$, $K > 0$ and $\sigma_{\max}$. Moreover in view of (15b), the root λ decreases monotonically with increasing ℓ. The corresponding stress is then given by (21b). These representations will of course involve given values of K, Y_0, Y_1 and the yet to be found values x_0, x_1.

The length ℓ of the body in reference space given through (21c) can be expressed in terms of stress σ as

$$\ell = \bar{\ell}(\sigma) := \frac{\sigma_{\max} - \sigma}{K\widehat{\lambda}(\sigma)}, \tag{26}$$

eq:ls

for all $\sigma < \sigma_{\max}$, where the function $\widehat{\lambda}(\sigma)$ is the inverse of the stress-stretch relation $\sigma = W'(\lambda)$ introduced in eq. (11). In view of (12)-(13), this shows that

$$\bar{\ell}'(\sigma) < 0, \quad \bar{\ell}(\sigma) \to +\infty \text{ as } \sigma \to -\infty, \quad \bar{\ell}(\sigma) \to 0^+ \text{ as } \sigma \to \sigma_{\max}^-. \tag{27}$$

eq:lsprop

The function $\bar{\sigma}(\ell)$ that is inverse to $\bar{\ell}(\sigma)$ obeys

$$\begin{aligned} &\bar{\ell}(\bar{\sigma}(\ell)) = \ell && \bar{\sigma}(\ell) \to \sigma_{\max}^- \quad \text{as} \quad \ell \to 0^+, \\ &\bar{\sigma}'(\ell) < 0 && \bar{\sigma}(\ell) \to -\infty \quad \text{as} \quad \ell \to +\infty \end{aligned} \tag{28}$$

eq:sl

so that in particular as the length ℓ of the bar in the reference configuration increases, the spring is increasingly compressed and the stress σ decreases monotonically.

Would be good to describe the behavior of the mechanical system in physical terms. Bit confusing with $\sigma_{\max} < 0$ and > 0 etc. I haven't quite figured out what I want to say so I have written down anything for your consideration. Suppose during some motion ℓ is increasing monotonically. Then is λ decreasing and ...

subsec:DAEdiff

5.2. *Diffusion*

eq:dsol

The solution of the system of equations (3) yields

See comment earlier about y_1 and M_1.

$$\begin{cases} \mu(y,t) = M_1 \dfrac{y-y_0}{y_1-y_0} + \mu_0 \dfrac{y_1-y}{y_1-y_0}, & \forall\ y_0(t) \le y \le y_1(t) \quad (29a) \quad \texttt{eq:dsol1} \\ h(y,t) = -m \dfrac{M_1-\mu_0}{y_1-y_0} \quad (29b) \quad \texttt{eq:dsol2} \\ \mu_0 = M_1 + \dfrac{\varrho}{m}\,(y_1-y_0)\,\dot{x}_0 \quad (29c) \quad \texttt{eq:dsol3} \end{cases}$$

and we recall that $y_1 - y_0 = \lambda\ell$. Using (21c) and (24) one can express μ_0 in terms of the force σ,

$$\mu_0 = M_1 + \frac{\varrho}{Km}(\sigma_{\max} - \sigma)\,\dot{x}_0\ . \quad (30) \quad \texttt{eq:mu0s}$$

Observe that (30) can be used to eliminate the unknown chemical potential μ_0 from the other equations where its appears, namely (7a), (29a) and (29b).

Finally we note that if x_0 and x_1 are known, then as noted previously y_1 can be determined from (20), (24) and (25), $y_0 = Y_0$ being of course known. If in addition $\dot{x}_0$ is known then the chemical potential and flux fields are fully determined through (29).

subsec:DAEaccr

5.3. *Accretion*

eq:asub

Using (30) and noting that $\sigma_0(t) = \sigma_1(t) = \sigma(t)$, we rewrite the pair of kinetic equations (7) as

$$\begin{cases} \dot{x}_0(t) = -\dfrac{1}{B_0}\dfrac{\varrho(M_1 - M_{B,0}) + W^*(\sigma(t))}{1 + \frac{\varrho^2}{mB_0K}(\sigma_{\max}-\sigma)}, \quad (31a) \quad \texttt{eq:asub1} \\ \dot{x}_1(t) = \dfrac{1}{B_1}\left(\varrho(M_1 - M_{B,1}) + W^*(\sigma(t))\right) \quad (31b) \quad \texttt{eq:asub2} \end{cases}$$

We now introduce forces $\sigma_{\alpha 0}$, $\sigma_{\alpha 1}$ exploiting the bijectivity of $W^*(\sigma)$ in $\mathbb{R}$

$$\sigma_{\alpha 0}\ :\ -W^*(\sigma_{\alpha 0}) = \varrho(M_1 - M_{B,0})\ , \quad \sigma_{\alpha 1}\ :\ -W^*(\sigma_{\alpha 1}) = \varrho(M_1 - M_{B,1})\ , \quad (32) \quad \texttt{eq:salpha}$$

From the monotonicity (15a) of W^*, it follows that

$$\sigma_{\alpha 0} < \sigma_{\alpha 1}. \quad (33) \quad \texttt{eq:sa0<sa1}$$

Further more let the forces $\Delta\sigma$, σ_{asym} be defined by

$$\Delta\sigma \coloneqq \sigma_{\text{asym}} - \sigma_{\max} \coloneqq \frac{mB_0K}{\varrho^2} > 0\ , \quad (34) \quad \texttt{eq:sasym}$$

eq:afin

This allows us to write

$$\begin{cases} \dot{x}_0(t) = R_0(\sigma) \coloneqq -\dfrac{\Delta\sigma}{B_0}\dfrac{W^*(\sigma(t)) - W^*(\sigma_{\alpha 0})}{\sigma_{\text{asym}} - \sigma}, \quad (35a) \quad \texttt{eq:afin1} \\ \dot{x}_1(t) = R_1(\sigma) \coloneqq \dfrac{1}{B_1}\left(W^*(\sigma(t)) - W^*(\sigma_{\alpha 1})\right) \quad (35b) \quad \texttt{eq:afin2} \end{cases}$$

for the accretion rates $\dot{x}_0(t)$, $\dot{x}_1(t)$ as functions $R_0(\sigma)$ and $R_1(\sigma)$ of the force, respectively.

Notice that $\sigma_{\alpha 0}$ and $\sigma_{\alpha 1}$ represent the values of force for which the accretion rates $\dot{x}_0(t)$, $\dot{x}_1(t)$ are zero. Furthermore, since the chemical potential of the solvent bath M_1 can be varied, according to their definitions (32), the values of $\sigma_{\alpha 0}$ and $\sigma_{\alpha 1}$ may also be varied, but not independently. In addition, for the admissible values (23) of the force σ smaller than $\sigma_{\max}$, relation (34) and the monotonicity (15a) of $W^*(\sigma)$ tell us that

$$R_0(\sigma) \lessgtr 0 \ \text{ for } \sigma \lessgtr \sigma_{\alpha 0} \text{ and } \sigma < \sigma_{\max}\,, \quad R_1(\sigma) \gtrless 0 \ \text{ for } \sigma \gtrless \sigma_{\alpha 1}\,. \tag{36}$$

eq:R>0

For $R_1(\sigma)$ we can also easily infer its properties from those of W^*: it is a convex, monotonically increasing function whose image is all $\mathbb{R}$ and whose derivative tends to 0^+ for $\sigma \to -\infty$ and to $+\infty$ for $\sigma \to +\infty$. Thus in particular, $\sigma_{\alpha 1}$ is the unique zero of $R_1(\sigma)$.

Looking at the first derivative of $R_0(\sigma)$,

$$R_0'(\sigma) = -\frac{\Delta\sigma}{B_0}\,\frac{W^*(\sigma) - W^*(\sigma_{\alpha 0}) + W^{*\prime}(\sigma)(\sigma_{\text{asym}} - \sigma)}{(\sigma_{\text{asym}} - \sigma)^2}\,, \tag{37}$$

eq:R0'

we observe that it is strictly negative when conditions $\sigma > \sigma_{\alpha 0}$ and $\sigma < \sigma_{\text{asym}}$ are satisfied.

subsec:DAEeq

5.4. *Differential algebraic equation*

The model under consideration reduces to the following differential algebraic equation Rohan: I have changed the sign on the middle line below.

eq:lsdae

$$\begin{cases} \dot{\ell} = R_1(\sigma) - R_0(\sigma) \\ \quad = \dfrac{1}{B_1}\,(W^*(\sigma) - W^*(\sigma_{\alpha 1})) + \dfrac{\Delta\sigma}{B_0}\,\dfrac{W^*(\sigma) - W^*(\sigma_{\alpha 0})}{\sigma_{\text{asym}} - \sigma}, & \text{(38a)} \quad \texttt{eq:lsdae1} \\ \ell = \bar{\ell}(\sigma) = \dfrac{\sigma_{\max} - \sigma}{K\ W^{*\prime}(\sigma)} & \text{(38b)} \quad \texttt{eq:lsdae2} \end{cases}$$

in which $\ell(t)$ and $\sigma(t)$ are sought under initial conditions, see (8),

$$\ell(0) = x_{10} - x_{00}, \quad \sigma(0) = W'\left(\frac{Y_{10} - Y_0}{x_{10} - x_{00}}\right)\,. \tag{39}$$

eq:lsinit

sec:treadmill

6. Existence and stability of treadmilling solutions

In a so-called treadmilling solution the length ℓ of the bar in the reference configuration does not vary with time: $\dot{\ell} = 0$, and this corresponds to values of the force for which $R_0(\sigma) = R_1(\sigma)$. We distinguish two subcases and analyze them separately.

subsec:sa0>smax

6.1. $\sigma_{\alpha 0} \geq \sigma_{\max}$*: no treadmilling*

In this case it follows from (33) and (23) that

$$\sigma < \sigma_{\max} \leq \sigma_{\alpha 0} < \sigma_{\alpha 1}\,.$$

The inequalities (36) tell us that for values of force in this range, $R_0(\sigma)$ is positive and $R_1(\sigma)$ negative. Thus there is no value of force at which they have the same value. It therefore follows that a treamilling solution does not exist in this case.

If we consider an initial value problem with the bar having some finite material length length $x_{10} - x_{00}$ at $t = 0$, then since $\dot{\ell}$ is negative according to (38a), the bar progressively loses all of its monomers till it reaches $\ell = 0$ and $\sigma = \sigma_{\max}$.

subsec:sa0<smax

6.2. $\sigma_{\alpha 0} < \sigma_{\max}$*: at most one treadmilling solution*

In this case there can at most one treadmilling solution for values of σ between $\sigma_{\alpha 0}$ and $\sigma_{\alpha 1}$. In fact, according to equations (36),(37), we know that both $R_0(\sigma)$ and $R_1(\sigma)$ are negative and monotonic in that range. As shown in Figure 3, R_1 is an increasing function of σ that attains value zero in $\sigma = \sigma_{\alpha 1}$ while R_0 is a decreasing function that has value zero in $\sigma = \sigma_{\alpha 0}$. There is

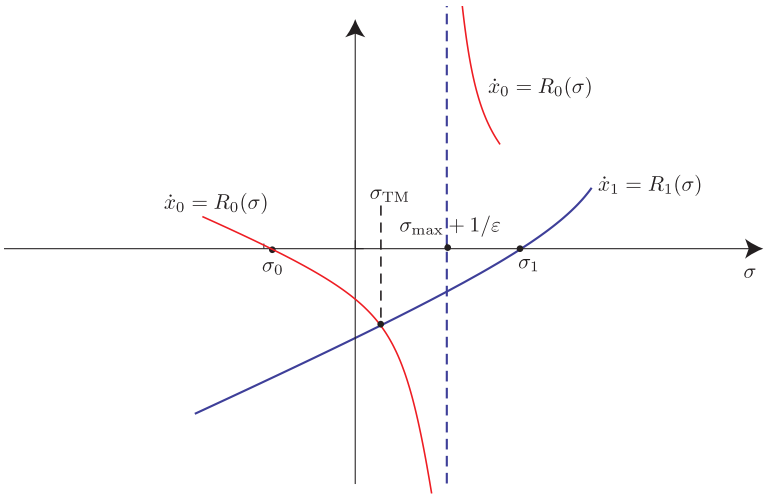

Figure 3: Graphs of $\dot{x}_0 = R_0(\sigma)$ and $\dot{x}_1 = R_1(\sigma)$. The figure has been drawn for the case $\sigma_{\rm asym} < \sigma_{\alpha 1}$ though this is not necessary. Likewise the origin need not be in the interval $(\sigma_{\alpha 0}, \sigma_{\alpha 1})$. To be redrawn.

fig:tm

therefore certainly one value of force called $\sigma_{\rm TM}$ for which R_0 and R_1 have the same values and the material length ℓ of the bar is constant in time. However, for the solution to be admissible, the force $\sigma_{\rm TM}$ in the bar at treadmilling has

to be smaller than $\sigma_{\max}$, see eq. (23), and this occurs if at $\sigma_{\max}$, R_0 and R_1 have already crossed, that is if

$$R_1(\sigma_{\max}) > R_0(\sigma_{\max})\,. \tag{40}$$

eq:tmcond

By substituting eq. (35) into (40) above and exploiting once again the bijectivity of W^*, we can express the condition of admissibility of the treadmilling solution as

$$\sigma_\beta < \sigma_{\max} \tag{41}$$

eq:sb<smax

where

$$\beta = \frac{B_0}{B_1} > 0 \quad \text{and} \quad \sigma_\beta \;:\; W^*(\sigma_\beta) = \frac{1}{1+\beta} W^*(\sigma_{\alpha 0}) + \frac{\beta}{1+\beta} W^*(\sigma_{\alpha 1})\,.$$

From the monotonicity of W^*, it is clear that $\sigma_{\alpha 0} < \sigma_\beta < \sigma_{\alpha 1}$. The definitions of $W^*(\sigma_{\alpha 0})$ and $W^*(\sigma_{\alpha 1})$ are in turn given in eq. (32).

Thus in summary, necessary and sufficient condition for the existence of a treadmilling state under the hypothesis (33) is eq. (41). When this inequality holds, there is a unique treadmilling stress $\sigma_{\rm TM}$ at which

$$\dot\ell = 0 \quad \text{and} \quad \dot x_0 = \dot x_1 = R_0(\sigma_{\rm TM}) = R_1(\sigma_{\rm TM}) < 0.$$

The corresponding stretch $\lambda_{\rm TM}$ is given by $\lambda_{\rm TM} = \widehat\lambda(\sigma_{\rm TM})$; the growth rates at the two ends are $\dot x_0^{\rm TM} = \dot x_1^{\rm TM} = R_0(\sigma_{\rm TM}) = R_1(\sigma_{\rm TM})$; the length of the body in reference space is $\ell_{\rm TM} = (\sigma_{\max} - \sigma_{\rm TM})/(K\lambda_{\rm TM})$; the length of the body in physical space is $\lambda_{\rm TM}\ell_{\rm TM}$; and the chemical potential at the growing end is $\mu_0^{\rm TM} = M_1 + \varrho(\sigma_{\max} - \sigma_{\rm TM})\dot x_0^{\rm TM}/(Km)$.

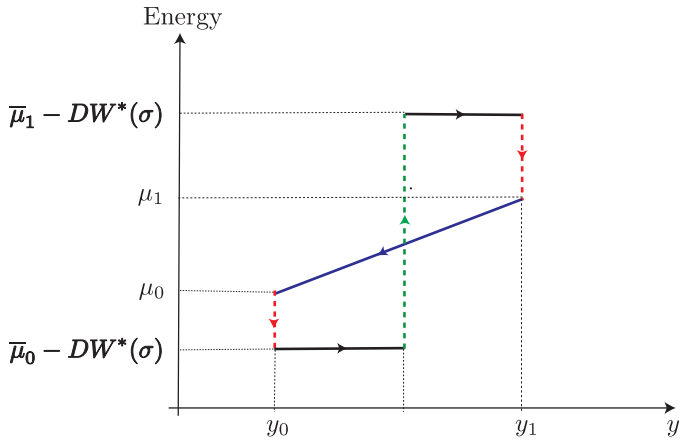

Figure 4: Energy of a monomer unit as it undergoes treadmilling. To be redrawn and described in the text.

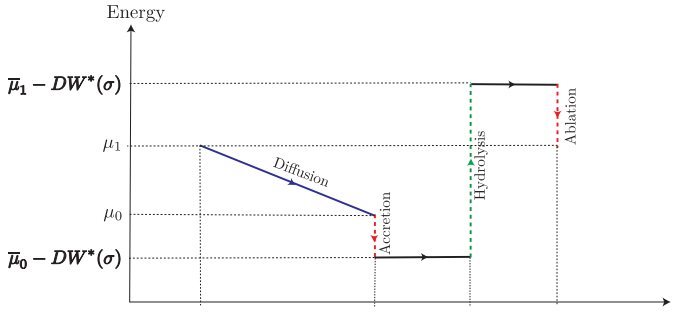

Figure 5: Energy of a monomer unit as it undergoes treadmilling.To be redrawn and described in the text.

6.3. Stability of treadmilling state

We now perturb the treadmilling state described in the preceding subsection. The perturbation of equation (11), $\lambda = \widehat{\lambda}(\sigma)$, yields

$$\delta\lambda = \widehat{\lambda}'(\sigma_{\rm TM})\delta\sigma$$

Operating analogously on equation (21c), $K\lambda\ell = \sigma_{\max} - \sigma$, gives

$$K\widehat{\lambda}(\sigma_{\rm TM})\delta\ell + K\ell_{\rm TM}\delta\lambda = -\delta\sigma$$

Combining the two preceding equations provides a relation between the perturbations $\delta\ell$ and $\delta\sigma$,

$$K\widehat{\lambda}(\sigma_{\rm TM})\,\delta\ell + \left(K\ell_{\rm TM}\widehat{\lambda}'(\sigma_{\rm TM}) + 1\right)\,\delta\sigma = 0. \tag{42}$$

eq:psell

From the expression (38a) of $\dot{\ell}(\sigma)$ we obtain

$$\delta\dot{\ell} = (R_1'(\sigma_{\rm TM}) - R_0'(\sigma_{\rm TM}))\;\delta\sigma.$$

Combining this with (42) yields

$$\delta\dot{\ell} = -F(\sigma_{\rm TM})\delta\ell \qquad \text{where} \quad F(\sigma_{\rm TM}) = \frac{R_1'(\sigma_{\rm TM}) - R_0'(\sigma_{\rm TM})}{K\ell_{\rm TM}\widehat{\lambda}'(\sigma_{\rm TM}) + 1}\,K\widehat{\lambda}(\sigma_{\rm TM}).$$

The treadmilling solution is stable if the ordinary differential equation $\delta\dot{\ell}(t) = -F(\sigma_{\rm TM})\delta\ell(t)$ has exponentially decaying solutions[1], and this occurs if and only if $F(\sigma_{\rm TM}) > 0$. Since $\widehat{\lambda}(\sigma_{\rm TM}) > 0, \ell_{\rm TM} > 0$ and $\widehat{\lambda}'(\sigma_{\rm TM}) > 0$ it follows that the treadmilling solution is stable if and only if

$$R_1'(\sigma_{\rm TM}) > R_0'(\sigma_{\rm TM}). \tag{43}$$

[1] If $\delta\ell(t)$ vanishes exponentially then so do the perturbations of the various other quantities.

It is illuminating the use the monotonic relation (26) between the stress σ and the referential length ℓ to re-plot Figure 3 on the $\ell, \dot{\ell}$-plane. This effectively involves (a) reversing the direction of the σ-axis since ℓ decreases monotonically when σ increases, and (b), since $\ell = x_1 - x_0$, plotting the difference $\dot{\ell} = \dot{x}_1 - \dot{x}_0 = R_1(\sigma(\ell)) - R_0(\sigma(\ell))$ on the vertical axis. This is shown schematically in Figure 6. Observe how, if $\ell > \ell_{\rm TM}$ at some time then $\dot{\ell} < 0$ and so $\ell(t)$ will decrease until it reaches the treadmilling value $\ell_{\rm TM}$. Likewise if $\ell < \ell_{\rm TM}$, $\ell(t)$ will increase to $\ell_{\rm TM}$.

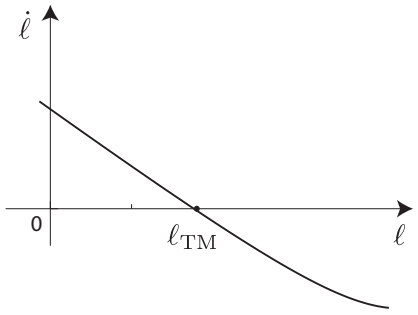

Figure 6: Graph of $\dot{\ell} = \dot{x}_1 - \dot{x}_0 = R_1(\sigma(\ell)) - R_0(\sigma(\ell))$ versus ℓ where $\sigma(\ell)$ is given through (21c). fig:ell

sec:end

7. Conclusions

Acknowledgements

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sec:appA

Appendix A. Examples of strain energy densities

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