Dynamical Riemannian Geometry and Plant Growth

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1 Introduction

Mathematical modeling of biological systems has, in recent years, caught the attention of an eclectic mix of biologists, mathematicians, computer scientists and physicists. The variety and complexity of problems encountered so readily in Nature makes biological models an excellent test-bed for nonlinear dynamics, statistics and a number of abstract computational theories. In plant leaves, features such as ruffles, symmetric vein patterns and buckling have not been explained at the cellular level, and despite displaying geometric elegance, have only been examined mathematically in a handful of descriptive, rather than predictive ways. It is our aim to fully describe the structure of plant leaves using the techniques of differential geometry, fluid flow mechanics and numerical simulations.

There are two main assumptions that provide the basis for such an analysis. The first is that the cells that make up a plant leaf are vanishingly small compared to the size of the leaf, so that a leaf can be described as a 2-dimensional differentiable manifold embedded in a flat, 3-dimensional space. The second assumption is that nutrients and hormones are distributed continuously throughout the leaf. Indeed, biological data supports this assumption, and it has been a key component of previous work done in the study of plant growth [1]. Interpreted mathematically, such an assumption permits the use of flow equations to describe the dynamics of nutrients, hormones and growth in the leaf. Combining the two assumptions, the problem of leaf growth can be explored as transport of material on a curved background space.

Though it is relatively straightforward to choose physical assumptions to work with, we cannot forget that the goal is to model an intricate living system. The fact that leaves are often symmetric in vein patterns and shape is particularly striking, since in physics a symmetry indicates a conserved quantity. Does symmetry in growth allow for an efficient plant? Furthermore, how does the geometry of a leaf affect the flow of nutrients and hormones in a plant, and hence its growth? Indeed, these types of questions require the factual knowledge of biology as well as insights into the geometric structure of plants.

Even from these simple considerations, we already see the purpose of this work is twofold. On the one hand, we have started with a simple, unanswered question in biology that

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might well be asked by a child: why are leaves shaped the way they are? Our approach, however, incorporates mathematics that is common to many physical systems but in itself is only partially understood. By having a physical system to emulate using our equations, we hope to not only discover how geometry presents itself in Nature, but also gain a better understanding of the equations that scientists in a variety of disciplines use today.

2 The Geometry and Growth of Plants

Interest in plant geometry and growth is by no means a new field of study. Scientists have tried to quantify both how plants grow and what is is that might determine their geometry for the past century, with efforts coming from three main directions: computer science, quantitative biology and structural mechanics. The approaches to understanding plant geometry range from static models involving single rule based models to analogues with mechanical systems. Similarly models of growth can focus on the cellular scale to the organism over all where continuum systems are applied. An all too brief review of some of the approaches which have had an influence on what will follow is given below.

2.1 Static Geometric Models

2.1.1 Growth and Form - Mapping One Species to Another

In 1917, biologist D'Arcy Thompson published a seminal work titled 'On Growth and Form' [2]. In it he argued that speciation can be understood in terms of geometry, mechanics and basic physical principles. With striking visual examples, he shows that simple mathematical transformations lead to variations in form that we perceive as different species. Though not outwardly contesting Darwin's ideas, which were already dominant at the time, Thompson does emphasize that efficient geometries are found everywhere in the natural world, thereby pointing to principles other than just the survival of the fittest in shaping new generations of plants and animals. In the 1000 plus pages of his work, Thompson discusses and derives the mathematics of a myriad of different phenomena: honeycomb packing, logarithmic spirals of shells, stress lines in bones (and how these can be used to build better bridges), cell structure, et cetera, et cetera.

Thompson did not, however, postulate a testable model for his observations. True to the spirit of early 20th century biologists, his work was to catalogue and describe. Although the word "growth" appeared in the title of his manuscript, very little discussion of the mechanism for growth was provided. However, his underlying motive of understanding organisms through the prism of geometry was incredibly original for its time, and is especially close to the concept we attempt to work with. Indeed, it has already been a source of inspiration for many students of biomechanics and quantitative biology.

2.1.2 L-Systems

L-systems, named after Aristid Lindenmayer, are algorithms for describing the fractal nature of many plants [3]. They arise from formal grammars where a plant is represented by a string of symbols which signify, for example, a stem and branches.

A formal grammar is an algorithm that acts on a set of symbols. From an initial string, each iteration of the algorithm generates a new string. For example, one can start with the symbol S and the rule $S \to qS$, which leads to the string qqqqqqqS after seven iterations. For a stem S with branches b, one could try starting with S and the rule $S \to SbS$. The first three iterations are: SbS, SbSbSbS, SbSbSbSbSbSbS.

As can be seen even with a few simple examples, this type of recursive algorithm readily gives self-similar patterns. The connection to plants is that they often display self-similar, fractal patterns. Indeed, L-systems produce intricate models of tree branches, simple shrub plants and flowers. With the addition of a few parameters to control things like branching angle, rate of growth and the like, a multitude of realistic plant models can be produced.

The focus of L-systems, however, is on the large scale architecture of a plant rather than the individual parts of a plant. Hence, our chosen approach is complimentary to L-systems and is aimed at the next smallest level of plant form.

2.2 Fitting to Given Time Dependent Functions

In many cases, plant growth undergoes three separate phases. Initially the growth is slow and as the plant matures it goes through rapid growth stage, after which it slows to reach a maximum size. In some cases the plant will shrink in its old age. The general shape of a growth curve can be described by a sigmoidal function of time. Different sigmoidal functions (e.g. Gompertz, logistic, error, arctan, hyperbolic tangent, etc.) have been used to model the growth patterns observed in plant structures. Associated with these functions are various parameters that hopefully one can relate to actual measurement processes. However, the functions do not arise out of a dynamic model, where different variables are evolved from initial data (along with a set of appropriate spatial boundary conditions). The functional models provide a means for classifying growth but unfortunately are unable to provide information about what interactions among the dynamical variables control growth.

2.2.1 Observations of Tobacco Leaf Growth

Since the early 1930s, particular interest has been devoted to documenting the growth and morphology of tobacco (*Nicotiana tabacum*) leaves [4]. The earliest experiments were done by J.S. Huxley who imprinted regularly spaced ink dots on a maturing tobacco leaf and monitored how these dots moved relative to each other as the leaf grew. This lead directly to the ideas of relative growth rates rather than absolute growth rates, and hence the first steps toward a differential and geometric approach of analysing plants.

In later decades, a common genetic cause for growth was found for plants, and studied most intensively in tobacco and arabidopsis plants. Tests on these plants have verified that the growth hormone auxin is responsible for the rate of plant growth. If genes governing the production of auxin are turned off, the resulting plant is stunted to a fraction of its normal height. Conversely, if auxin levels are increased by, for instance, physically applying more auxin to localized areas on a leaf, that portion of the leaf will grow much faster.

In more recent tobacco leaf research, biologists have been able to describe in great detail the steps of tobacco leaf growth by examining it cell by cell. Others have even attempted to characterize the time evolution of certain plant parameters (notably the relative growth rate) by fitting regression functions to plant growth data [5]. Hence, the growth of a tobacco leaf is known from a macroscopic scale down to the cellular level, but only in a descriptive capacity. This details, however, are of great value in our research because they provide trustworthy data to emulate.

2.3 Edge Buckling due to Mechanical Stresses

Another recent development on the biomechanical front has been to look at how stresses in a 2-dimensional sheet yield buckling patterns along its edges [6]. The stresses can be produced either by tearing a sheet while it is under tension, or by increasing the amount of material on the sheet along its edge. Both approaches yield ruffled patterns similar to a lettuce leaf edge, and have a fractal structure. Despite visually accurate patterns and control parameters that produce a variety of shapes, the basic mechanisms used here explain only the final shape of a surface and not its development from one surface to another.

2.4 Continuum Mechanics Approach

One of the first attempts at using continuum dynamics to describe plant growth were published by W. Silk and R. Erickson [1] in the late 1970s. Their arguments rested on employing a continuity equation when describing various parameters in plants like hormone distributions. Indeed, the experimental data they use shows continuous distributions, especially when materials are averaged over the whole cell, indicating that the cells transfer materials between each other rather than concentrating materials more in certain cells than others. This is not so surprising - cells have permeable walls and the materials passed between cells are in a water solution.

The other emphasis in Silk and Erickson's work is on choosing between Eulerian and Lagrangian representations of the coordinates on which the equations exist. In an Eulerian system, the coordinates are external to the plant (i.e. the plant has been put inside a box with, say, a Cartesian system on its axes). In a Lagrangian system, the coordinate origin is bound to a particular feature of the plant, for example the apex of the stem. As Silk and Erickson show, the latter representation often reveals stationary material distributions that an Eulerian system would not show as readily. In terms of what different observers perceive, these results tell us that an external observer would see materials pushed towards the growing regions of the plant, while the plant experiences a constant supply of the materials it needs to grow at a certain rate.

Silk and Erickson did not take their research into the realm of testing predictions, but were able to describe certain elements of plant growth in the language of fluid mechanics. Their approach is the closest to the one proposed in this work; they showed preliminary results that indicate the validity of fluid dynamics in modeling plant growth. What Silk and Erickson did not consider is how the curved geometry of the plan leaf can affect the material distributions therein. This aspect will be a main focus of our work.

3 Constructing A Dynamic Geometric Model

3.1 Leaves as Differentiable Manifolds

The mathematical analysis of a surface requires defining a continuous space of appropriate dimension to the problem at hand. Once a space, or manifold, has been defined, the tools of differential geometry can be employed to explore the properties of that space.

These tools of differential geometry all stem from considering calculus on a curved space. Of particular interest for our purposes is correctly defining dynamics - quantities that change over space and time - in curved space. Essentially, one would like to know how the dynamics of a system are changed because of it's curved geometry, and how the geometry reacts to the dynamics when the system is set in motion.

A good illustration of this principal is found in general relativity, where the dynamics of particles are affected by the curvature of spacetime, but the sources of curvature are massive particles. Hence, there is constant feedback between the moving, massive particles and the geometry of the spacetime they move through.

In the case of plants, the geometry of a leaf or tendril clearly affects the motion and deposition of material through it. Correspondingly, though, where material (such as water and nutrients) travel to dictates how the plant will grow and hence its geometry.

We cannot, however, omit the fact that plants are inherently discontinuous at the cellular level, whereas differentiable manifolds are by definition smooth. In this point rests our aforementioned first assumption: that at a macroscopic level, the geometry of plants can be described by a smooth geometry. Indeed, it is plain to see that under normal circumstances, plants do look smooth to our eyes. Moreover, cells are themselves flexible and all but the hardest ones can bend, elongate or compress to accommodate the general shape of the leaf or tendril. Finally, in analogy to theoretical physics, we currently know that at the smallest scales our universe is discontinuous and governed by quantum mechanics, but we also know that large-scale dynamics are accurately represented by general relativity. Since the question pursued in this work pertains to the macroscopic geometry of plants, it is not unfounded to apply the corresponding mathematics of differential manifolds to attempt a solution.

3.2 Mathematical Preliminaries - Riemannian Geometry

In this section the fundamentals of Riemannian Geometry are introduced in preparation for what follows. The basic geometrical object in Riemannian geometry is the metric tensor \mathbf{g} with components $g_{ik}(\mathbf{x})$. Given a set of coordinates $\{x^i\}$ (i=1,n) that describe points on a n-dimensional manifold (geometry), the distances ds between infinitesimal coordinate displacements dx^i are given by:

$$ds^2 = g_{ik}dx^i dx^k. (1)$$

where the Einstein summation notation is used such that any pair of repeated indices implies a summation using that index over the range from 1 to n. It must be remembered that the coordinates themselves do not determine the distances between them unless the metric components are exactly one. For example one often uses angular coordinates θ to

distinguish between points on a circle of radius R. The distance between θ_2 and θ_1 along the circle however is given by $\Delta s = R\Delta\theta$ where $\Delta\theta = \theta_2 - \theta_1$. The factor multiplying the difference in the coordinates is represented by a metric coefficient.

As a basic example, let us take flat 2D space with the Cartesian coordinates (x, y). The distance between two points is

$$ds^2 = dx^2 + dy^2, (2)$$

from which we can read the coefficients of the metric tensor to be $g_{11} = 1 = g_{22}$ and $g_{12} = 0 = g_{21}$. Often, the metric tensor for an *n*-dimensional space is represented by an $n \times n$ symmetric array. The flat space metric is then

$$\eta_{ik} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \tag{3}$$

In curved geometries, a non-tensorial quantity called the affine connection is required to ensure that derivatives of tensor quantities also form tensors. In general, partial derivatives of tensor quantities are not themselves tensors. The connection coefficients are objects that allow one to form tensor derivatives (also called covariant derivatives) through a cancellation of the non-tensorial terms appearing in the partial derivatives. If the connections are determined from the metric tensor they are often called Christoffel symbols and are are determined from a combination of partial derivatives of the metric by:

$$\Gamma_{bc}^{a} = \frac{1}{2}g^{ad} \left(\frac{\partial g_{bd}}{\partial x^{c}} + \frac{\partial g_{dc}}{\partial x^{b}} + \frac{\partial g_{bc}}{\partial x^{d}} \right). \tag{4}$$

To complicate matters even further, the components of vectors and higher order tensors will depend on whether they are computed with respect to the coordinate displacements (contravariant components), or with respect to directions orthogonal to the coordinate displacements (i.e. as gradients and known as covariant components). The tensor transformation laws for the components will depend upon how the components are computed, and the derivatives of the tensor components will depend upon how the the non-tensorial partial derivative terms are removed.

The covariant derivatives of covariant and contravariant components of a vector \mathbf{A} are given by:

$$\nabla_k A_i = \frac{\partial A_i}{\partial x^k} - \Gamma^j_{ik} A_j \tag{5}$$

$$\nabla_k A^i = \frac{\partial A^i}{\partial x^k} + \Gamma^i_{jk} A^j. \tag{6}$$

respectively.

On a curved manifold covariant derivatives do not commute (although mixed partial derivatives do). A measure of the strength of the non-commutativity for a covariant vector is given by the Ricci identity.

$$\nabla_i \nabla_j A_k - \nabla_j \nabla_i A_k = R_{kij}^{\ell} v_{\ell}$$

where R_{kij}^{ℓ} is the Riemann curvature tensor given by:

$$R_{jk\ell}^{i} = \frac{\partial \Gamma_{j\ell}^{i}}{\partial x^{k}} - \frac{\partial \Gamma_{jk}^{i}}{\partial x^{\ell}} + \Gamma_{j\ell}^{m} \Gamma_{mk}^{i} - \Gamma_{jk}^{m} \Gamma_{m\ell}^{i}.$$

Another measure of curvature is provided by the Ricci curvature tensor $R_{ik} = R_{i\ell k}^{\ell}$ or:

$$R_{ik} = \frac{\partial \Gamma_{ik}^m}{\partial x^m} - \frac{\partial \Gamma_{im}^m}{\partial x^k} + \Gamma_{ik}^n \Gamma_{nm}^m - \Gamma_{im}^n \Gamma_{nk}^m.$$
 (7)

which can be thought of as a metric weighted average of the Riemannian curvature. The advantage of the Ricci tensor is that it has fewer components, is easier to compute and has the same transformation properties as the metric tensor. It does have the disadvantage of sometimes being identically equal to zero even though the Riemann tensor components from which it is constructed may be non-zero.

The curvature tensors constructed above are called intrinsic curvature measures since they are computed only from information contained in the metric components within the manifold's geometry. There is no reference to higher dimensional spaces within which the *n*-dimensional manifold might be embedded. Therefore whether a geometry is curved or not is something that can be computed from the properties of the geometry itself. Thus Riemann was able to complete Gauss' programme which was to provide a method of determining the curvature of a surface (e.g. that of the Earth) without having to go off of the surface into a three dimensional embedding space.

Due to a remarkable series of theorems [7] it has been shown that any Riemannian space can be embedded into a higher dimensional flat (non-curved) space. In many cases the dimension of that flat space is N = n + 1 although there are important exceptions where the dimension of the embedding space may be even higher.

3.3 Dynamical Riemannian Geometry

The next step in constructing a dynamical or time evolving geometry is determine the equations that govern the time dependence of that geometry and the objects that couple to the geometry. Once again, Einstein's theory of general relativity is provides one possibility where the 4-dimensional (pseudo-Riemannian) manifold is described by a single time coordinate in addition to three spatial coordinates. Due to the symmetry between space and time, the general properties of the Einstein equations are that they are essentially hyperbolic. This means that gravity can change due to the propagation of waves that carry information at a finite velocity from one point in the manifold to another.

On the other hand biological (and chemical) processes occur through diffusive flows which are governed by parabolic equations. Fortunately so-called curvature flow equations have exactly this this property. The best known case is the Ricci flow where the evolution of the metric is determined directly from the Ricci tensor by

$$\frac{\partial g_{ik}}{\partial t} = \kappa R_{ik}.\tag{8}$$

where κ is a real constant. Pure Ricci flow (with $\kappa - 2$) describes spaces that contract in the direction of positive curvature and expend in the direction of negative curvature.

Note that this PDE has both a diffusive and reactive term. In fact this is no coincidence. In the early 1980's, the mathematician R. Hamilton [8] wrote down the equation for Ricci flow so that manifolds could be evolved through a heat-like process to find out if an arbitrary manifold is isomorphic to some simpler geometry by smoothing out the irregularities of the arbitrary manifold. Just as a hot spot in a metal rod will diffuse until the rod is equally heated throughout its length, a curved manifold can diffuse its curvature, causing a time evolution of the space that effectively flattens it out. The motivation for introducing Ricci flows was initially to provide an application to the Thurston geometrization conjecture [9] which subsequently led to the resolution of the Poincaré conjecture [10].

While Ricci flow is a purely intrinsic flow, extrinsic (or mean) curvature flow provides an alternative set of differential equations for the metric in terms of the coordinates of the higher dimensional space within which the original space is embedded. Assuming that the coordinates of the higher dimensional space are given by $X^{\mu}(\mathbf{x})$ (where Greek indices $\mu = 1, \dots, N$ are used to label coordinates in the higher dimensional embedding space), the components of g_{ik} can be written as:

$$g_{ik} = G_{\mu\nu} X^{\mu}_{,i} X^{\nu}_{,j}$$

where $X^{\mu}_{,j} = \partial X^{\mu}/\partial x^{j}$ and $G_{\mu\nu}$ is the metric tensor of the embedding space which is often taken to be the flat space metric, $\eta_{\mu\nu} = \mathrm{diag}(\pm 1, \cdots, \pm 1)$.

Following the results of Tapia [11] one can translate the mean curvature flow equations:

$$\frac{\partial \mathbf{X}}{\partial t} = \nabla^2 \mathbf{X}$$

(where the indexed coordinates X^{μ} have been replaced by the vector \mathbf{X} , and the Laplacian operator, $\nabla^2 = g^{ij} \nabla_i \nabla_j$) into a flow equation for the metric \mathbf{g} :

$$\frac{\partial g_{ik}}{\partial t} = \kappa \nabla^2 \mathbf{X} \cdot \nabla_{ij} \mathbf{X}.$$

In the above equation the inner product represented by the \cdot operator is taken with respect to $\eta_{\mu\nu}$.

Curvature flows have primarily remained in the realm of mathematicians, and are just beginning to be applied in physical contexts [12]. The intuition behind curvature flows for botanical growth seems appealing, though, when one considers that young plants, often with tightly curved leaves, must somehow develop into mature, flatter leaves; in other words, a plant's geometry and curvature are time dependent. A curvature flow process would at once be an elegant and physically motivated application of such a theory.

For most cases leaves and petals when considered on the large scale have negligible thickness and can therefore be considered as 2-dimensional surfaces. A 2-dimensional manifold is also *conformally flat*. This means that the metric can be written in a form where a single function of the spatial coordinates multiplies the 2-D flat metric described above. This is consistent with the fact that the Riemann curvature tensor in 2-dimensions has only one independent component. Thus introducing a set of two spatial coordinates

(u, v) the metric on any 2-D structure can be written in terms of a single scale factor f(u, v; t).

$$g_{ik} = f(u, v; t) \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \tag{9}$$

The fact that f is time dependent indicates that the distances between points on the manifold can change over time. Clearly, working with a single function rather than three independent parameters is always advantageous, and will prove to be so in subsequent calculations.

The Ricci tensor describing the curvature of this manifold at any moment in time also has one independent component given by:

$$R_{11} = R_{22} = \frac{\kappa}{2f} \left[\frac{\partial^2 f}{\partial u^2} + \frac{\partial^2 f}{\partial v^2} - \frac{1}{f} \left[\left(\frac{\partial f}{\partial u} \right)^2 + \left(\frac{\partial f}{\partial v} \right)^2 \right] \right]$$
(10)

Just as a 2D space will be used when considering leaves, a 1D space can be used to represent roots and tendrils, and spaces that have a symmetry in one of their two coordinates. The metric tensor for a 1D manifold is even simpler than in the 2D case as there is only one coordinate axis and only one parameter that describes how the manifold is shaped:

$$g_{11} = f(u;t). (11)$$

3.4 Coupling Material Flow, Growth and Geometry

The basic premise on which Silk and Erickson based their study of plant growth was that material flow in the leaf should be governed by the laws of material transport. This makes sense since the leaf relies on the flow of nutrients and growth hormones to each cell in order to grow. The cells in turn create more cells through cell division and this accounts for the increase in spatial dimensions. Furthermore, the growth is symplastic. That is the cell growth and formation is smooth and coordinated in such a away that the cells once formed do not migrate. This makes the continuum description easier than in the case of animal tissue growth where the cells can slide over one another. The equations governing tissue growth should account for the flow of material throughout the medium as well as the change in distances between fixed coordinate locations on the body. It is therefore natural to impose a metric whose coefficients depend on both space and time.

Since plant growth is an example of an open, non-equilibrium dynamical system, we apply the philosophy presented in Kardar's text [13] that the equation of motion is the fundamental object of interest in describing systems that lack a Hamiltonian formulation. The equations of motion should include all terms consistent with the symmetry of the problem since "in a generic situation an allowed terms is present and only vanishes by accident". Furthermore for a spatio-temporal field $h(\mathbf{x},t)$ one can expect that in the presence of dissipative dynamics and over long enough time scales inertial terms (i.e. those proportional to $\partial_t^2 h$) are irrelevant.

In general the evolution of h is governed by an equation of the form:

$$\partial_t h(\mathbf{x}, t) = f[h, \mathbf{x}, t] + \phi[\mathbf{x}, t]$$

where the first term on the RHS governs the deterministic dynamics and the second introduces stochastic terms. If the interactions are short ranged the driving terms in the function f at (\mathbf{x}, t) depends on h and a few low order spatial derivatives:

$$f[h, \mathbf{x}, t] = f[[h(\mathbf{x}, t), \nabla h(\mathbf{x}, t), \cdots \mathbf{x}, t]]$$

Therefore we can expect a feedback system where the flow of material during growth creates stresses that change the leaf's geometry which in turn affects the rate of flow of material.

Once again, this is not that far removed from the ideas of general relativity. In the context of spacetime, Einstein postulated that the movement of massive objects such as planets, stars and galaxies is governed by the shape of the spacetime through which they move, but that the geometry of spacetime is shaped by massive objects residing in it.

When the plant leaf is viewed as a curved 2-dimensional space, then it is natural to think of the material flowing on it as reacting to the curvature it must navigate, just as we react to the curved spacetime around our planet by experiencing gravity. This aspect is, however, missing from Silk and Erickson's work, in which they applied fluid flow like models based in a flat background space.

In order to incorporate curvature effects into a fluid flow model, we must translate our assumptions into valid differential equations involving tensors quantities, such as scalars, vectors and higher rank tensors. Tensor equations, when properly formulated, are invariant with respect to arbitrary coordinate choices and therefore provide fundamental relationships between dynamical variables. By extending the theory of Silk and Erickson we introduce three dynamical variables, (1) the metric tensor which describes the geometry of the curved manifold that makes up the biological organ, (2) the material flow velocity of the material that causes the growth of the organ itself and (3) the density of the material that makes up the organ. Each variable will depend on both spatial and temporal coordinates and equations of motion will be developed tin a manner following the guidelines discussed in the preceding paragraphs.

The equation for the the evolution of the metric tensor, describes changes in the leaf's geometry in response to the stresses induced by the flow of material in the leaf. In addition the curvature of the leaf may also induce changes in the metric tensor. A vector equation for the velocity field of the material flowing on the leaf should include diffusive, advective, damping, pressure and external force terms, as well as a reaction of the flow to the leaf's geometrical structure. Finally, a scalar equation for the density of the material that makes up the leaf can be written should be in the form of a continuity equation having both sources and sinks. If tensorial equations are to have an intrinsic meaning, they must be independent of the the coordinates chosen to describe of measure the components of the objects in question. Therefore we will develop a set of dynamical equations where the variables in the equations all obey the same transformation rules. Such a restriction requires the use of self-consistent expressions not only in the actual dynamical variables but also in how their derivatives with respect to spatial coordinates appear in the equations.

First, let us construct the equation for the evolution of the metric. We would like the geometry of the leaf to respond to the flow of material. In other words, a change in the flow of material should affect the time evolution of the geometry:

$$\frac{\partial g_{ik}}{\partial t} \propto \nabla_i v_k + \nabla_k v_i. \tag{12}$$

In biology, $\partial v^k/\partial x^i$ (or in this case its covariant equivalent $\nabla_i v_k$) is called the growth tensor [14], and can be measured experimentally. It is a measure of how the velocity field on the leaf varies spatially. In continuum mechanics, $\gamma_{ij} = 1/2(\partial v_i/\partial x^j + \partial v_j/\partial x^i)$ is the deformation tensor or in fluid dynamics the strain rate tensor. Since a Riemannian metric tensor g_{ik} is itself symmetric, a symmetrized form of the growth tensor (i.e. the strain rate or deformation) is introduced to account for this fact. From a dimensional analysis point of view the time derivative of the metric has units of inverse time, exactly those units for the growth tensor.

Likewise, the curvature of the plant should be able to change over time, changing from a highly curved young leaf to a more flat mature leaf. This is where curvature flow affects the geometry and this represents a nonlinear feedback of the geometry back onto itself:

$$\frac{\partial g_{ik}}{\partial t} \propto R_{ik},\tag{13}$$

where R_{ik} is the Ricci curvature, as discussed in Section 3.2.

The final ingredient in the geometric evolution is the possible presence of a nonlinear stress:

$$\frac{\partial g_{ik}}{\partial t} \propto v_i v_k. \tag{14}$$

Taken together, these proportionalities form the most generalized set of tensorially consistent quantities involving all the possible second-rank tensors under consideration. The metric tensor time evolution is therefore governed by

$$\frac{\partial g_{ik}}{\partial t} = \kappa R_{ik} + \kappa_1 v_i v_k + \kappa_2 [\nabla_i v_k + \nabla_k v_i], \tag{15}$$

where κ_i are real constants reflecting the strength with which each term affects the evolution.

We now turning our attention to the vector equation for the leaf's velocity field. Most of the terms are borrowed from standard fluid mechanics and represent, respectively, advection, damping, external forces, pressure gradients and diffusion. From this point of view the model is similar to that introduced by Silk and Erickson:

$$\frac{\partial v^i}{\partial t} \propto -v^k \nabla_k v^i + \frac{1}{\rho} [v^i + F^i + g^{ik} \nabla_k P] + g^{lm} \nabla_l \nabla_m v^i. \tag{16}$$

The additional term needed to have the flow respond to curvature is introduced by a "force" representing motion along the geodesics of the geometry. The introduction of geodesic flow appears not only in general relativity but in condensed matter physics where they have been found experimentally to be related to the strain tensor patterns observed in sheets of disordered material [15]. The non-linear (quadratic) coupling of the flow velocity with itself, together with the viscous, dissipative terms above provides a reaction-diffusion type equation for the velocity field:

$$\frac{\partial v^i}{\partial t} \propto -\Gamma^i_{jk} v^j v^k. \tag{17}$$

Together, the time evolution of the velocity field reads

$$\frac{\partial v^i}{\partial t} = -c\Gamma^i_{jk}v^jv^k - c_1v^k\nabla_kv^i + \frac{1}{\rho}[c_2v^i + c_3F^i + c_4g^{ik}\nabla_kP] + c_5g^{lm}\nabla_l\nabla_mv^i$$
 (18)

where c_i are real constants.

Lastly, a scalar equation can be written to describe changes in the leaf's density over time as a result of sources (or sinks) represented by the function $S(\mathbf{x}, t)$ and flux of material flowing into or out of the a closed region of the leaf:

$$\frac{\partial \rho}{\partial t} = S(\mathbf{x}, t) - \nabla_i(\rho v^i) \tag{19}$$

It is important to note that in all the equations presented above, the use of ∇_i indicates a covariant derivative as presented in section 3.3. This is yet another way that geometry affects the evolution of the dynamical variables describing the system.

4 One-Dimensional Plant Growth

In considering a geometric model of plant growth, it would be advantageous to study a simple system first, and then proceed to build a more general model. This can be done by looking at growth in one-dimensional. This is not without immediate application. For example the growth of stems, blades of grass, and tendrils might well be approximated by one-dimensional systems. Similarly plants with circular symmetry, such as the lotus leaf, can have geometries described by a single radial coordinate.

Reducing the system to 1 spatial dimension and a 1-dimensional velocity field eliminates the possibility of finding spatio-temporal chaos, as the parameter space of a chaotic system must be at least 3-dimensional. Hence, a 1-dimensional plant promises to be a well-behaved system, which is advantageous when performing numerical simulations on a system so poorly understood. Also, building intuition about the simpler scenario becomes all the more important when moving into the 2-dimensional model.

4.1 Assumptions and Approximations

One-dimensional geometries have a Riemann-tensor that vanishes, i.e. 1D systems have no intrinsic curvature. This means that the nonlinear feedback that would normally appear in coupling the Ricci tensor to the metric now vanishes identically and the evolution of the metric would be governed directly by the fluid flow.

In order to provide a nonlinear coupling between the scale factor and its derivatives with respect to the spatial coordinates, we introduce a "pseudo-curvature" term that contains terms linear in the Laplacian of the scale factor and quadratic in the first spatial derivatives. This will act as a substitute for the Ricci tensor in the 1D case. In addition

to this, it is assumed that the leaf consists of a constant density material. This seems to be a reasonable assumption based upon experience and clearly indicates that the flux of material is then driven by an external source that sustains the growth, at least for early times. In addition external forces such as gravity and imposed pressure gradients will also be ignored in favour of focusing more on the internal dynamics.

Choosing the spatial coordinate to be x, the 1D metric scale factor f(x,t) the flow velocity v(x,t) and the material density $\rho(x,t)$ obey the following equations:

$$\frac{\partial f}{\partial t} = \frac{\kappa}{2f} \left[\frac{\partial^2 f}{\partial x^2} - \frac{1}{f} \left(\frac{\partial f}{\partial x} \right)^2 \right] + \kappa_1 f^2 v^2 + \kappa_2 \left(2f \frac{\partial v}{\partial x} + v \frac{\partial f}{\partial x} \right)$$

$$\frac{\partial v}{\partial x} = \frac{\kappa_2 \left(\partial f \right)}{2\pi} \left[\frac{\partial v}{\partial x} - \frac{1}{f} \left(\frac{\partial f}{\partial x} \right) \right]$$
(20)

$$\frac{\partial v}{\partial t} = -\frac{c_0}{2f} \left(\frac{\partial f}{\partial x} \right) v^2 - c_1 v \left[\frac{\partial v}{\partial x} + \frac{1}{2f} \left(\frac{\partial f}{\partial x} \right) v \right] - c_2 v$$

$$-c_3 \left[\frac{1}{f} \frac{\partial^2 v}{\partial x^2} + \frac{1}{2f^2} \left(\frac{\partial^2 f}{\partial x^2} v + \frac{\partial f}{\partial x} \frac{\partial v}{\partial x} - \frac{1}{f} \left(\frac{\partial f}{\partial x} \right)^2 v \right) \right]. \tag{21}$$

Admittedly, these equations, even with the simplifying assumptions are rather complex. However there are situations where some well known dynamical systems can be recovered from the general dynamics in the appropriate limiting cases.

For example the velocity equation (when $c_1 = c_2 = 0$) reduces to a reaction-diffusion equation for the velocity:

$$\frac{\partial v}{\partial t} = -\frac{c_0}{2f} \left(\frac{\partial f}{\partial x} \right) v^2 - c_3 \frac{1}{f} \frac{\partial^2 v}{\partial x^2} + \cdots$$
 (22)

When f = 1, and $c_0 = c_3 = 0$, $c_1 = 1$) one obtains Burger's equation [16] if $-c_3$ is identified as a viscosity parameter:

$$\frac{\partial v}{\partial t} = -c_1 v \frac{\partial v}{\partial x} - c_3 \frac{\partial^2 v}{\partial x^2}.$$
 (23)

This is not altogether surprising, given the relationship between these equations and those describing fluid flow. The coupling to a dynamical background geometry is what introduces the largest number of terms in the equations.

Intriguingly though, the metric tensor evolution has hints of a process not originally inscribed in its architecture. The so-called pseudo-curvature term that replaces the Ricci tensor in the 1-D case reduces to a Kardar-Parisi-Zhang (KPZ) type equation [17]. The KPZ system was designed to study rapid crystal growth (particularly from the deposition of material) and is an evolution equation for the surface height $h(\mathbf{x}, t)$ where x is a coordinate measured along the boundary between the surface and the air (or vacuum).

$$\frac{\partial h(\mathbf{x},t)}{\partial t} = \nu \nabla^2 h + \frac{\lambda}{2} (\nabla h)^2 + \cdots.$$

In our case writing the scale factor as a perturbation of flat space $f \approx 1 + h$ and setting $\kappa_1 = \kappa_2 \approx 0$ leads to:

$$\frac{\partial h}{\partial t} \approx \frac{\kappa}{2} \left[\frac{\partial^2 h}{\partial x^2} - \left(\frac{\partial h}{\partial x} \right)^2 \right] + \cdots$$
 (24)

What in 2-dimensional space is associated with the Ricci flow, in 1-dimension becomes similar to physical processes normally associated with growth processes. While; the structure of the equations is similar, they describe different growth dynamics. The KPZ system describes growth perpendicular to the coordinate x whereas our equation describes a continuous growth in the direction of the x-coordinate.

An obvious steady state solution can be found by letting $\partial f/\partial t = 0$ and $\partial v/\partial t = 0$. In that case,

$$f = C_1 + C_2 e^{-bx} (25)$$

$$v = 0 (26)$$

where C_1 , C_2 and b are real constants. Physically, this would correspond to a leaf that has stopped growing since the material velocity goes to zero, but the leaf has a non-zero length.

The evolution equations at hand can also be studied numerically. Having both spatial and temporal aspects, a finite differencing scheme must be chosen carefully so as to achieve accurate results as well as long-term stability. We choose to employ, a semi-implicit Dufort-Frankel scheme for the Laplacian operator since it provides a means for using larger time steps than an explicit scheme while maintaining a numerically stable evolution. It is most often used in heat-type equations; for the heat equation in particular, the Dufort-Frankel scheme is as follows:

$$\frac{u_j^{n+1} - u_j^{n-1}}{2\Delta t} = \alpha \frac{u_{j+1}^n - u_j^{n+1} - u_j^{n-1} + u_{j-1}^n}{(\Delta x)^2},\tag{27}$$

where $t = n\Delta t$ and $x = j\Delta x$ and α is a constant of proportionality.

The Dufort-Frankel method leads to an explicit scheme in calculating the time-evolving values of a function and is robust enough to allow time and spatial differencing values to be comparable when $\alpha \sim 10^{-2}$.

4.2 Results and Discussion

The generic behaviour of the scale factor for all cases is that the scale Numerical solutions to the equations were constructed for a wide range of parameter values. This allowed one to emphasize different effects to determine which terms are dominant and which one can regulate the growth patterns. In addition a variety of initial conditions for the spatial distribution of the scale factor and the flow velocity were studied.

In what follows we present some results for evolutions obtained with simple initial conditions given by a scale factor set to unity every where and a velocity profile that is an exponentally decreasing function of spatial position. The following values for the

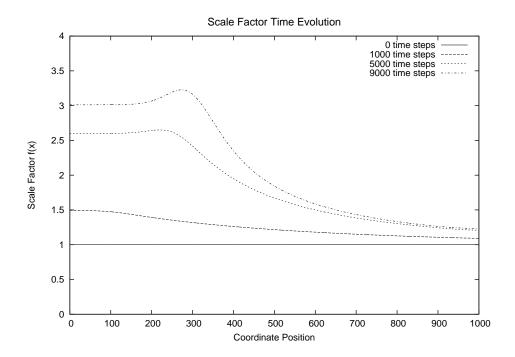


Figure 1: Plots of the evolution of the scale factor f(x,t). The plots are "snapshots" (at specified values of t) of the spatial distribution of the scale factor as a function of the coordinate position x.

constants κ_n and c_n

$$\kappa = -0.05,$$
 $\kappa_1 = 0.02,$ $\kappa_2 = -0.08,$ $c = 0.1,$ $c_1 = 0.01,$ $c_2 = c_3 = c_4 = 0$ $c_5 = 0.0001$

The evolution for both the scale factor and the material velocity are shown in Figures 1 and 2 respectively.

The generic behaviour of the scale factor for all cases is that the scale factor grows in time, as it should. This means that the distances between the fixed points on the plant increase with time. It is interesting to notice that the early in the evolution the scale factor is a monotonically decreasing function of position. At later times the scale factor grows in the intermediate region, indicating that the growth occurs most noticeably in this region. This is exactly what has been observed in the spatial distribution of growth patterns observed in 1D systems such as blades of grass (Festuca arundinacea)[18] and the primary root of corn (Zea mays)[19].

The velocity distribution of is shown in Figure 2 where initially the velocity is a decreasing function of position and as the growth occurs (i.e. the system undergoes an increase in length) the speed at which the material is transported decreases to zero. While it would appear that these figures indicate that there is no back-reaction effect on the plant due to the change on scale factor, simulations that de-couple the curvature from the evolution (i.e. an evolution for f(x,t) = 1, for all x and t) leads to unbounded growth.

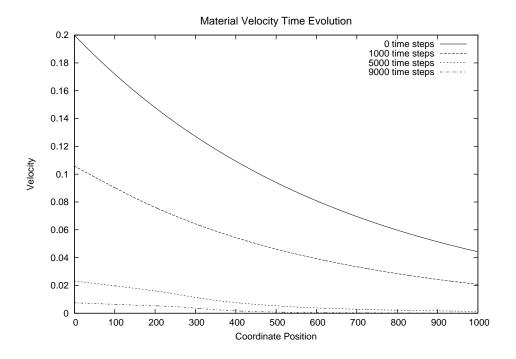


Figure 2: Plots of the evolution of the velocity v(x,t).

The effect of stretching and curvature (or in this case the nonlinear KPZ term) leads to a regulation of the overall increase in length.

Overall, it is easy to find sets of parameters for which growth is initially rapid, then tapers off as the plant ages, and finally stops growing. This correlates well with patterns seen in tobacco leaf and other plant growth. In order to compute the overall growth of the system one needs to define the length of the system in terms of the scale factor:

$$L(t) = \int_0^{x_{\text{max}}} f^{\frac{1}{2}}(x, t) dx.$$

Figure 3 shows how the total size of the system changes as a function of time for two different choices of spatial boundary conditions. In both cases presented here there is a rapid growth phase that eventually dies out when some maximum length is reached. At late times the transport velocity goes to zero everywhere along the structure. Not only does the the geometry regulate the growth but changes in the boundary conditions placed upon far tip of the structure changes the long term growth pattern. If the boundary condition is a Neumann condition where the derivative of both f and v vanish, then the growth leads to a constant late time length. On the other hand a Neumann condition where the derivative is a given small non-zero negative value, leads to a small and slow shrinking of the overall length as a function of time.

Figure 4 which plots fixed coordinate positions as a function of time demonstrates that the largest changes early in the evolution occur in the region where the velocity was the largest. The growth in the outer region is smaller and the largest contributions to the overall length come from the inner region. This corresponds exactly to patterns

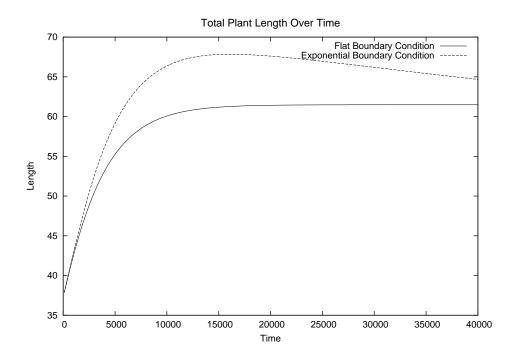


Figure 3: Plots of: The behaviour of the overall length L as a function of time. In both cases the initial conditions are the same $(f(x,0) = 1, v(x,0) = v_0 e^{-alphax})$ but the spatial boundary conditions are different and this leads to two different patterns of growth at both intermediate and late times.

one observes in actual plant growth. This figure can be compare directly with Figure 3 appearing in [19] where fixed positions on a a primary root of a corn plant are indicated by stripes painted on them. Similarly the coordinate locations on blades of grass are measured from pin-pricks made on the young blades [18]. Both observations show that the distribution of growth as a function of position along the organ takes the form of an inverted "U". The region where the maximum segmented growth appears is often called the "elongation zone" and this is exactly the behaviour one sees develop in the scale factor evolution shown in Figure 1.

What is interesting is to plot the growth tensor profile at different times in the evolution (See Figure 5). It can be seen that a local peak in the growth tensor forms in the inner region of the plant and that the peak "propagates" outward as the structure grows. Eventually this peak in the growth tensor will dissipate as the velocity begins to vanish everywhere at late times. This phenomena is consistent with experiments on linear growth where the elongation zone seems to move with wave-like behaviour outward during the growth process.[19]. The formation of the such a disturbance from monotonic initial data and its eventual "propagation" through the system is a phenomenon that needs more careful study.

Clearly the model presented in this manuscript is able to reproduce many of the features one expects from plant growth. The advantage of using a time dependent metric is that its use can be directly related to the types of experimental measures one makes

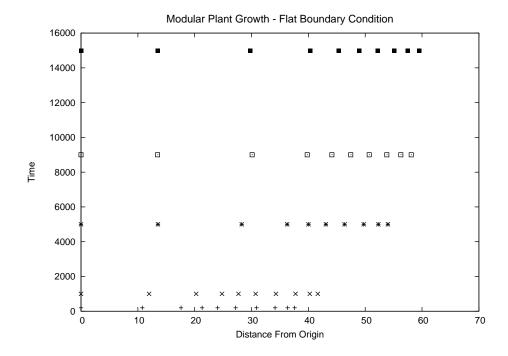


Figure 4: Plots of the spatial distribution of growth occurring at specific intervals over the entire length of the plant. The marks represent the constant coordinate positions on the plant. This corresponds to experimental methods that make permanent marks on a growing plant that are used to monitor growth over a period of time.

in studying plant growth. Accepting the fact that the specification of coordinates is fixed on the plant once the points on the plant are marked, the metric tensor then becomes the most natural way to turn the coordinate displacements into distance measurements especially on a curved surface.

The relationship between the metric scale factor and the behaviour of other quantities introduces a dynamical system where the material transport and the change in scale are intimately related through nonlinear reaction-diffusion type processes. This too is what one would expect from a time dependent system where diffusive processes dominate the dynamical evolution.

The results shown above, while encouraging, will require a great deal more effort if one is to understand the evolution of geometry coupled to growth. A more quantitative analysis of the parameters, along with the initial and boundary conditions will be performed in order to link the simulations directly to the measurements. This should help provide a means for understanding what exactly the parameters describe.

As with many nonlinear PDEs, the boundary conditions imposed on the system are essential to its behaviour. With a simple reflective boundary, the system evolves towards a flat steady state solution, while with an exponential function fit at the boundary, the metric tensor achieves an exponential steady state. This corresponds to the analytic solution explored in Section 4.1, but it is unknown whether one solution is more biologically relevant than the other.

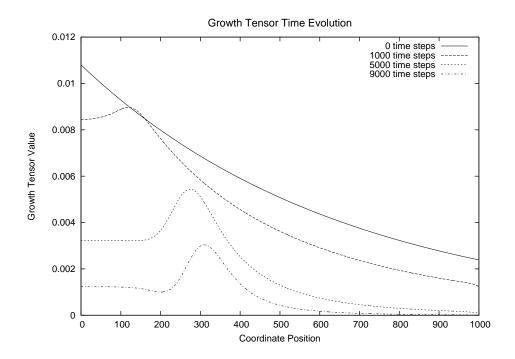


Figure 5: The evolution of the symmetrized growth tensor $\gamma_{ij}(x,t)$. (at specified values of t). The peak in the growth tensor is seen to move into the elongation zone in a manner reminiscent of a propagating wave.

Collectively, the results indicate that geometry plays an active role in material transport across the system, and hence the plant's growth. By influencing the flow rate of nutrients and hormones, the geometry of the leaf can produce unbounded growth, impede growth altogether, or regulate it in a nontrivial fashion.

5 Future Work

Numerical studies of the 1-dimensional plant model have provided promising results regarding the role of geometry in growth, but there are aspects of the model that remain poorly understood. These are largely tied to a lack of knowledge about the biophysics of plant growth.

Both the initial conditions and the boundary conditions are, at this point, assigned with no basis in biology, in part because biologists do not give these types of questions direct consideration, and therefore there is no standardized data for these quantities. There are, however, indirect clues in certain biomechanical studies of plant growth, and further work will include distilling these studies to better understand the physics behind how a plant starts its growth and how nutrients flow at the base and edges of leaves.

Another aspect that requires attention is the meaning of the various parameters included in the equations. Ideally these parameters would reflect gene expressions in the plant itself; this would allow for a model in which varying the parameters corresponds

to modeling different species of plants. Lacking direct evidence for such a correlation though, statistical sampling of the parameters may be an adequate method to decide plausible values for physically realistic plants.

There is also a somewhat philosophical consideration that acts as a hidden assumption in this model. In discussing the role of curvature and curvature flows, it is important to decide whether one considers the extrinsic curvature or the intrinsic curvature of the space. For the plant, this translates to deciding whether the plant knows it is growing in 3 dimensions or 2.

Mathematically, the two approaches have different strengths. In the extrinsic approach, we are guaranteed that simulations will produce physically realizable shapes, or else fail as soon as a nonphysical shape is encountered. The trouble is in keeping track of that shape because extrinsic curvature is a scalar-valued quantity and so cannot be directly incorporated into the time evolution calculations of the metric tensor.

On the other hand, the current approach of intrinsic curvature evolves the dynamics in a lower dimensional space, and treats the problem of what the leaf looks like separately. Unfortunately, embedding problems like this one are difficult to solve and have the potential to produce ambiguous or unphysical shapes.

Deciding this problem in 1-dimension may prove very helpful before venturing into the more complicated 2-dimensional model. Indeed, the very dynamics of the two approaches may well be different and in this way provide necessary information on which is the more physically relevant.

6 Conclusion

A dynamical model that couples a non-flat Riemannian geometry to physically measurable dynamical variables has been developed in order to understand both the increase in size and the formation of structure in growing plants. The use of a metric with a scale factor that depends upon both space and time leads naturally to a system that changes its scale and at he same time has leads to non-zero curvature.

In many dynamical systems derived from a least-action principle, one introduces all the terms that are allowable into the expression for the Lagrangian and/or Hamiltonian and then obtains the dynamical equations of motion from standard procedures. In the case of systems far from equilibrium, one must introduce the equations of motion directly again incorporating all allowable terms. This process seems to have met with success in this case and or one-dimensional toy model does capture in a general way many of the properties associated with biological growth.

The fact that the geometry plays a role in regulating the growth and leads to an asymptotic solution at late time is encouraging evidence that the geometry of a system may indeed affect the growth and vice versa.

What values of the coupling parameters correspond to directly to real plant observations remain to be explored. At least for 1-D models there seems to be very little variation in the overall pattern for growth in changes in the parameters. There is still room for exploration in the 1-D cases that should lead to even more realistic evolution.

One change is to alter the Ricci flow to mean-curvature flow. The mean (extrinsic)

curvature of a 1-D structure does not vanish as it does for the Ricci (intrinsic) curvature. The fact that the extrinsic curvature can written explicitly was a function of the spatial coordinate (it is a curve embedded in a 3-D flat space) makes it easier to specify the initial conditions. The flow equation for the scale factor of the metric can still be computed but now it is in terms of the equation for the curve. This has the advantage also that the curve can be easily embedded in a higher dimensional flat space explicitly and makes for easier and more intuitive visualization.

Secondly the 1-D case can be extended to 2-D spaces with a high degree of symmetry. Examples of lotus leaves that are circular will have intrinsic curvature. Similarly the evolution of *Acetabularia* algae with a circular cap that undergoes and evolution from a positively curved cap to one that is flat to one with negative curvature poses the challenge of understanding what it is that causes the change in the sign of the curvature.

Thirdly what role does the continuity equation play in the evolution? If the density of the structure is not constant how does that effect the overall growth of the system. This adds another degree of freedom to the system and that alone should induce some interesting dynamics.

Finally full 2-D simulations of leaves and petals are likely to show a variety of different behaviours. A system with three (or more) dynamical variables will be more difficult to simulate but pattern formation, spatio-temporal chaos, and and other strongly nonlinear phenomena might be expected to occur as they do in other higher dimensional systems. In addition the boundary conditions become more complex. Since the simple spatial boundary conditions in the 1D model affect the over all evolution one can expect even more complicated situations where the spatial boundaries themselves are changing.

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8 References

References

- [1] W.K. Silk & R.O. Erickson, "Kinematics of plant growth", J. Theor. Biology, 76, 481, (1979).
- [2] D. Thompson, On Growth and Form, (reprint of 1942 2nd ed.), Dover, New York (1992).
- [3] P. Prusinkiewicz & A. Lindenmayer, *The Algorithmic Beauty of Plants*, Springer, New York, (1990).
- [4] G.S. Avery, "Structure and development of the Tobacco Leaf", Am. J. Botany, 20, 565, (1933)
- [5] A. Khamis and Z. Ismail, "Comparative Study on Nonlinear Growth Model to Tobacco Leaf Growth Data", *J. of Agronomy*, **3**, 147, (2004).
- [6] J. Dervaux and M. Ben Amar, "Elastic growth in thin geometries", Origins of Life: Self-Organization and/or Biological Evolution, 79, (2009).
- [7] M. Janet, "Sur la possibilité de plonger un espace riemannien donné dans un espace euclidien", Ann. Soc. Pol. Math. 5, 36, (1926), also J. Nash, "The embedding problem for riemannian manifolds" Ann. Math 63, 20 (1956).
- [8] R. Hamilton, "Three-manifolds with positive Ricci curvature", J. Diff. Geom, 17, 255, (1982).
- [9] W.P. Thurston, "Three-dimensional manifolds, kleinian groups and hyperbolic geometry", Bull. Am Math. Soc., 6, 357, (1982).
- [10] G. Perelman, "The entropy formula for Ricci flow and its geometric applications", arXiv:math.DG/0211159, "Finite extinction time for solutions to the Ricci flow on certain three-manifolds", arXiv:math.DG/0307245, and "Ricci flow with surgery on three-manifolds", arXiv:math.DG/0303109.
- [11] V. Tapia, "Evolution of curvature tensors under mean curvature flow", Rev. Colomb. de Matemáticas, 43, 175 (2009).
- [12] E. Woolgar, "Some applications of Ricci flow in physics", Can. J. Phys., 86, 645, (2008).
- [13] M. Kardar, *The Statistical Physics of Fields*, Cambridge University Press, Cambridge, (2007).
- [14] J. Nakielski, *Planta*, "The tensor-based model for growth and cell divisions of the root apex. I. The significance of principal directions", **228**, 179 (2008).

- [15] D. Jeulin, W. Li, & M. Ostoja-Starzewski, "On the geodesic property of strain field patterns in elastoplastic composites", *Proc. Roy. Soc. A*, **464** 1217, (2008).
- [16] J.M. Burgers, The Nonlinear Diffusion Equation, Riedel, Boston (1974).
- [17] M. Kardar, G. Parisi, and Y.-C. Zhang, "Dynamic Scaling of Growing Interfaces", *Phys. Rev. Lett.*, **56**, 889, (1986).
- [18] H. Schnyder, C.J. Nelson, J.H. Coutts, "Assessment of Spatial Distribution of Growth in the Elongation zone of grass leaf blades" *Plant Physiol.* **85**, 290, (1987).
- [19] R.E. Sharp, W. Silk, T. Hsiao, "Growth of Maize Primary Root at low water potentials: Spatial distribution of expansive growth", *Plant Physiol.* 87, 50, (1988).