

# Statement of Research Interests

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The following begins with a description of a problem that has been a central subject of my work, namely the study of tiling patterns in growing plant apices. This motivates other problems in pattern formation, mechanics and growth in biological systems, and the geometry of differential equations. Finally, I describe some recent work in mathematical epidemiology and modeling in linguistics.

## Tiling Planforms and Symmetries in Plants

Inspecting a sunflower head such as that of Fig. 1 (a), one may notice first the diamond-shaped seeds that tile the disk. Families of spirals catch the eye, and if one counts the numbers of spirals in each family, one typically arrives at successive members of the Fibonacci sequence 1, 1, 2, 3, . . . . The spirals families seem to blend into each other so that lower members of the Fibonacci sequence are observed near the center of the disk and higher numbers as one works ones way out. Yet, there is a self-similarity in that locally the pattern is nearly the same throughout the disk. Variations of these observations are observed throughout the plant world. Often it is hexagons rather than diamonds that tile, or the planform may be dominated by ridges (see Fig. 2). Smooth transitions between spiral families may give way to more abrupt transitions that display defects. The mathematician finds in these *phyllotactic patterns* a source of questions on the tiling of surfaces, and the scientist asks what physical or chemical mechanisms are behind their formation. Together, the task is to combine experimental data with PDE models whose analysis reveals both the underlying symmetries inherent in the bifurcations to these patterns and the parameter combinations that connect the variety of patterns to the mechanisms behind them. With the view that patterns are universal objects in that very different physical mechanisms may give rise to similar results, *Alan Newell* and I have developed a program that aims to make a clear distinction about what is generic to a mathematical model for phyllotaxis and what relies on the specific mechanism under investigation.

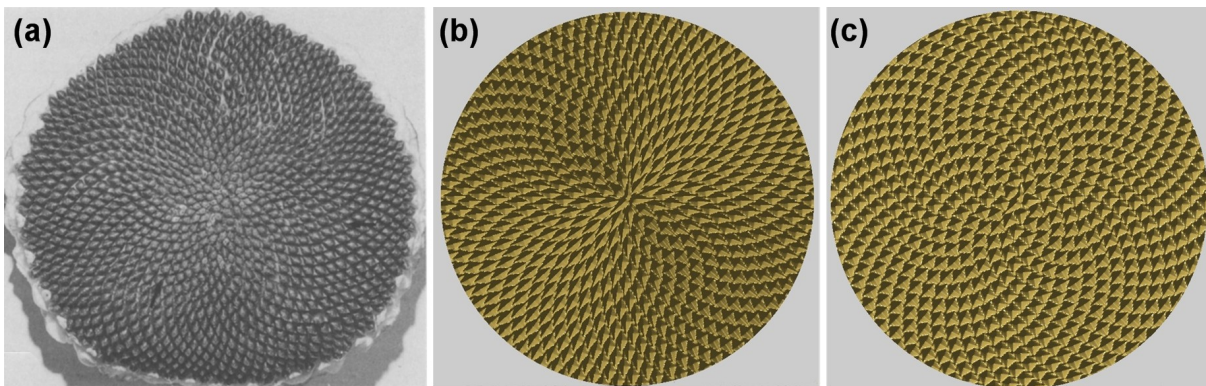


Figure 1: A sunflower head (a) and theoretical reproductions (b,c)

## BIOPHYSICS AND BIOCHEMISTRY: TWO PLAYERS AND THEIR EQUATIONS

Underlying the genesis of phyllotactic patterns is a rich interaction of biophysical and chemical mechanisms whose respective roles are only beginning to be understood. Our first model was based on the experiments of P. Green and colleagues in the 1990s, who correlated the regions of compressive stress on a plant shoot to regions where the phyllotactic patterns are formed and demonstrated through experiments that mechanical forces influence pattern choice. In [5, 9, 10], we model a plant as a thin, compressed shell (the plant's outer skin, its *tunica*) attached to an elastic foundation (the plant's squishy corpus) and study how the shell buckles under the influences of compressive stresses that arise from growth. The elastic energy that is minimized by this buckling is a functional  $\mathfrak{E}(w, \Sigma_{ij})$  of the shell deformation  $w$  and the in-plane stress tensor  $\Sigma_{ij}$ . The key observation is that the energy is minimized on configurations for which

$$w(\vec{x}) = \sum_{\nu=1}^n \left( A_{\nu} e^{i\vec{k}_{\nu} \cdot \vec{x}} + A_{\nu}^* e^{-i\vec{k}_{\nu} \cdot \vec{x}} \right) \quad (1)$$

consists of *triads* of periodic deformations, meaning that the wavevectors  $\vec{k}_\nu$  form a Fibonacci-like sequence with  $\vec{k}_\nu + \vec{k}_{\nu+1} = \vec{k}_{\nu+2}$ . This is seen via a Galerkin approximation of the Föppl-von Kármán-Donnell (FvKD) equations, which are the Euler-Lagrange equations for the energy  $\mathfrak{E}(w, \Sigma_{ij})$ . The analysis relies on reducing the problem to solving differential equations for the *order parameters*, namely the wavevectors  $\vec{k}_j$  and amplitudes  $A_\nu$ , which parameterize the space of possible patterns. This we discuss further below. First, there is another mechanism to be added to the picture. Experimental work in the past five years has revealed how an instability involving the diffusion and transport against diffusion of the growth hormone auxin plays a central role in plant development. Auxin essentially acts to promote growth, so that a nonhomogeneous distribution of auxin results in nonhomogeneous growth. We have developed our model so that the FvKD equations are extended to a set of equations for the deformation  $w$ , the Airy function  $F$  (a potential for the stresses  $\Sigma_{ij}$ ), and a growth function  $g$  related to the auxin concentration distribution. The FvKD equations

$$w_t + \nabla^4 w + P\nabla^2 w - [F, w + w_0] + \kappa w + \gamma w^3 = 0, \quad (2.a)$$

$$\nabla^4 F + \nabla^2 g + \frac{1}{2}[w, w + w_0] = 0, \quad (2.b)$$

are completed with an equation governing the function  $g$ . In (2),  $(x, y, w_0(x, y))$  is the graph of the middle surface of the original, unbuckled tunica shell, and the bracket is defined by  $[F, w] = F_{xx}w_{yy} + F_{yy}w_{xx} - 2F_{xy}w_{xy}$ . The first equation is a force-equilibrium equation, and the second equation is a compatibility equation expressing Gauss's Theorema Egregium. Indeed, in FvKD theory, stresses are linearly related to strains (changes that buckling induces on the metric of the shell's middle surface) so that (2.b) relates a potential for changes in the metric to change in Gaussian curvature. The effect of the growth term  $\nabla^2 g$  is to change the intrinsic, natural, metric on the surface.

Even without the growth term  $\nabla^2 g$ , a variety of patterns as illustrated in Fig. 2 is possible, depending on the anisotropies of the system and the geometry of the pre-buckling surface  $(x, y, w_0(x, y))$ . An important effect of the growth term can be understood by comparing Fig. 1 (b) with Fig. 1 (c). The maxima of each of the surfaces in these graphs lie at the same points, but the diamond-shaped tiles observed in Fig. 1 (b) contrast with the nearly square-shaped tiles of Fig. 1 (c); the change of natural metric as measured by  $\nabla^2 g$  affects the shapes of the tiles relative to the underlying lattice. In [6], we further study how the biomechanical and biochemical mechanisms can cooperate or compete to choose the winning pattern.

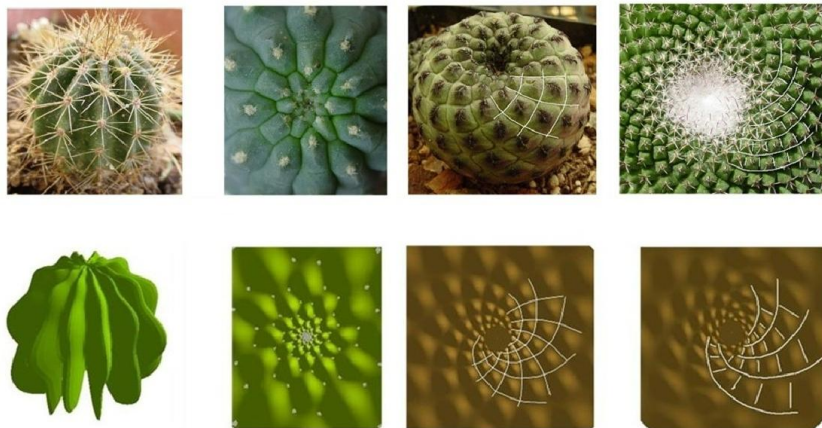


Figure 2: Planforms of ridges, hexagons, diamonds and offset diamonds on real plants (top row) and theoretical reproductions (bottom row).

#### SYMMETRIES AND SELF-SIMILARITY

Graphed in Fig. 1 (b,c) are functions of the form (1), where both the amplitudes and the wavevectors are functions of the radial coordinate. Starting from a PDE model such as (2), the task is to calculate the functions  $A_\nu(r)$  and  $\vec{k}_\nu(r)$ . Let us write

$$w(r, \theta) = \sum A_\nu(r) \cos(\vec{k}_\nu(r) \cdot (r, \theta)) = \sum A_\nu(r) \cos(l_\nu(r)r + m_\nu\theta),$$

where again  $\vec{k}_\nu + \vec{k}_{\nu+1} = \vec{k}_{\nu+2}$ . As  $\theta$  is an angle, the  $m_\nu$  are integers; think of them as forming the Fibonacci sequence  $m_1 = 1, m_2 = 1, m_3 = 2, \dots$ . For a fixed value of  $r$ , the order parameter equations for the amplitudes  $A_\nu$  read

$$\frac{\partial A_\nu}{\partial t} = \sigma(\vec{k}_\nu)A_\nu + \sum \tau(\vec{k}_\nu, \vec{k}_p, \vec{k}_q)A_p^*A_q^* + \text{quartic terms}, \quad (3)$$

where the cubic term is summed over all triads of wavevectors such that  $\pm\vec{k}_p \pm \vec{k}_q = \vec{k}_\nu$ . In form, this system of equations is generic in that it governs bifurcations from rotationally symmetric states to states with say,  $D_4$  (squares) or  $D_6$  (hexagons) symmetry. The details of the microscopic mechanisms lie in the coefficients  $\sigma, \tau$ , and these coefficients determine the optimal choice of wavevector sequence  $\vec{k}_\nu$ . Depending on  $r$ , solutions with  $D_4$  or  $D_6$  symmetry may be preferred, or neither symmetry may be compatible with the boundary conditions. However, a continuous symmetry can be expressed in the existence of functions  $\mathcal{A}$  and  $\mathcal{L}$  such that

$$A_\nu(r) = \mathcal{A}\left(\frac{r}{m_\nu}\right), \quad l_\nu(r) = \mathcal{L}\left(\frac{r}{m_\nu}\right).$$

The functions  $\mathcal{A}$  and  $\mathcal{L}$  can be calculated from the PDE model by numerically solving the amplitude equations (3), in which case the exact forms of  $\mathcal{A}$  and  $\mathcal{L}$  depend on the coefficients  $\sigma$  and  $\tau$ . In [8], I further show how functions  $\mathcal{A}$  and  $\mathcal{L}$  can be derived starting not with a PDE model, but rather by making reference to a global invariance condition which demands that the lattice determined by the wavevectors  $\vec{k}_\nu$  vary as little as possible with  $r$ . In particular, the sequence  $l_\nu$  is related to the sequence  $m_\nu$  by  $\frac{l_{\nu+1}}{l_\nu} = \lim_{\nu \rightarrow \infty} \frac{m_\nu}{m_{\nu+1}}$ . Classical theorems on the continued fraction expansions and the approximation of irrational numbers, such as  $\frac{l_{\nu+1}}{l_\nu}$ , by rational numbers, such as  $\frac{m_\nu}{m_{\nu+1}}$ , come into play.

#### CURRENT WORK AND GOALS

A relatively simple PDE that shares features similar to the system (2) is the Swift-Hohenberg equation, which in one dimension reads

$$\partial_t u = (\epsilon^2 - (1 + \partial_x^2)^2)u - u^3,$$

where  $u(x, t)$  is defined on  $\mathbb{R} \times \mathbb{R}^+$  and  $\epsilon > 0$  is a small parameter. It is known that this equation has nonlinearly stable solutions  $u(x, t) = u_{\epsilon, \omega}(x)$  of the form

$$u_{\epsilon, \omega}(x) = \sum_{n \in \mathbb{Z}} u_{\epsilon, \omega, n} e^{i\omega n x}.$$

This gives hope that solutions of the form (1) to a two-dimensional Swift-Hohenberg equation can be calculated exactly. The continuous invariance of the solution (1) as expressed by the functions  $\mathcal{A}, \mathcal{L}$  also suggests that the techniques of Lie groups applied to differential equations could be applicable, and I plan to pursue this line of thought.

Defects are also often observed in plant patterns, particularly as the plant grows in size so that transitions between patterns are induced. In our previous work, we identified transition types and their relation to defects such penta-hepta pairs observed in many plants. Currently, we are looking in more detail at how the wavevectors  $\vec{k}_\nu$  can vary in space. Spatial dependence of the wavevectors introduces spatial derivatives into the order parameter equations.

Essential for the further development of this work is close collaboration with biologists. I am currently working with **Todd Cooke** (Biology; University of Maryland). The mathematics described above has suggested relationships between the relative positions of the tiles and their shapes, and our first goal is to compare these predictions with real plants. As the patterns arise on plants as microscopically small deformations at the tip of the plant shoot, it is therefore necessary to make scanning electron microscope images of plant tips. Our results so far have gone beyond the relationship between tile shape and relative position to also show how the model captures many features of the three-dimensional shape of the pattern. The long-term goal of my work with Cooke is to develop experiments, informed by the results of the models, aimed at better understanding the interaction of mechanics and chemistry on the patterning. I also envision the development of biologist-friendly MATLAB code to aid in the development of plant pattern analysis.

The microscopic images of plant patterns are also offering us a look at the shapes of the cells. Various patterns of hexagonal or diamond shapes are also observed at the cell level. Cell growth and division is to a large extent dependent on stresses in the plant. In current work with **Isaac Chenchiakh** (University of Bristol), we are aiming to develop a mathematical framework to understand how stress states give rise to cell shape patterns.

The self-similar lattice structures in disks discussed above have analogs in three dimensions. With **Barbara Shipman** (University of Texas at Arlington), I plan to investigate three-dimensional tilings of balls in  $\mathbb{R}^3$ . This has potential applications to the study of the packing and shape of seeds.

### Mechanics, Growth, and Geometry: Current Projects

#### GROWTH IN ANISOTROPIC DISKS

With **Stuart Antman** (University of Maryland) and **David Bourne** (Max-Planck-Institute for Mathematics in the Sciences), I am analyzing growth in anisotropic disks. Antman and Negrón-Marrero [1] studied radially symmetric equilibrium states of anisotropic nonlinearly elastic disks and show how anisotropy gives rise to phenomena not suggested by solutions for isotropic bodies. As many biological materials have anisotropic material properties, we are looking at how these results carry over to growing anisotropic bodies. We consider an axisymmetric deformation of a disk

$$\chi(s, \theta) = (\rho(s), \theta)$$

with deformation gradient

$$F = \nabla\chi = \begin{pmatrix} \rho'(s) & 0 \\ 0 & \frac{\rho(s)}{s} \end{pmatrix} \doteq \begin{pmatrix} \nu & 0 \\ 0 & \tau \end{pmatrix}.$$

Following Rodriguez, *et. al.* [7], growth is modelled by decomposing  $F$  multiplicatively as

$$F = AG \doteq \begin{pmatrix} \nu_e & 0 \\ 0 & \tau_e \end{pmatrix} \begin{pmatrix} \nu_g & 0 \\ 0 & \tau_g \end{pmatrix},$$

where  $A$  corresponds to the elastic component of the deformation and  $G$  comes from growth. The stresses  $N(s)$  and  $T(s)$  depend only on the elastic part of the deformation and the equilibrium equation takes the form

$$\frac{d}{ds}[sN(\tau_e, \nu_e)] = T(\tau_e, \nu_e).$$

Using an exponential change of variables, this equation can be transformed into an autonomous system of ODE which can then be studied in the phase plane.

#### GROWTH OF MOLLUSK SHELLS

Many mollusk shells show similar patterns of ridges and bumps as those seen on plants. **Régis Chirat** (Paleontology; Université Claude Bènard, Lyon) and I have recently studied these patterns and suggest that they too arise from growth-induced mechanical stresses as the shell forms [2]. Various measurements such as the wavelength of the patterns as well as the angles between ridges and the shell edge depend on the curvature of the shell in agreement with theory. Currently we are considering another class of structures that emerge on mollusk shells and are exemplified in Fig. 4. These have an analogue in plants as well, namely in the ripples that form at edges of plant leaves (Fig. 4). In recent theoretical and experimental work, leaf ripples are understood as the result of a growth-induced intrinsic metric of the form  $ds^2 = \rho(y)dx^2 + dy^2$ , where  $x$  is the coordinate parallel to and  $y$  the coordinate perpendicular to the leaf edge, and  $\rho(y)$  is a decreasing function of  $y$ . Mollusks offer an opportunity to study both ripple-like and phyllotactic-like patterns in a single organism.



Figure 3: Ripple patterns at the edges of a mollusk shell and a leaf

**Partha Guha** (Bose Research Institute, Calcutta) and I have shown how the FvKD equations (2) can be linearized with the aid of the hodograph transformation which interchanges the dependent and independent variables [4]. Currently, we are looking at extending the work of Fokas and Gelfand [3] on the integrability of the Gauss-Codazzi equations for surfaces immersed in Lie groups and Lie algebras. Motivated by the work of Zakharov [12], who studies the integrability of the Gauss-Lamé equations for finding orthogonal coordinate systems in Euclidean space, we are looking at orthogonal coordinate systems expressed in Lie groups and Lie algebras.

FACETED STRUCTURES

For the purpose of optimizing the effective stiffness of building material, **Frank Mirtsch** (Engineering; Technische Hochschule, Berlin) has developed techniques whereby compressed sheets of metal or other material buckle into hexagonal or diamond planforms similar to those seen on plants. Particularly unique to his set of work is the formation of faceted hexagons in which the buckled surface consists of tent-like structures with flat sides (Fig.). The Gaussian curvature is concentrated on points. Similar concentrations of Gaussian curvature are obtained in paper crumpling and in the context of the Cross-Newell phase diffusion equation (CNPDE)

$$\theta_t + \nabla \cdot \vec{k}B(k) = 0,$$

where  $\vec{k} = \nabla\theta$  and  $k = |\vec{k}|$ . The equation arises in the study of modulated patterns (the function  $B(k)$  then depends on the microscopic nature of the pattern-forming system), and numerical analysis reveals that the Gaussian curvature of the phase surface  $(x, y, \theta(x, y))$  accumulates first on lines and then on points under the evolution of the CNPDE. The work of Prof. Mirtsch has been largely experimental, relying on trial and error to produce the desired structures. The hope is to provide theory, motivated by the studies of plants and the CNPDE, to inform his work.

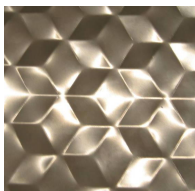


Figure 4: A faceted hexagonal structure.

**Continuous Diversity in Linguistic Modelling**

Together with **Sérgio Faria** (Universität Göttingen), I have developed a model for the evolution of the vowel pronunciation in natural languages. We consider the question of how vowel systems that have, in the case of American English, been stable for thousands of years, begin to change so that significant differences are noticed within a few generations. The object of our study is an age-structured population, the individuals of which are distinguished by their pronunciation of a given vowel. The processes of aging, birth, and death follow a standard demographic model of McKendrick and von Foerster, while the evolution of language by teaching and social interaction is based on the theory of mixtures with continuous diversity.

A mixture with continuous diversity is a multicomponent medium made up of an infinite number of mutually interacting species whose distinctive properties vary smoothly from one to another. The mathematical modeling of such systems can be traced back to Euler’s studies of the demography of structured populations and similar mathematical formulations have since proven useful in a range of topics, including crystal structure, gas dynamics, and anisotropic fluids.

Continuous diversity is relevant in this study in that vowels sounds can be represented in a continuous two-dimensional space that essentially parameterizes the position of the tongue in the mouth. Different speakers have slightly different pronunciations of the same vowels in a common language. The fundamental quantity of this study is a speaker number intensity  $n^*(\sigma, \alpha, t)$ , depending on a continuous pronunciation parameter  $\sigma$ , age  $\alpha$  of a speaker, and time  $t$ .

## Mathematical Epidemiology

My first foray into mathematical epidemiology involved a study with *Henry Tuckwell* (Max-Planck-Institute for Mathematics in the Sciences) and *Alan Perelson* (Los Alamos Laboratories) on the the early stages of HIV infection. In [11], we estimate with a simple stochastic model the probability that a new host becomes infected with HIV after the physical transfer of a number of virus particles from an infected source person.

In current work with Tuckwell, we consider a population for which the viral load and populations of infected and noninfected cells in each individual are governed by a system of ordinary differential equations, the parameters of which vary randomly from individual to individual. We have studied the distributions of the nature of the fixed points of the system and are looking at how random parameters affect dynamics in population networks.

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