

The Mathematics of Phyllotaxis

Introduction

Phyllotactic patterns (from the Greek *phyllo* (leaf) and *taxis* (order)) arise whenever a vascular plant produces at its growing tip a series of similar botanical elements, such as leaves, scales or flowerets. The most common and well known of such patterns is one where the elements are arranged in two families of spirals winding in opposite directions. The numbers of spirals in each of these families are, remarkably often, successive numbers in the Fibonacci sequence 1, 1, 2, 3, 5, 8, 13, 21, ... where each term f_n is the sum of the previous two: $f_n = f_{n-1} + f_{n-2}$. (See Fig. 1).

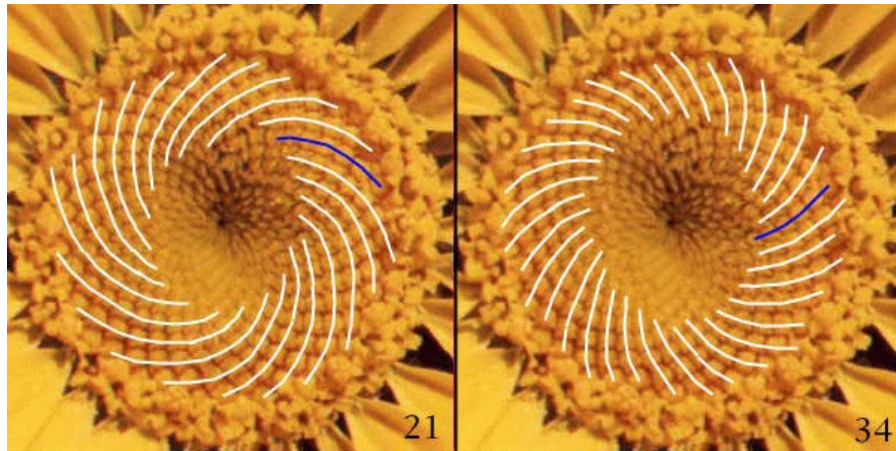


Figure 1: A Marguerite flower with the two families of spirals marked, Fibonacci numbers 21 and 34.

These structures arise as the primordia (microscopic growth spurs that eventually give rise to the botanical elements) appear periodically at the circular edge of the apical meristem or apex (the growing tip of the plant) at a constant divergence angle from their predecessor and move radially away from the meristem. This angle, when the pattern is of the Fibonacci spiral type, is very close to $222.5^\circ \dots = 360(1/\tau)$ (or $137.5^\circ = 360 - 222.5^\circ$), where $\tau = \lim f_{n+1}/f_n = (1 + \sqrt{5})/2 \simeq 1.61803$ is the famous golden mean. The descriptive theories of Phyllotaxis (“Fundamental Theorem of Phyllotaxis”, Adler [1], Jean [7]) elucidated the relationship between Fibonacci patterns and a divergence angle close to 222.5° or 137.5° . The following fundamental questions remain, to our knowledge, widely open to investigation:

Question 1. What are the biochemical or biophysical mechanisms of primordium formation and interaction at the apex of vascular plants?

Question 2. How do these mechanisms favor a convergence to constant divergence angles and hence regular spiral structures (or whorled structures, see Section 2)?

Question 3. Why, among all possible regular spiral patterns, are the Fibonacci spirals favored?

Question 4. What other less common patterns are possible, in nature, experimentally or theoretically and what are the mechanisms of transition between these different patterns?

As mathematicians we can lay no claim as to the answer of Question 1. We propose to study and improve on models based on hypotheses general enough to be compatible with most of the mechanisms conjectured by biologists. We hope that an understanding of which models better answer Questions 2, 3 and 4 will also provide clues for Question 1. The models we study fulfill the further requirement that they are not only

numerically, but mathematically tractable as well, and provide at least partial answers to Questions 2, 3, and 4.

In the difficult task of choosing (or creating) a model of Phyllotaxis, one is faced with conflicting criteria. A large part of the literature offers geometric studies of models with no time evolution, involving only spiral patterns (Levitov [11], Adler [1]). The global mathematical analysis of these models is compelling. Unfortunately, they cannot explain the convergence to (and hence the stability of) regular spirals patterns from general initial conditions. The obviously dynamical aspect of plant growth compels one to choose time evolution, Partial Differential Equations models of the type pioneered by Turing (reaction diffusion) or Green et al.(buckling). There are several problems with this choice: the actual biochemical or biophysical mechanisms of primordia formation and interaction is still subject to debate, and hence the actual P.D.E.'s proposed may not be the ones relevant to biology. Moreover, the phase space of time evolution P.D.E.'s is infinite dimensional, and does not lend itself easily to a rigorous, global analysis of the system. In light of this, we chose to study the iterative models of the French physicists Douady and Couder [3], [4] (see also the systems proposed by Schwabe [13], Koch, Bernasconi and Rothen [8]) seem like a good compromise: they are simple enough to be cast in finite dimensional, discrete dynamical systems, yet they are compatible with most of the biological mechanisms proposed nowadays. Finally, they offer a bridge to the geometric models, whose beautiful mathematics can be brought to bear. As researchers in Dynamical systems, who have worked in a variety of setting (discrete, continuous, variational), we feel well suited for the task of analyzing these models and providing bridges between them and other models. The relative simplicity of the systems and of our analysis should make their feature accessible to biologists, and thus enhance their applicability.

Douady and Couder proposed two types of models. The first type, based on hypotheses proposed by Hofmeister in 1868, assumes that primordia form at constant intervals of time. We will call it the "Time Periodic model". The second type of model, based on the work of M. and R. Snow (1935) replaces the time periodicity hypothesis by the assumption that primordia appear when and where there is enough space. This model, that we call here "Threshold model" also gives rise to the spiral patterns exhibited by the Time Periodic model, as well as to whorled patterns (see Section Threshold).

Until now, we have concentrated on a study of the Time Periodic model of Douady and Couder. In this context we have obtained significant results about Questions 2, 3, 4 above. In the following section, we present these results, obtained while one of the PI's, Chris Golé, was supported by an NSF grant (# 9796309). We outline the work that remains to be done in the analysis of this model, as well as its relevance to botany. In Section 2, we present a plan of work on the Threshold model, including its relationship with the Time Periodic model. In Section 3 we propose different ways to refine the models, making them more realistic while keeping them accessible to analysis. In Section 4, we present our already extensive collection of interactive java applets, available from our web site as well as our plan to develop a fully integrated web site where people around the globe will be able to use the models and explore their underlying structures.

1 The Time Periodic Model

Douady and Couder based their model on the following assumptions:

1. The apex has a circular symmetry (i.e. it is a disk, cone, cylinder, or paraboloid).
2. The primordia are formed on the boundary of the apex and move radially away from the center at a speed that is only function of their distance to the center.
3. New primordia are formed at periodic time intervals (the plastochrone T).
4. The incipient primordium forms in the largest available space left by the previous ones.
5. Outside a certain perimeter, the primordia do not change their angular positions.

From these premises, Douady and Couder performed two kinds of experiments: one is a purely physical system involving drops of ferrofluids in a magnetic field, repelling one another. The other experiment is an iterative numerical model which can be seen as a simulation of the physical system. Both exhibit all the spiral structures encountered in nature. For an implementation of this numerical scheme, click on Dynamical Model in our web site www.math.smith.edu/~phylllo/phylllo.html

We took the numerical iteration scheme as the basis of our study. We put it in a Dynamical Systems framework in which spiral patterns appear as fixed points. It is worth noting here that, although Douady

and Couder and others have used the phraseology of dynamical systems, this conceptual step had not been performed before and hence neither was any rigorous mathematical analysis of the dynamics¹.

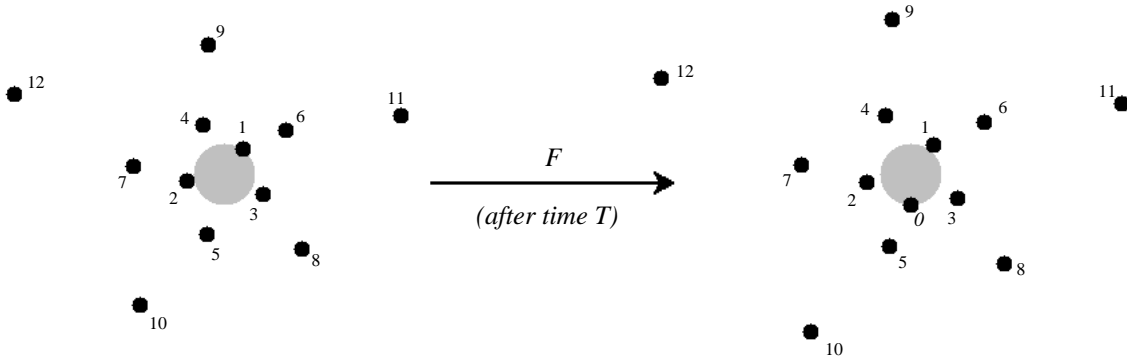


Figure 2: The map F . On the left, a few of the concentric circles and the divergence angle θ_4 are shown. The map F takes the primordia configuration at time t (left) to the configuration at time $t + T$ (right), where a new primordia has emerged. Each primordia is located now in the subsequent concentric circle. Angular coordinates are preserved.

We now describe our discrete dynamical system. We define a map F whose iterates model the evolution in discrete time increments of the primordia arrangement (see Fig. 2). In the *circular or centric representation*, the primordia are arranged in concentric circles C_k , $k = 0, 1, 2, 3, \dots$ of radii $r_k = e^{kG}$ with one primordium per circle, where G is a parameter proportional to the plastochrone T and can be seen as the exponential growth rate of the apex. We think of the meristem as the circle of radius 1. After time T (see Fig. 2), each primordia is shifted from circle C_k to circle C_{k+1} in radial direction away from the meristem. In polar coordinates, the primordia preserve their angular coordinates. The angular coordinate increments between successive primordia, the *divergence angles*, are denoted by $\theta_1, \dots, \theta_n$. One can also choose to study the *cylindrical representation*, e.g. corresponding to phyllotaxis of plant stems. In this model the radial coordinates become the vertical coordinates $r_k = kG$. We remark that other growth laws and other geometries can be assumed without change in the analysis.

The map F is defined on a torus of large dimension n , with angular coordinates $(\theta_1, \dots, \theta_n)$ ($n = 200$ in our implementation). The image $(\Theta_1, \dots, \Theta_n)$ of a point $(\theta_1, \dots, \theta_n)$ by our map F is given by the following prescription:

$$\begin{aligned} \Theta_1 &= f(\theta_1, \dots, \theta_n) \\ \Theta_2 &= \theta_1 \\ &\dots \\ \Theta_n &= \theta_{n-1} \end{aligned} \tag{*}$$

where f returns the divergence angle Θ_1 between the incipient primordium on the unit circle and the primordium of the previous generation. This divergence angle is chosen to minimize a (repelling) potential energy of the form:

$$W = \sum_{k=0}^n U(d_k),$$

where d_k is the distance between the k^{th} primordium and the incipient one on the unit circle and U is a repelling potential, e.g. $U(d) = d^{-s}$ for some s . Our graduate student Scott Hotton came up with the following approximating potential. It turned out to be a very useful, simplifying template:

$$X = \max_k U(d_k).$$

¹a notable exception to this is the work of Kunz (Kunz' thesis) who independently came across a similar dynamical system and performed a (local) analysis of the linear stability of the fixed points.

This simple approximation, which only keeps the contribution to the potential energy by the primordium closest to the incipient primordium already contains the essence of the geometric information of the system with the potential W above. We think of X as a the relevant potential energy when the stiffness of the potential (e.g. s in $U(d) = d^{-s}$) goes to infinity and we have rigorous results about the correspondence of the models with energies W and X (see later in this section). Minimizing X easily gives rise to the following minimax principle: the incipient primordium chooses the location on the unit circle where the minimum distance to all primordia is maximized.² Hence, with the energy X the actual form of the decreasing potential U becomes irrelevant, and the choice of location of the incipient primordium is entirely geometric.

1.1 Results on the Time Periodic System

Regular spirals as fixed points. The configuration is a *regular spiral* if $\theta_l = \theta_j = \theta, \forall l, j$. In this case the primordium k is, expressed as a complex number, $p_k = e^{k(G+i\theta)} = p_1^k$. All the primordia are included in the so-called *generative spiral* $p_1^{\mathbb{N}}$. There are usually two closest primordia (exceptionally a third), say p_j, p_k , in which case the configuration has two families of j and k visible spirals, or parastechies each. The *parastechies* generated by p_j are of the form $p_u(p_j^{\mathbb{N}}), u \in \{0, \dots, j-1\}$. In our applet Spiral in www.math.smith.edu/~phyll0/phyll0.html, all such spiral configurations are shown, together with the corresponding parastechies. In our applet Cylinder, we show the regular spiral configurations on the (opened up) cylinder: they appear as regular lattices in the plane. In this case, each parastechy is a line belonging to one of two families of parallel lines.

One can easily show that fixed points of the map F defined in (*) above must satisfy $\theta_{k+1} = \theta_k$. Hence *the divergence angles in a configuration fixed by F must be equal: the configuration forms a regular spiral (However, not all spirals are fixed points of the map).*

Stability and Structural Stability. The prescription of Θ_1 in the definition of F is sometimes not well defined: several divergence angles may minimize the energy. However everywhere else, F is smooth. We proved that, where it is defined, the spectrum of the differential DF was always strictly included in the unit disk. Hence F is a contraction on any convex neighborhood that does not contain discontinuities. This has very strong consequences on the dynamics of F : any fixed point is asymptotically stable, and so is any periodic orbit of F . Moreover, these orbits or any attracting set that the map contains is isolated and must persist under perturbation of the map (structural stability of hyperbolic invariant sets). Hence *the recurrent structures (e.g. spirals) of this system are stable under perturbations of the initial conditions, as well as perturbations of the system itself.*

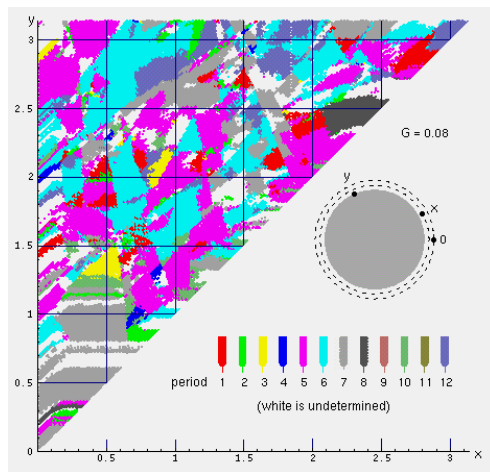


Figure 3: Basins of attraction of periodic orbits in a plane of the phase space, shaded according to the period of the attractor.

²This answers a question of Adler [2] as to the connection between his “minimax” principle (set in the more restrictive context of spiral configurations), and the model of Douady and Couder: the minimax principle of incipient primordium location is a stiff limit of Douady and Couder’s principle of energy minimization.

Periodic Configurations. We have found periodic points of the above map F . These would correspond to a primordia configuration with divergence angles $\theta_1, \dots, \theta_p, \theta_1, \dots, \theta_p, \theta_1, \dots, \theta_p, \dots$, with p denoting the *period*. Biologists have observed similar patterns (see Tucker [14]). The spontaneous appearance of these patterns in our model are not the product of a process akin to crystalization as suggested by Lyndon ([12], p. 113). Rather, they are, as the regular spirals, some of the natural and important features of our dynamical systems which produces and arranges primordia sequentially. We remark again that by the global contraction property of F , every periodic orbit of the dynamical system is both asymptotically and structurally stable. We have carried out a number of computer experiments simulating iterations of the map F finding orbits with different periods (and different orbits of same period). We describe here one such experiments. Figure 3 shows a graphical summary of the results. We start with three primordia placed with divergence angles $0 \leq x \leq y \leq \pi$. After some iterates of the map F , the configuration of the primordia indeed converges to a stable periodic sequence of divergence angles. In the figure, each point of the X - Y plane represents an initial choice of the two divergence angles between the three initial primordia. The point (x, y) is color coded depending on the period p of the divergence angles of the asymptotic configuration reached.

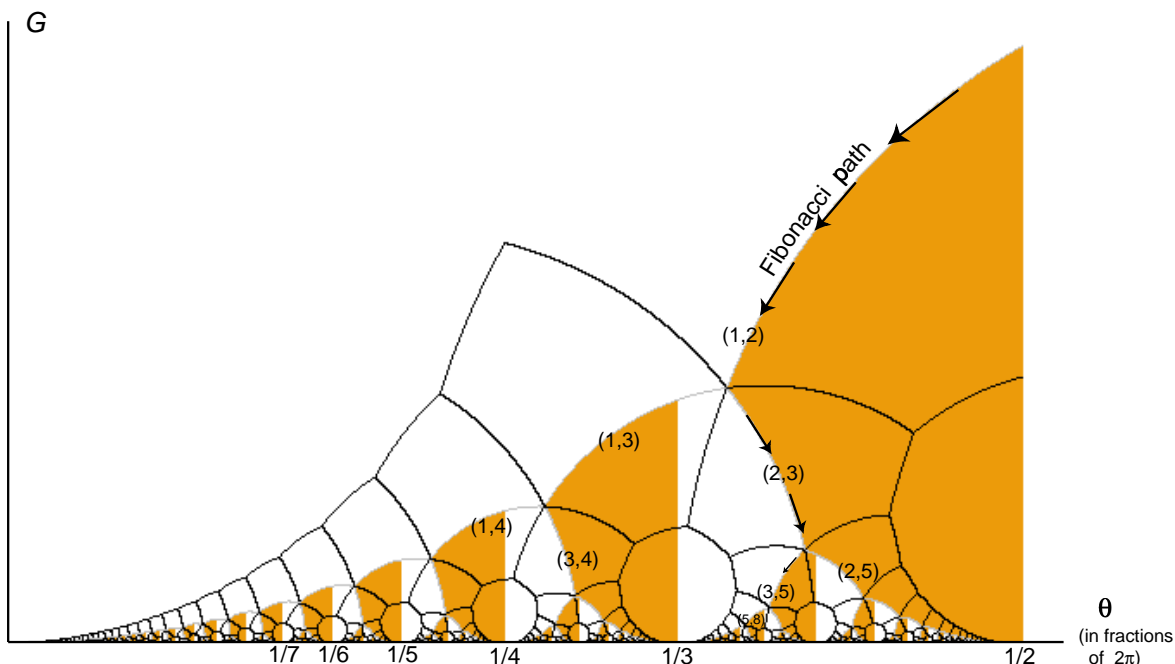


Figure 4: Bifurcation diagram for the “stiff” potential X for the cylindrical model. The branches of the bifurcation diagram appear at the interface of the shaded region, (where $\frac{\partial X}{\partial \Theta} < 0$), and the white region (where $\frac{\partial X}{\partial \Theta} > 0$). We have underlined the most famous, Fibonacci branch. All the points on this branch represent regular spiral patterns (with growth rate G and divergence angle θ) that are fixed points of the system. This diagram appears in our applet Cylinder at www.math.smith.edu/~phyllo/phyllo.html.

Bifurcation Diagram and the Fibonacci Spirals. Not all regular spirals ($\theta_k = \theta_j$ for all k, j) are fixed points of F . If the spiral configuration is given by the divergence angle θ , then it is a fixed point of F whenever $\theta = f(\theta, \dots, \theta)$. Implicit in our definition of F , and hence W or X is the dependence on the growth parameter G . To emphasize this dependence, we will now denote F, W, X as F_G, W_G and X_G respectively. The *bifurcation diagram* of the family W_G or X_G is a convenient way to represent the set of all fixed points of F_G as G varies:

$$\text{Fix}(F) = \{(\theta, G) \mid F_G(\theta, \dots, \theta) = (\theta, \dots, \theta)\}.$$

From the definition of F_G , this is easily seen to be a subset of:

$$\Gamma(W) = \left\{ (\theta, G) \mid \left. \frac{\partial W_G(\theta, \dots, \theta, \Theta)}{\partial \Theta} \right|_{\Theta=\theta} = 0 \right\}$$

(the set of all critical points: fixed points only correspond to global minimizers of $\Theta \mapsto W$). In Figure 4 we show the bifurcation diagram $\Gamma(X)$ in the cylindrical representation. This diagram appears interactively in our applet Cylinder in www.math.smith.edu/~phylllo/phylllo.html.

Although it is given different interpretations by different authors, this diagram is now well understood: it is a truncated version of the so-called Van Iterson diagram, formed by circular arcs perpendicular to the θ axis (hyperbolic geodesics). The grid of black curves (all circular arcs) defines regions where the parastechny numbers are constant. The crucial use of $\Gamma(X)$ in understanding the predominance of the Fibonacci sequence is the following: as G decreases from a relatively high value, the only branch of fixed points that can be followed continuously is one that starts at $\theta = \pi$ (the *decussate mode* where primordia are born successively opposite to one another) and meanders down through hexagonal regions of constant parastechny numbers (j_n, k_n) . In the cylindrical model, it is relatively easy to see that, along this and any other branch continuous branch of local minima, $(j_n, k_n) = (k_{n-1}, k_{n-1} + k_{n-2})$. *This explains, given a steady decrease of the growth rate (observed in plants) and the fact that these fixed points are all attractors, the predominance of spiral structures whose parastechny numbers are successors in the Fibonacci sequence.* It also explains the rarer cases in which configurations have parastechny numbers in Fibonacci like sequence (where the first two terms are other than 1 and 1, corresponding to other branches of the diagram).

Using our thorough understanding of the relatively simple diagram $\Gamma(X)$ and its relation to hyperbolic geometry, we can prove that, for sufficient stiffness of the potential $U(d) = d^{-s}$ (i.e. for all $s > s_0$), all the branches of the bifurcation diagram $\Gamma(W)$ traverse the same regions of constant parastechnies numbers as those of $\Gamma(X)$. This improves on the work of Kunz [9] where only a subset of the set of branches could be dealt with at any given finite stiffness, and where lesser control of each branch was obtained. It is also similar to work by Levitov [11], where an assumption on the symmetry under $SL(2, \mathbb{N})$ of W is made (this is not the case here). Finally, our work provides the mathematical rigor that these otherwise brilliant work by physicists sometimes lack. *This result gives an answer to Question 2 in the context of the Time Periodic model.*

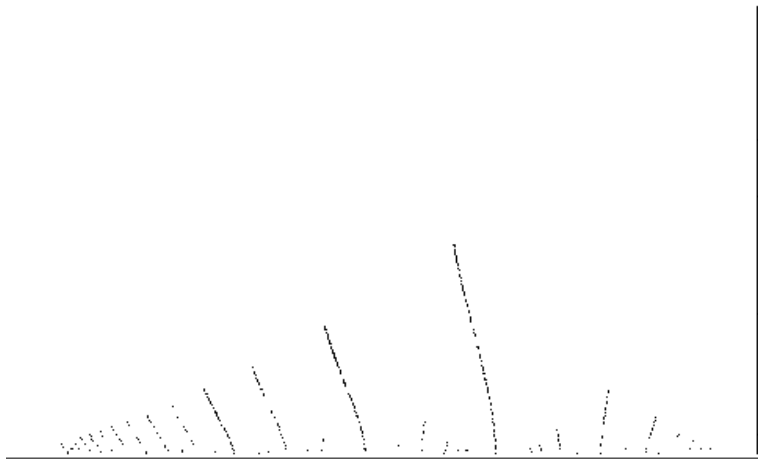


Figure 5: The traces of the set of discontinuities in the (θ, G) plane ($\theta \in [0, \pi]$).

Discontinuities. We have started a systematic study of the discontinuities of the map F . They form codimension 1 submanifolds of the phase space (with possible singularities). We have looked at the trace of these discontinuities in the bifurcation diagram plane (see Fig. 5). This picture was obtained numerically by marking, for each G , the lattice configurations (given by θ) that yield discontinuities for the map F_G . We also have an analytic formula for these curves (they are cubics), and can use them to get complete information about the diagram $Fix(F)$ of fixed points from $\Gamma(X)$. We believe that discontinuities are instrumental in the understanding of the dynamical system defined by F .

1.2 Open Problems on the Time Periodic Model

Periodic Orbits vs. Chaos. Fig. 3 offers a tantalizing suggestion: basins of attraction of periodic orbits seem to be (almost) filling this particular plane of the phase space. *Is the phase space a union of basins of attraction of periodic orbits, or are there orbits that are not asymptotically periodic (e.g. are there chaotic attractors)?*

Periodic Orbits vs. Botany. Tucker (1961) collected botanical data on the divergence angles of *Michelia*. He found patterns where the divergence was not constant but repeated periodically (e.g. he observed a period 8 sequence of $134^\circ, 94^\circ, 83^\circ, 138^\circ, 92^\circ, 86^\circ, 136^\circ, 310^\circ, 134^\circ, \dots$). This seems to justify the relevance of our dynamical systems model beyond the prediction of regular spiral patterns. We plan to involve our colleagues Dany Adams (development biologist) and Phil Reid (botanist) (proposed consultants in this project) and student assistants in trying to reconcile the botanical data on these periodic sequences with the numerical data given by our model. This is made possible by the outstanding collection of plants in our planthouse and botanical garden at Smith College, as well as the plant growing and microscopy facilities.

Discontinuities. We want to study discontinuities of our system thoroughly. In particular, we want to elucidate the relation between these discontinuities and the boundaries of the domains of attraction of the different attractors. We suspect that discontinuities may explain a phenomenon observed in Douady and Couder (1996a): “disordered” arrangements occur as the order formation of two (consecutive) primordia is switched.

Different Geometries. Our mathematical analysis of the model could easily be carried out with different meristem shapes (e.g., elliptical) as well as with different geometries of the underlying surface (e.g., plane, paraboloid, cone and cylinder). If the boundary of the meristem is circular we will prove that, as $G \rightarrow 0$, the bifurcation diagrams converge to a Universal one. As for the asymmetric shapes, we suspect that they could be responsible for the dislocations observed in some plants (reference to Scott’s picture).

2 The Threshold Model

It is well known that plant meristems exhibit other structures than spiral configurations. The most common one is the decussate mode, where 2 primordia are born at the same time at opposite points of the boundary of the meristem, followed by two others opposite primordia interlocking with the first pair at an angle of 90° . More generally, one can observe whorled modes where groups of n primordia are born at once, interlocking with the previous group at a bisecting angle. Even more general structures exist, where the interlocking angle between groups of n primordia is not bisecting. These structures, called multijugate, exhibit n generative spirals. In this section, we review some of the numerical results obtained by Douady and Couder in their Threshold model which implements the hypothesis of the Snows. We then outline our proposed mathematical analysis of the model. We note that almost no such analysis has been performed to date.

2.1 The Snows’ Hypothesis.

In 1935, M. and R. Snow performed a series of experiment where they sliced the apex of *Epilobium hirsutum* (Snow & Snow (1935)). In the most common outcome of the experiment, two shoots would grow out of the apex, each exhibiting spiral modes, instead of the decussate mode common to that plant. This showed that, all other growth parameters being equal, a different initial geometrical condition at the apex could yield both decussate or whorled modes. The Snows suggested a new hypothesis replacing the third hypothesis in the time periodic model:

A new primordium is born when and where there is sufficient space.

One of the corollaries of this hypothesis is that several primordia may be born at the same time, hence allowing whorled modes. Another consequence is that time periodicity of the birth of the primordia is not imposed (although it is often observed in steady states).

2.2 Douady and Couder's Implementation of the Snows' Hypothesis.

The iterative model that Douady & Couder propose for implementing the Snow hypothesis is, as their Time Periodic model, iterative. It also exhibits the spontaneous formation of global (spiral or whorled) patterns from simple, semi-local laws of optimization. The fundamental difference between the mechanism Douady and Couder's implementation of the Threshold model and that of their Time Periodic model is the following:

-Instead of being born at periodic intervals of time, primordia are born when and where (on the edge of the meristem) the potential energy is below a certain threshold. If several sites around the meristem have their energy below that threshold, several primordia are allowed to sprout at once. It is not difficult to see that this threshold condition is equivalent to the Snows' hypothesis of "enough space".

Here are some of the experimental phenomena observed by Douady & Couder with their Threshold model:

-The system exhibits time periodic steady states that are whorled and multijugate modes, as well as the spiral modes of the Time Periodic model (although these might have different stability than in the Time Periodic model, where all are stable).

- The model also exhibits transitions between these different modes. These transitions occur when the packing efficiency of the primordia (i.e., the rate at which the primordia fill the space) of another mode becomes greater than that of the present mode.

-The new relevant growth parameter is the quotient Γ of the size of the inborn primordium (given by the value of the threshold of the energy) divided by that of the apex. The system seems to be more sensitive to initial conditions, and different laws of decrease of Γ with time yield different transitions to different modes. Nonetheless, this experimental bifurcation diagram shows remarkable connections between the former Time Periodic diagram and the corresponding multijugate diagrams which coexist in a kind of patchwork.

2.3 Agreement of the model with botany.

The model is in good qualitative agreement with botany for the following phenomena, among others (Douady and Couder [5]):

1. Fibonacci spiral phyllotaxis
2. Transitions between decussate or other whorled modes and spiral modes (and vice versa)
3. Coexistence of decussate and spiral modes
4. Transition to multijugate modes

That a model of Phyllotaxis exhibits rising phyllotaxis is, given the frequency of the phenomenon, a prerequisite. One of the striking features of the Threshold model of Douady & Couder is that it also exhibits (3), that is the very phenomenon the Snows based their hypothesis on. In that sense, this model can be seen as a verification of the Snows' hypothesis.

The model has a more limited agreement with Botany for the transition between different whorled modes (e.g. (3,3) to (4,4)). These transitions can occur within one or two generations in nature, which the model can only do in many more generation, often transiting through spiral modes. In general, transients might be much faster in nature, pointing to a greater stability of the steady modes in nature than observed in the model.

2.4 Mathematical analysis of the Threshold Model.

There is, to our knowledge, almost no rigorous mathematical treatment of Douady & Couder Threshold model in the literature (Kunz' thesis [10] offers the promising beginning of an analysis). We propose to work on the following questions:

Establish the Proper Setting Create a dynamical system—possibly multivalued—reproducing the main elements of the Douady & Couder iterative scheme of the Threshold model. This dynamical system will include time as one of its variables. It could still be discretized by choosing very small time steps. As in the Time periodic model, we can hope that the Threshold model given by the X potential will serve as a reference model.

Spiral and whorls as fixed points Identify the spiral and whorled modes as fixed points of this dynamical system and study their stability.

Stability It is doubtful that there would be a global contraction in the Threshold model as in the Time Periodic model, given the loss of stability of the spiral structures observed by Douady and Couder [4] (and Schwabe [13], in a related model). But these losses of stability correspond to transition from spiral to whorled patterns. Hence an understanding of the regions of stability of the different recurrent orbits is fundamental in this system.

Bifurcation Diagram Study the bifurcation diagram of the Threshold model. In particular: a) What is its relationship between the bifurcation diagram of the Threshold model and that of the Time Periodic model? We suspect that, as it appears in the experimental diagram of Douady and Couder, this diagram will be made of pieces of the diagrams for multijugate Time periodic models (where n primordia are systematically deposited at each generation, instead of one; these diagrams are rescaled copies of the one in Fig. 4.) b) How is the “branching” between the various diagrams related to the curves of discontinuity? To stability?

Transition vs. packing efficiency Verify mathematically that transitions between modes occur when the packing efficiency of a mode supplants that of the mode present in the model. Relate packing efficiency to dynamical stability and the discontinuities of the model.

3 Proposed Improvements on the Models

Although in remarkable agreement with many phenomena in Botany, the models present limitations. These limitations were already pointed out in Douady & Couder [5]. The limitation of the Time Periodic model is that it does not produce whorled structures. This is the reason to study the Threshold model. The most striking lack of agreement with botany of the Threshold model is on the speed at which transitions occur between different modes. Mathematically, the rate of convergence to fixed points of the dynamical system is too low. One way to palliate this is to use a combination of the following:

- a) Allow angular readjustment of the primordia after they are born.
- b) Implement a time dependence of the repulsive potential generated by each primordia. This would model in a continuous growth of the primordia instead of the sudden births in our present models.
- c) Spread the primordia spacially by defining them as Gaussian distribution instead of points (See .

The intuitive reason for these modification to yield faster convergence is that both create more flexibility in otherwise rather rigid models. Stability means that the effect of a small perturbation from a steady states gets rapidly dampened. Allowing rearrangements of primordia would help this dampening effect. This modification could be performed on either the Time Periodic or the Threshold models of Douady & Couder. However, these modifications would be most interesting in the Threshold model, where more instability is observed.

4 Communication and Visualization

One important goal we have in our research is to make our work accessible to all scientists, including students.

Web Site. Visualization of the models is an essential tool in communicating the concepts of Phyllotaxis. We will continue to develop our web site (see the prototype at www.math.smith.edu/~phylllo/phylllo.html) centered on interactive programs (applets) in java. One program, “Dynamical Model” simulates the Time Periodic model with the X potential. “Spiral” (developed with one of our undergraduate students) shows all the (exponential) spiral patterns possible mathematically, while “Cylinder” shows the cylindrical spiral representations as they relate to the bifurcation diagram of Fig. 4. Further development of the web page will include:

1. A tutorial which fully integrates the applets as well as text and images.
2. An extended gallery of botanical examples (as, e.g. Fig. 1), classified according to phyllotactic type, or (at the user’s wish) according to botanical classifications. These examples would be taken from our extensive botanical garden and planthouse collection. Note that this would be a perfect project for undergraduate students, who could also be involved in creating microscope pictures of growing apical meristems.

3. New features to the programs, which will let the user choose the geometry as well as the potential interactively.
4. An applet simulating the Threshold model (a new applet), with different refinements implemented.

Our existing Dynamical Model applet as well as our future Threshold model will allow different scientists and agriculture engineers to explore botanical patterns, and test their hypotheses on our models. There is a great need for such programs in agriculture and in pure science, where observing a plant grow at the microscopic level can be very hard. This web site would also be (in fact has been) used for pedagogical purposes in mathematics as well as in biology.

Seminars and Interdisciplinary Courses. We plan to organize a multidisciplinary seminar at Smith. In a first phase, this seminar would seek to better coordinate the knowledge between the PI's and their consultants D. Adams and P. Reid in the biological sciences department. In a second phase, the seminar will be opened to biology, physics and mathematics students, partly to attract them to our research project. This seminar will yield a more formal, multidisciplinary course in which the computer visualization tools developed in our web site will be a source of labs and tutorials.

5 Conclusion

We have proposed a mathematical study of two iterative models of Phyllotaxis: the Time Periodic model and the Threshold model. Our approach is novel and firmly grounded in the theory of Dynamical Systems and provides a unifying view encompassing previously distinct approaches to Phyllotaxis. It has already yielded a proof of the stability of the regular spiral patterns as well as the existence of patterns with periodic divergence angles in the Time periodic model. Similar periodic patterns have been observed by botanists. A collaboration with our colleagues in biology could unravel the role of these patterns in plant growth. Our global understanding of the Time Periodic model will permit us to modify and study the effect of changes of geometry and shape of the apical meristem in plant growth.

We are well poised for the elaboration of a mathematical analysis of the Threshold model. This could provide further insight as to the transition from whorled to spiral structures, and *vice-versa*. We do not doubt that it will also yield previously unnoticed patterns.

We will work toward bridging the gap between our discrete models and P.D.E. models of, e.g., reaction-diffusion and physical buckling. This may help understand the true mechanisms of primordia formation.

Finally, during the span of our project, we will stress the accessibility of our theory and experiments. This will be done by consulting with our colleagues in biology, involving our female undergraduate students in all parts of our project, as well as by further developing our interactive web site.

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