A DYNAMICAL SYSTEM FOR PLANT PATTERN FORMATION

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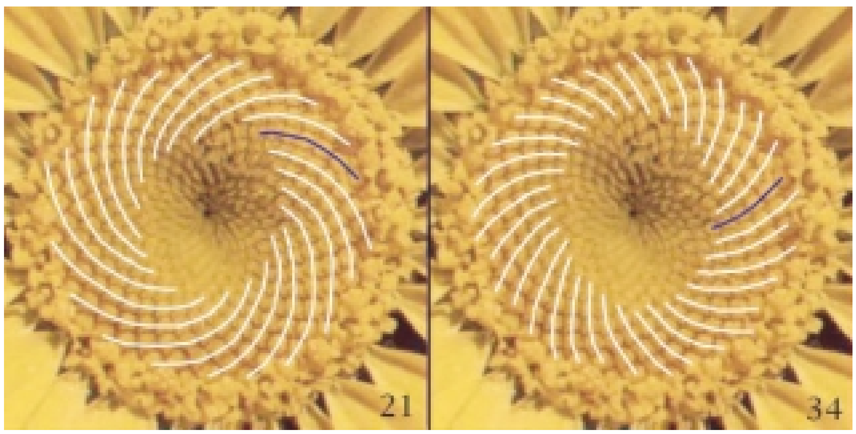
Phyllotaxis *(Greek: phylon=leaf, taxis = order)*



Botanical elements are commonly arranged so that:

- They form two families of spirals whose numbers are successors in the **Fibonacci sequence**:

$$1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, ...$$

- The "divergence" angle between two chronologically successive element tends to $360^o/\tau = 222.48^o$... where $\tau = \frac{1+\sqrt{5}}{2}$ is the **Golden Mean**.

Goals for our Models

- to reproduce and explain important features of botanical patterns
- to allow a thorough mathematical (and not only numerical) analysis
- to make predictions about phenomena either ignored or ill understood by botanists
- to be robust under perturbations and lend themselves to "upgrades"
- compatibility with some of the current biochemical or biomechanical models
- beauty and simplicity

Quick Review of Dynamical Systems

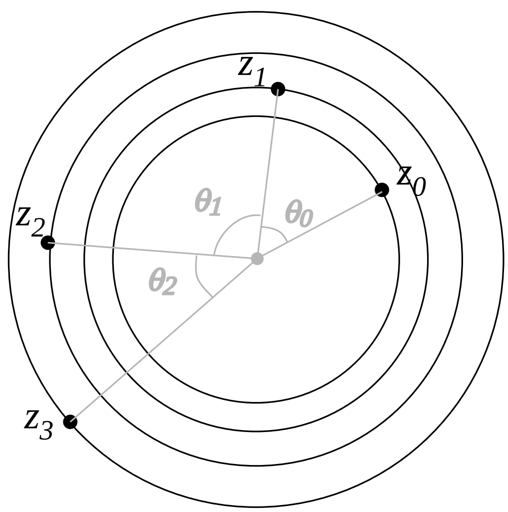
A discrete dynamical system is a map f from a "phase" space S to itself. The goal is to study the qualitatively different trajectories of points of S under iteration of f .

Ex: If $S = \mathbf{R}$ and $f(x) = x^2$, then the trajectory of the point 2 under f is 2, 4, 16, 256 etc. The trajectory of 1 is 1, 1, 1 ... etc. The point 1 is a fixed point for f.

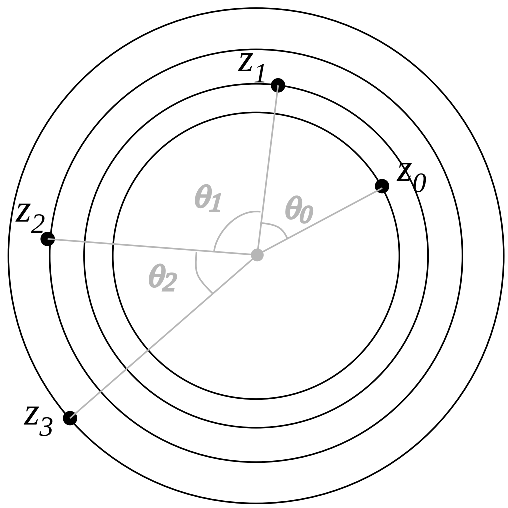
The fixed point 1 is unstable: trajectories of nearby points move away from it. On the other hand, the fixed point 0 is stable. This is due to the fact that $f'(1) = 2 > 1$, whereas $f'(0) = 0 < 1$.

The Phase Space

The configurations are made of primordia laying on a family of concentric circles C_k of radii $r_k = (G)^k$. There is one primordium z_k on each circle C_k. $G = r_{k+1}/r_k$ is the growth (Plastochrone) ratio.



Note: This is the centric representation. Statements are valid for the cylindrical representation as well.

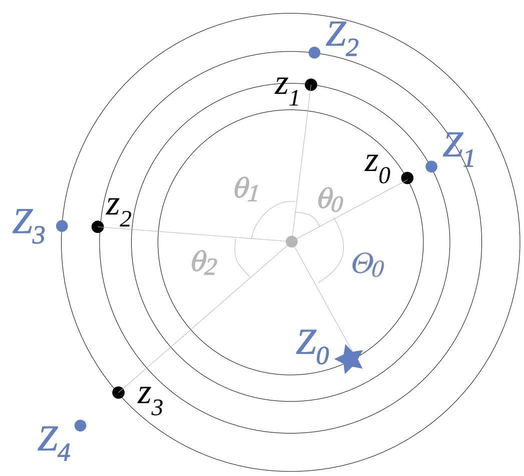


- The angle θ_k through the origin between particles z_k and z_{k+1} is the k^{th} divergence angle.

- Configurations are parameterized by $(\theta_0, \ldots, \theta_N)$: the phase space is the torus $\mathbf{T}^{N+1}$.

The Dynamical System

At each iterate, each primordium z_k moves radially, one circle up to Z_{k+1}.



A new primordium Z_0 is born on the central circle in the least crowded place. Mathematically, Z_0 goes to the minimum of a repulsive potential energy.

We get a torus map $F(\theta_0, \ldots, \theta_N) = (\Theta_0, \ldots, \Theta_N)$ of the form:

$$\begin{aligned} \Theta_0 &= f(\theta_0, \ldots, \theta_N) \\ \Theta_1 &= \theta_0 \\ &\vdots \\ \Theta_N &= \theta_{N-1} \end{aligned}$$

where $f(\theta_0, \ldots, \theta_N)$ gives the location on the central circle which minimizes the repulsive potential energy from the "old " primordia.

Note: F is really a one parameter family of Dynamical Systems, with parameter G.

- The potential energy is of the form:

$$W(\Theta) = \sum_{k=0}^{N} U(||Z_k - e^{i\Theta}||), \quad U(d) = d^{-s}$$

(or any similarly shaped potential U).

- The following simpler potential energy gives the same qualitative features:

$$X(\Theta) = \sup_{k \in \{1,\ldots,N\}} U(||Z_k - e^{i\Theta}||)$$

Results

- The fixed points of F are regular spirals, i.e.

$$\theta_0 = \ldots = \theta_N.$$

- All fixed points are (asymptotically) stable.

- The set of fixed points is completely described by the "bifurcation diagram" which, when G decreases slowly, explains the occurrence of Fibonacci spiral patterns.

- We can prove the existence of many stable periodic orbits.

Stability and Structural Stability

- F is a contraction in a large open set containing all the fixed points.

  The spectrum of the differential of F is in the unit disk, strictly so in a region containing all fixed points. Note: The map F is only defined on an open subset (of full measure) of $\mathbf{T}^{N+1}$, but it is smooth where defined.

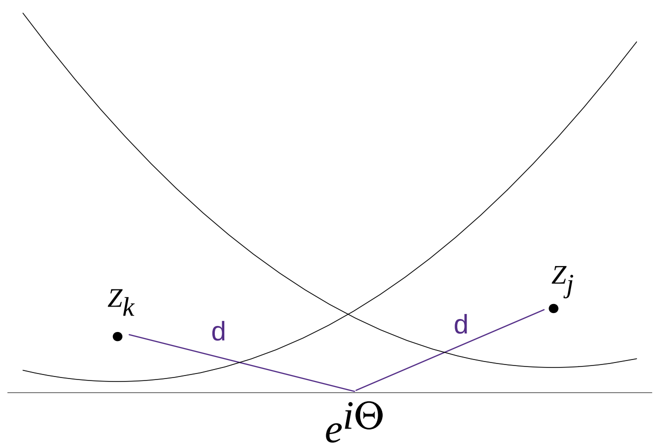
- Qualitatively, using the potential W gives the same fixed points behavior as using X.

  The bifurcation diagram of W is uniformly close in the *hyperbolic metric* to that of X.

To Build the Bifurcation Diagram

(Locus of fixed points)

With the X potential energy, the local minima occur at points $e^{i\Theta}$ on the central circle where the two closest primordia to $e^{i\Theta}$ are equidistant:



The local minima of $X(\Theta) = \sup_{k\in\{1,\ldots,N\}} U(||Z_k - e^{i\Theta}||)$ occur at the maxima of $\inf_k ||Z_k - e^{i\Theta}||^2$, represented here. At such a point, two primordia (Z_k and Z_j here) must be equidistant to $e^{i\Theta}$, and on opposite sides of it.

Periodic Orbits

We also find periodic orbits, that is configurations whose sequence of divergence angles is periodic. Botanists observed on *Michelia*:

$134^o, 94^o, 83^o, 138^o, 92^o, 86^o, 136^o, 310^o, 134^o, \ldots$

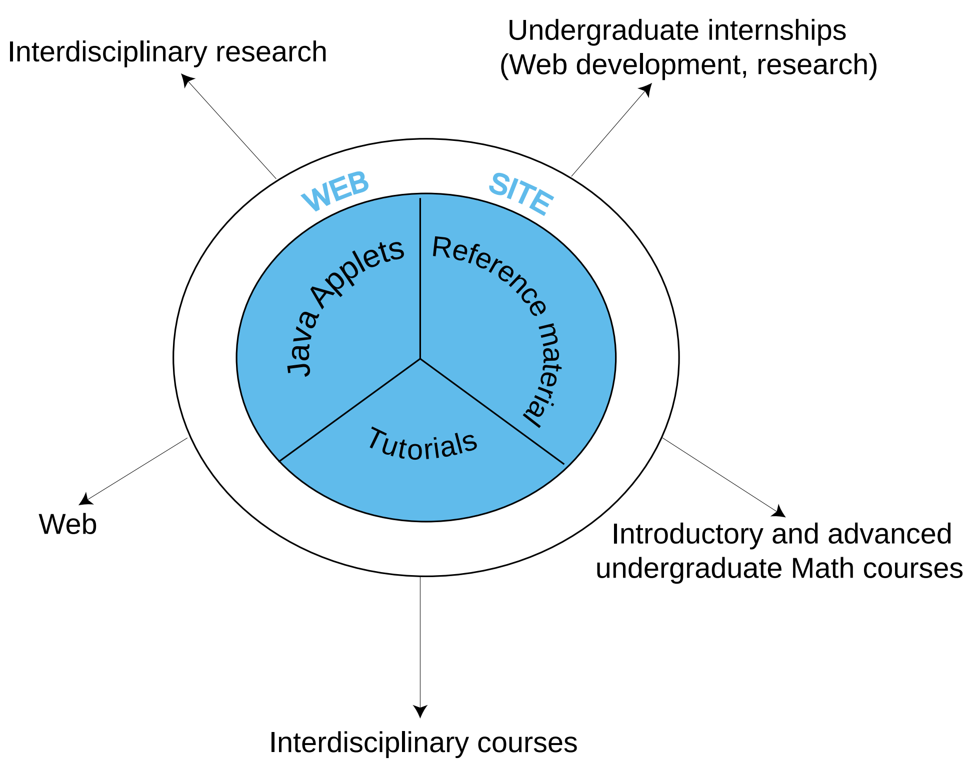
We find:

$130^o, 89^o, 89^o, 130^o, 89^o, 89^o, 130^o, 315^o, 130^o, \ldots$

Questions: Is the phase space filled with basins of attraction of periodic orbits? Is there chaos in this system?

The Phyllotaxis Project At Smith College

www.math.smith.edu/~phyllo



Differential DF of F

$$\begin{pmatrix}
0 & \dots & \dots & 0 & \overset{n}{a} & \dots & \overset{m}{1-a} & 0 & \dots & 0 \\
1 & 0 & \dots & \dots & \dots & \dots & \dots & \dots & \dots & 0 \\
0 & 1 & 0 & \dots & \dots & \dots & \dots & \dots & \dots & 0 \\
0 & 0 & 1 & 0 & \dots & \dots & \dots & \dots & \dots & 0 \\
 & & \ddots & \ddots & \ddots & & & & & \\
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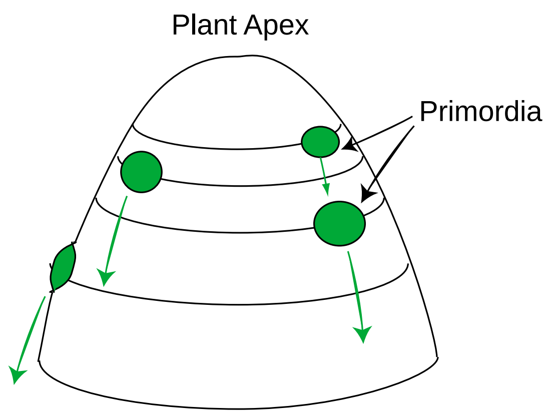
 & & & & & \ddots & \ddots & \ddots & & \\
 & & & & & & \ddots & \ddots & \ddots & \\
 & & & & & & & 0 & 1 & 0
\end{pmatrix}$$

for $a \in]0,1[$ (This is in the absolute angles coordinate system). We can prove that for fixed points, m and n are coprime, which makes the matrix *acyclic* and, by the Perron-Fröbenius theory, all its eigenvalues strictly inside the unit disk, except for one simple eigenvalue 1, which is discarded by symmetry.

Primordia Formation at the Apex of a Plant



~~Hofmeister's~~ Snow & Snow's Hypotheses

- ~~Primordia form periodically~~ not necessarily
- Once formed, they move radially away from the apex
- The new primordium forms when and where the older ones left it ~~most space~~ enough space.

(This allows both spiral and whorled patterns) **Back**