A DYNAMICAL SYSTEM FOR PLANT PATTERN FORMATION

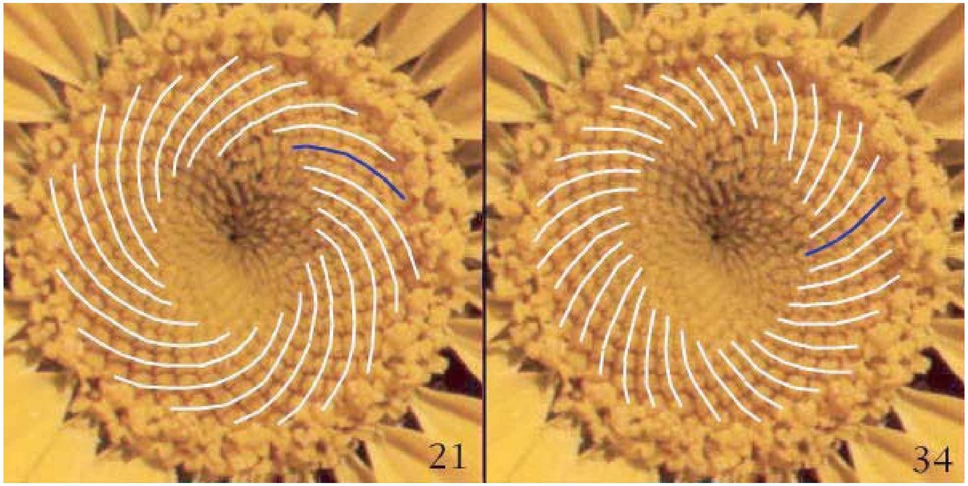
Pau Atela (Smith College)

Christophe Golé (Smith College)

Scott Hotton (Miami University)

www.math.smith.edu/~phyllo

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

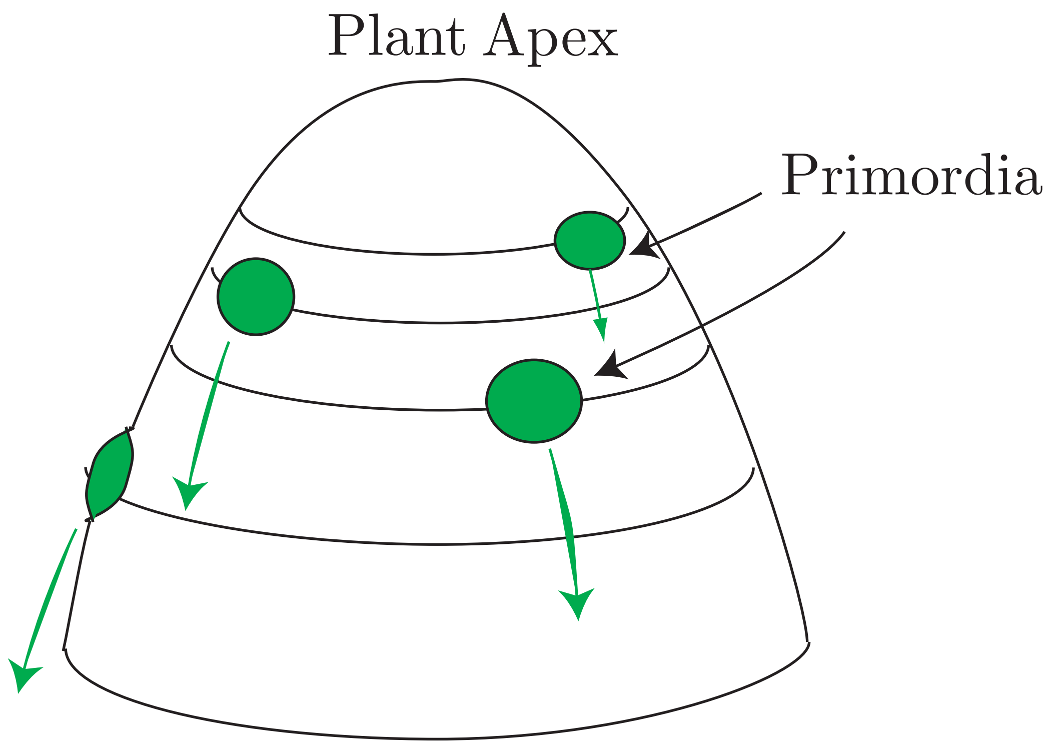
- to make predictions about phenomena either ignored or ill understood by botanists

- to be robust under perturbations and lend themselves to “upgrades”

- compatibility with some of the current biochemical or biomechanical models

- beauty and simplicity

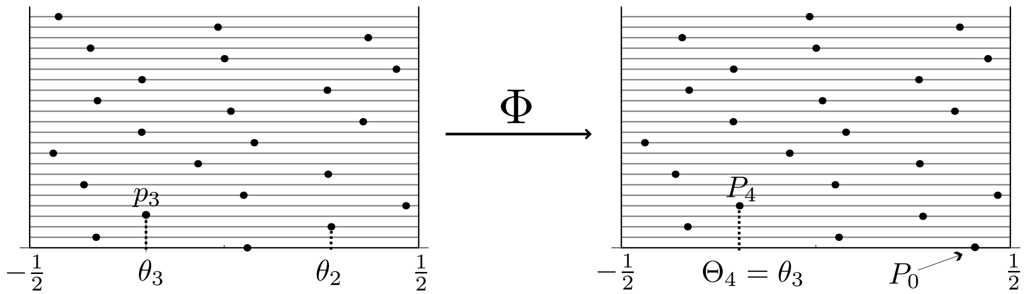
Primordia Formation at the Apex of a Plant



Hofmeister's Hypotheses (see also Snow & Snow)

- Primordia form periodically
- Once formed, they move radially away from the apex
- The new primordium forms where the older ones left it "most space"

The Dynamical System



- Configurations

  Points $\{p_0, p_1 \ldots, p_N\}$ on the cylinder, where $p_k = (\theta_k, y_k)$ and $y_k = ky$

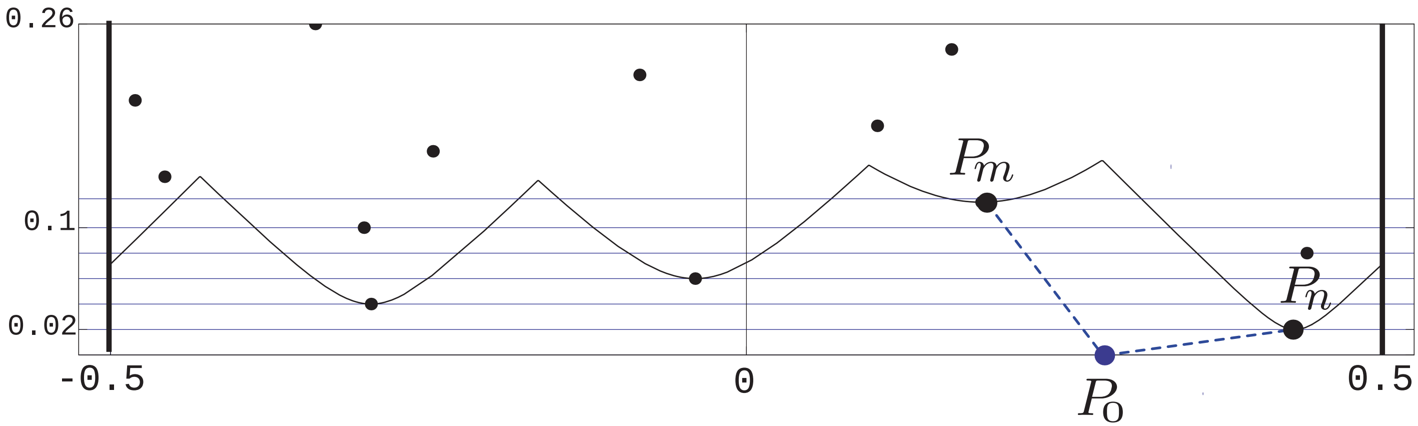
  Since the growth parameter y is constant (for now), configuration space is $\mathbb{T}^{N+1}$, parameterized by the absolute angles θ_k.

- Map Φ 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 implements the "least crowded" condition.

Maximin Principle



P_0 is in the least crowded place on $\mathbb{T}^1$, as measured by

$$\max_{P\in\mathbb{T}^1}\{\min_k Dis(P_k, P)\}.$$

Consequences:

- Equidistance: P_0 is equidistant to its nearest neighbours P_n, P_m.

- Opposedness: P_n, P_m are on opposite sides of P_0.

- Damping: A small variation in θ_m or θ_n induces a smaller variation in Θ_0:

$$0 < a = \frac{\partial\Theta_0}{\partial\theta_m} < 1 \quad \text{and} \quad \frac{\partial\Theta_0}{\partial\theta_n} = 1 - a$$

Fixed Points and Invariant Circles

Due to circular symmetry, consider the space of configuration *shapes* $\mathbb{T}^{N+1}/\mathbb{T}^1 = \mathbb{T}^N$ parameterized by divergence angles:

$$x_k = \theta_{k+1} - \theta_k$$

The map Φ gives rise to a quotient map ϕ on $\mathbb{T}^N$, of the form:

$$\begin{aligned} X_0 &= f(x_0, \ldots, x_N) \\ X_1 &= x_0 \\ &\vdots \\ X_{N-1} &= x_{N-2} \end{aligned}$$

- Fixed points of ϕ are cylindrical lattices: $x_k = X_k = x_{k-1}$.

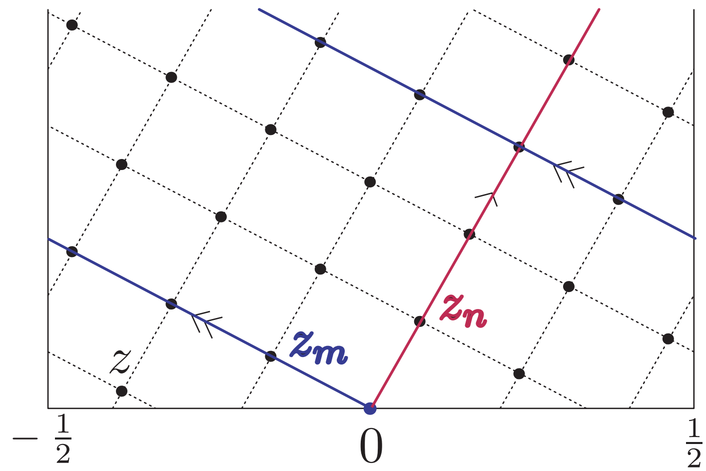
- All fixed points of ϕ are sinks: Damping condition and format of the differential $D\phi$.

- The fixed points of ϕ correspond to normally attracting invariant circles of Φ.

Cylindrical Lattices and Botany

A cylindrical lattice is a group $\{z_k\} = \{kx + iky\} \bmod 1$ ($\cong \mathbb{Z}$) generated by a single $z = x + iy$ in the cylinder $\mathbb{C}/\mathbb{Z}$. We only look at $k \geq 0$. Think of $z \in \mathbb{H}$.

The helixes seen in plants, called parastichies, are generated by joining points to nearest neighbors in the cylindrical lattice.



If $z_m = mz - \Delta_m$ and $z_n = nz - \Delta_n$, are nearest to 0, they generate subgroups $\cong n\mathbb{Z}$ and $m\mathbb{Z}$ on the cylinder.

Parastichies are cosets of these subgroups. There are n and m of them (resp.).

The pair (m, n) is the parastichy numbers. The pair $\{z_m, z_n\}$ generate the same *planar* lattice $\Lambda(z)$ as $\{z, 1\}$. We call them a cannonical or parastichy basis for $\Lambda(z)$.

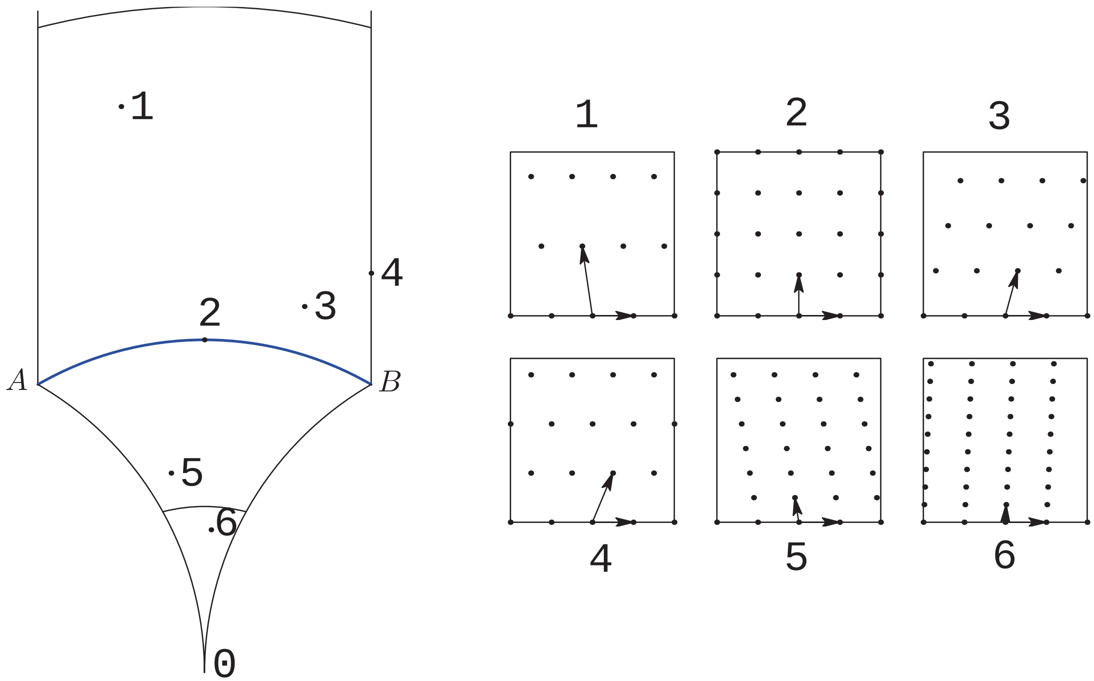
To understand why parastichy numbers follow the Fibonacci sequence in plants, classify lattices according to parastichy numbers, and study the fixed points bifurcation diagram.

Classification of Lattices

Use z to parameterize planar lattices $\Lambda(z)$ generated by $\{z, 1\}$. Partition upper half plane into regions where $\{nz, mz\}$ (mod 1) form a parastichy basis.

Start with the set Q where $z_1 = z$ and $z_0 = 1$ form a parastichy basis. Then proceed by homothecy.

$Q = Q^+ \cup Q^-$, where Q^+ (resp. Q^-) is the set of z such that $\{z, 1\}$ is a parastichy basis and $|z| \geq 1$ (resp. ≤ 1).



Q^- is the reflexion of Q^+ about the unit circle: if $\{z, 1\}$ parastichy basis of the lattice $\Lambda(z)$, then $\{1, 1/z\}$ is a parastichy basis of $\Lambda(1/z)$ by homothecy, and $\{1, 1/\overline{z}\}$ is a parastichy basis of $\Lambda(1/\overline{z})$.

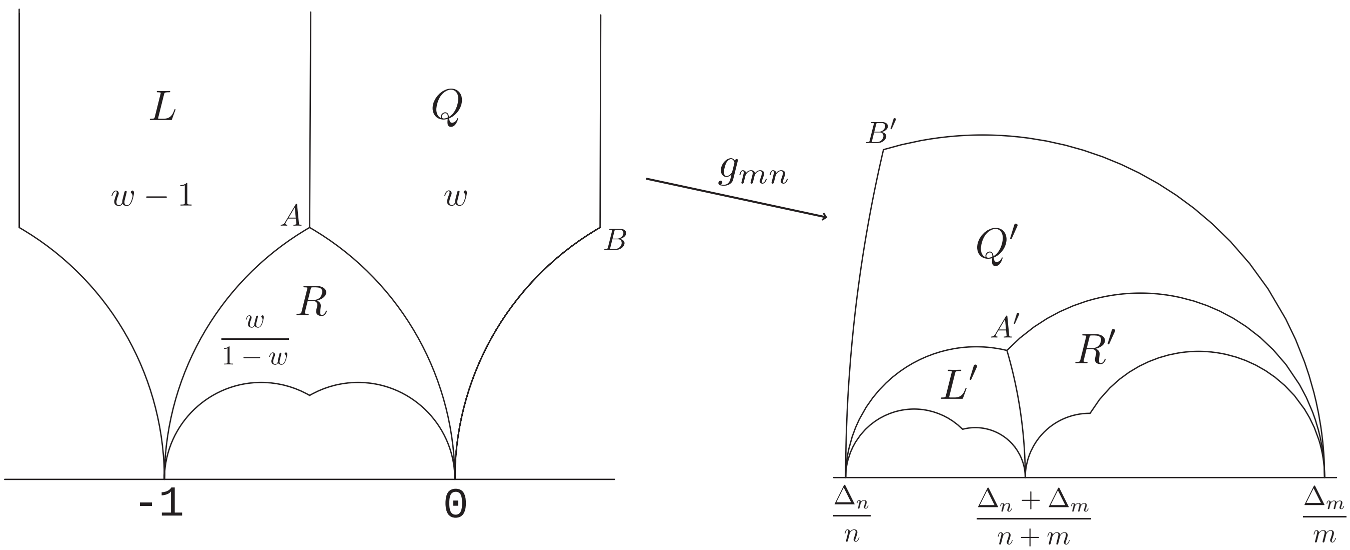
If $z \in Q^+$, then $|z| > 1$ and $|1/\overline{z}| < 1$, so $1/\overline{z} \in Q^-$.

Let z belong to the strip $Re(z) \in (0, 1)$.

If the pair $\{z_m, z_n\}$ is a parastichy basis for $\Lambda(z)$ then: $\{z_m/z_n, 1\}$ is a parastichy basis for the homothetic lattice $\Lambda(w)$ with

$$w = z_m/z_n = \frac{mz - \Delta_m}{nz - \Delta_n} \Leftrightarrow z = g_{mn}(w) \stackrel{def}{=} \frac{\Delta_n w - \Delta_m}{nw - m}$$

with $\Delta_m n - \Delta_n m = 1, \quad \left[\frac{\Delta_m}{m}, \frac{\Delta_n}{n}\right] \subset (0, 1)$.

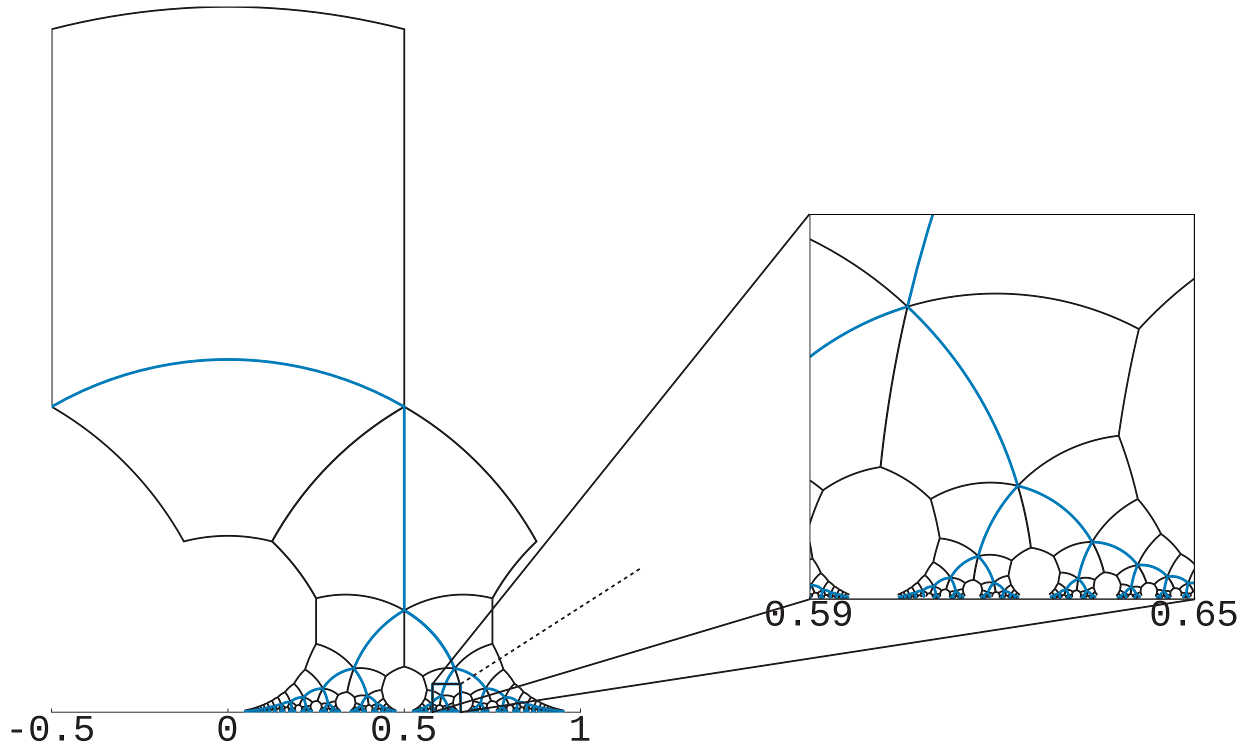


The images Q', R', L' of Q, R, L under g_{mn} are

$$Q' = Q_{mn}, \quad R' = Q_{m,m+n}, \quad L' = Q_{m+n,n},$$

where Q_{mn} is the set of z such that $\{z_m, z_n\}$ is a parastichy basis.

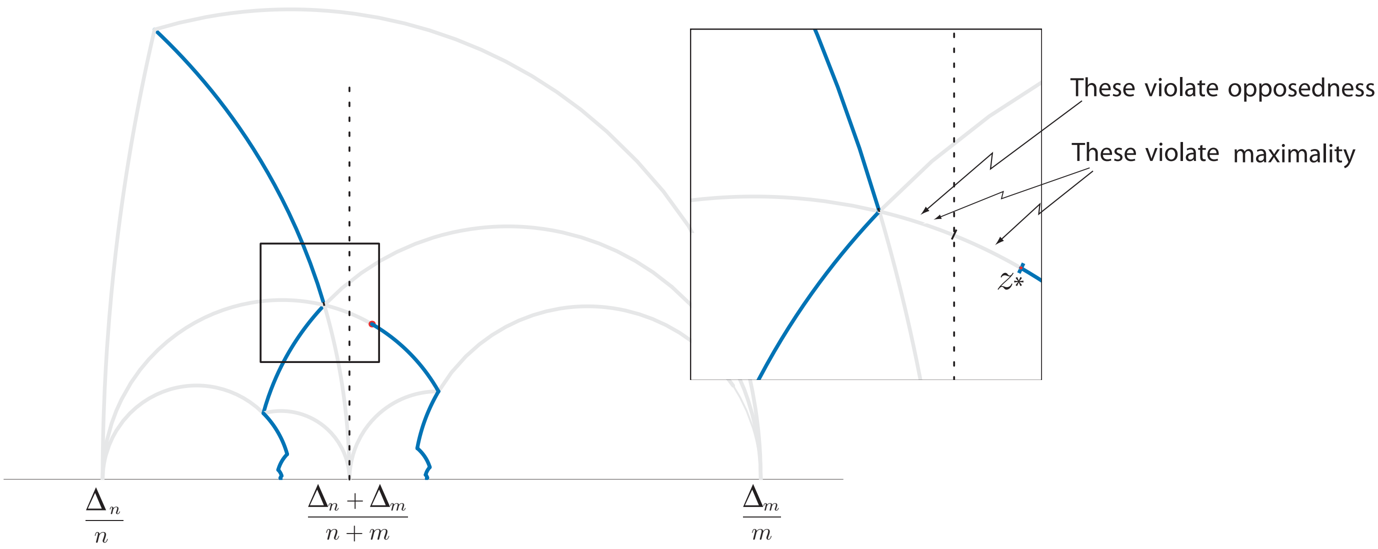
Van Iterson Diagram



The fixed point bifurcation diagram is a subset of the binary tree of rhombic lattices, shown in blue (equidistance condition).

Fibonacci Rule

Use the opposedness condition and maximality to prune the Van Iterson diagram:



As the parameter z moves down (it does in plants, at inflorescence, e.g.) only one branch is chosen at each branch point, moving through a sequence of Q_{mn} with m, n successors in a Fibonacci like sequence. The only branch starting high up is *the* Fibonacci sequence. The corresponding sequence of Δ_m/m tends to $1/\tau$.

Further Research

Periodic Orbits We also find periodic orbits, that is configurations whose sequence of divergence angles is periodic.

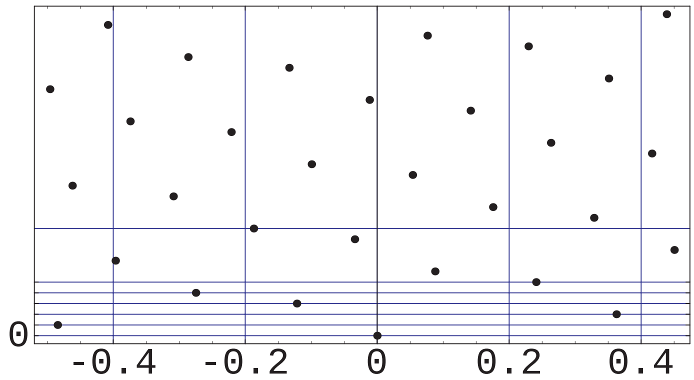
Botanists observed on *Michelia*:

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

We find numerically:

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

The following is a period 2 point (proven!)



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

Breaking the Symmetry Many flowers are elliptic. The spiral structure seems to survive for small ellipticity, and chaos seems to occur for larger perturbation. Mathematically: normally attracting invariant circles. Working with botanist Meicenheimer...

Spectrum of $D\Phi$

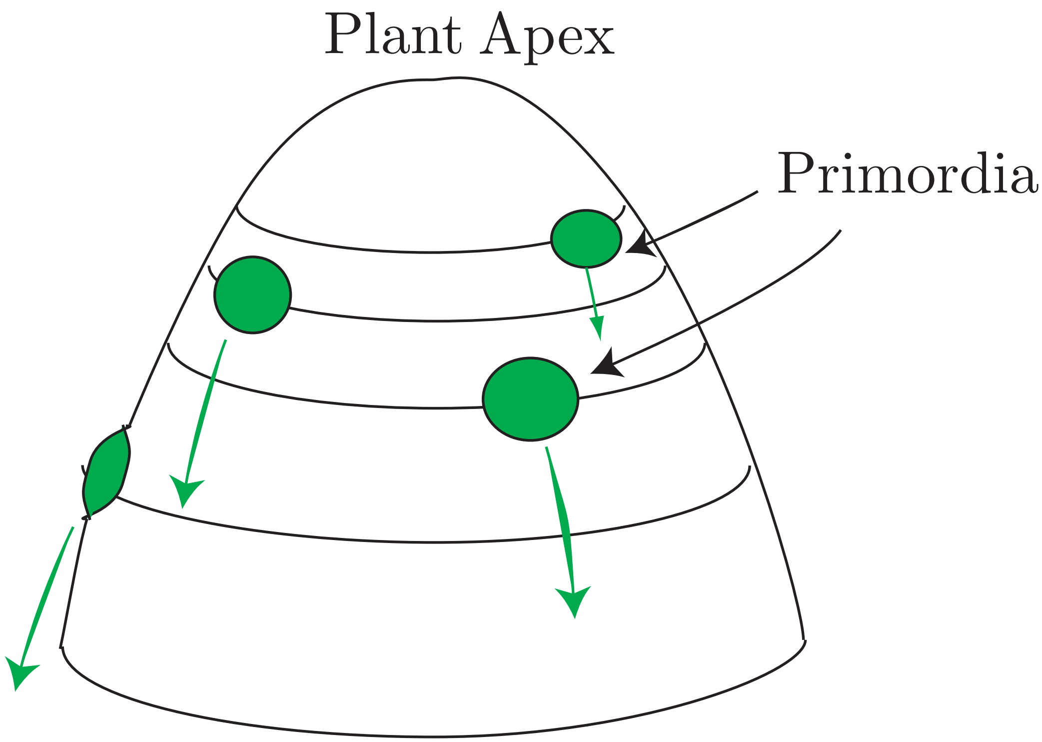
The differential of Φ is:

$$
\begin{array}{c}
\begin{array}{ccccccccc} & & & n & & m & & & \end{array} \\
\begin{pmatrix}
0 & \dots & 0 & a & \dots & 1-a & 0 & \dots & 0 \\
1 & 0 & \dots & \dots & \dots & \dots & \dots & \dots & 0 \\
0 & 1 & 0 & \dots & \dots & \dots & \dots & \dots & 0 \\
 & \dots & \dots & \dots & & & & & \\
 & & \dots & \dots & \dots & & & & \\
 & & & 0 & 1 & 0 & & & \\
 & & & & \dots & \dots & \dots & & \\
 & & & & & \dots & \dots & \dots & \\
 & & & & & & 0 & 1 & 0
\end{pmatrix}
\end{array}
$$

Thanks to the damping condition, a and $1-a$ are in $(0,1)$. Moreover, by lattice geometry, m and n must be coprime at a fixed point. This implies that the upper $m \times m$ submatrix A of $D\Phi$ is a nonnegative matrix, and A^q is strictly positive for q large enough.

Perron Fröbenius Theorem applies: all eigenvalues of A are less than its maximal one, which is 1. The rest of $D\Phi$ only contributes the 0 eigenvalue. The eigendirection of 1 is quotiented out in $D\phi$.

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)