Mathematical explanation of phyllotaxis

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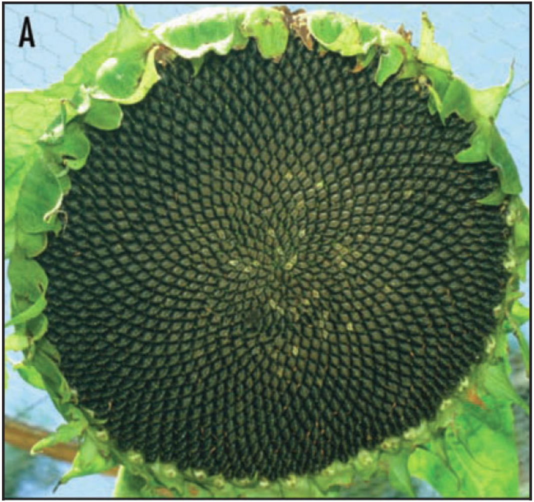
Phyllotaxy (= листорасположение) is a phenomenon of the arrangement of plant organs, e.g., leaves or branches around a stem, seeds on a pinecone or a sunflower, florets, petals, scales, and other units on a plant, which usually shows a regular character. It has attracted scientists for centuries (L. da Vinci, J. Kepler, J. W. Goethe, et al.)


A

There is a variety of phyllotaxy patterns among plants, but only two of them prevail. One of them, in which the leaves around a stem, or florets in a daisy flower, etc. are arranged in *spirals*, is the most widespread and at the same time intriguing. This type of phyllotaxy has been described in detail by brothers Bravais in 1837, by D'Arcy Thompson in 1917, and by many others in our time. The other one, the *whorled phyllotaxis* (example: pine or araukaria branches), is more comprehensible.

Whorled (мутовчатый) phyllotaxis

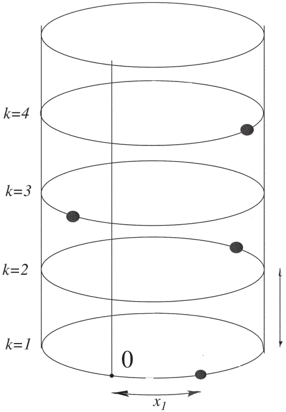
Here leaves are arranged in triplets: a triplet of leaves at each level.

Spiral phyllotaxis

Here florets are arranged in a spiral, one floret at each level.

Cylindrical model

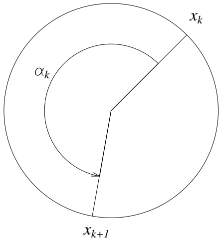
We assume a stem to be the semi-cylinder $\mathbb{T} \times [0, \infty)$, and the places where leaves (branches) attach to it to be its points $p_k = (2\pi x_k,\ h_k)$, $k \in \mathbb{N}, x_k \in [0, 1)$.
h_k is called the *internodal distance*, $x_{k+1} - x_k \mod 1$ *the divergence angle*.



Divergence angle

Usually it turns out that the divergence angle and the internodal distance are almost constant. This leads to the consideration of the case where x_k and h_k are arithmetic progressions: $x_k = xk$, $h_k = hk$.

The remarkable fact is that in most cases x is close to the golden mean $\tau = \frac{\sqrt{5}-1}{2} = 0.618\ldots$ or some number in its $PSL(2,\mathbb{Z})$-orbit on the real line.



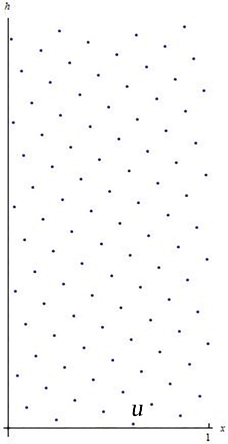
The set of points

$$p_k = (xk \bmod 1, hk)$$

representing the phyllotaxis with constant parameters x and h forms a lattice on the cylinder whose development we represent as the strip $[0,1] \times [0,\infty)$ with two border lines identified. This lattice is also the upper half of the lattice

$$L_{x,h} \subset \mathbb{R}^2$$

with base $u = p_1 = (x,h), v = (0,1)$ factorized by the subgroup $\{0\} \times \mathbb{Z}$.



Disk model

A similar representation of the phyllotaxis which one founds in a daisy flower or in a sunflower head may be obtained on the disk $\mathbb{D} = \{z \in \mathbb{C} \mid |z| \leq 1\}$ if we take the images of the points p_n under the mapping

$$(x_k, h_k) \mapsto e^{-h_k + i2\pi x_k}.$$

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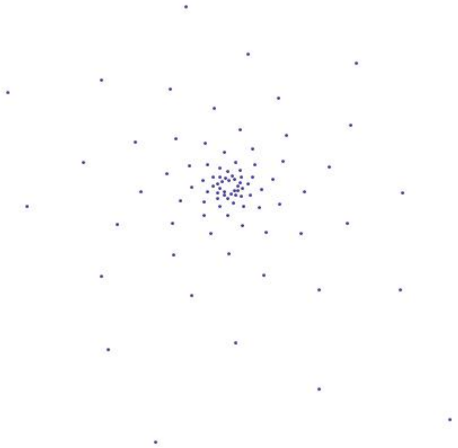
Simple transformations can also send one of the patterns above to a pattern on the cone.

Lattice image on the disk

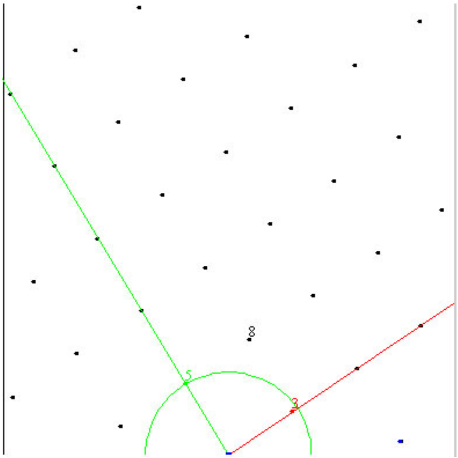


The spiral pattern described is an abstraction of the growth principle formulated by Hofmeister in 1868. This principle states that botanical units usually appear one by one periodically in time, each on its level. Thus, the points of the lattice receive chronological order which can be given by the level numbers.

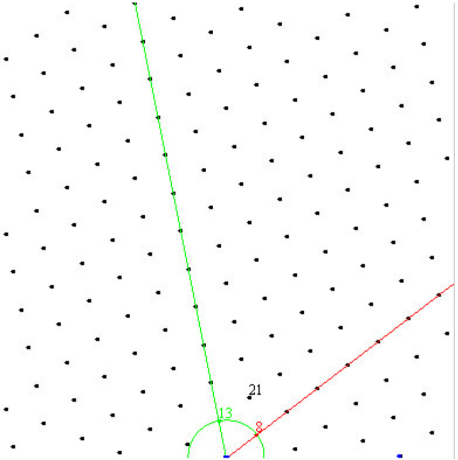
The *parastichies* are imaginary straight lines going through lattice points. The indices (= birth dates) of points in one parastichy L_k form a progression $mi + k, \ i = 1, 2, \ldots$. There are m such parallel parastichies. The best discernible parastichies form two families of m parastichies going clockwise around the stem and n parastichies going anticlockwise.

We call this pattern the (m, n)-phyllotaxis.

(3, 5)-phyllotaxis



(8, 13)-phyllotaxis



Most plants demonstrate spiral phyllotaxis of types (3,5), (5,8), (8,13), ..., i.e., the right and left parastichy numbers are usually made up of two consecutive Fibonacci numbers F_i, F_{i+1}.

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Recall that the cylinder lattice is determined by the parameters x, h. If you change h leaving x fixed, you will see that the most discernible parastichies go and come: one pair disappears, another becomes visible.

There is a simple rule that translates the divergence angle x into the series of parastichy numbers pairs (m, n) that appear while h decreases from ∞ to 0. Take the development of x into continued fraction

$$x = [0; k_1 k_2 k_3 \dots] = \cfrac{1}{k_1 + \cfrac{1}{k_2 + \cfrac{1}{k_3 + \dots}}}$$

and consider its rational approximates

$$r_i = [0; k_1 \dots k_i] = \frac{p_i}{q_i}.$$

Then the visible (at the convenient values of h) pairs of parastichies are given by $(m, n) = (p_i, q_i),\ i = 1, 2, \dots.$

Thus, the golden number $\tau = [0; 1, 1, 1, \dots]$ corresponds to the Fibonacci pairs (F_i, F_{i+1}) as in this case $F_i = [0; \overbrace{1, \dots, 1}^{i}]$ and we come to the sequence of rational approximants

$$[0;1] = \frac{1}{1},\ [0;1,1] = \frac{1}{2},\ [0;1,1,1] = \frac{2}{3},\ [0;1,1,1,1] = \frac{3}{5}, \dots .$$

This correspondence gives a practical means to measure the divergence angle on a real biological object in which units are far from being points and it is very difficult to find the consecutive units because chronological neighbors are very far from each other in space. Instead, one can simply count the left and right parastichies and take the ratio $\frac{m}{n}$ as an approximation to x such that $|x - \frac{m}{n}| < \frac{1}{mn}$.

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For example, one can count on a good sunflower head 144 left and 255 right parastichies (or vice versa). This gives the golden number with accuracy $3 \cdot 10^{-5}$!!!

Two problems:

Why phyllotactic pattern is usually a lattice?

How does a plant know the golden number?

- Some researchers tried to find the explanation of the existence of parastichies by looking for morphological relationship between their units.

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- In more recent time theories based on local mechanisms of consecutive appearance of the units prevailed.

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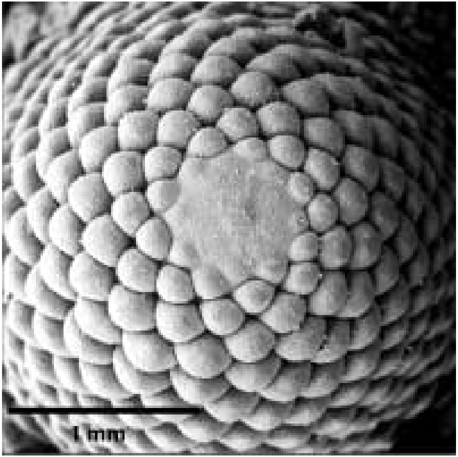
The character of the appearance of the primordia in the meristem area suggested the geometric (a search for the least crowded place) and the diffusion-inhibition models (a search for the least inhibitor concentration place).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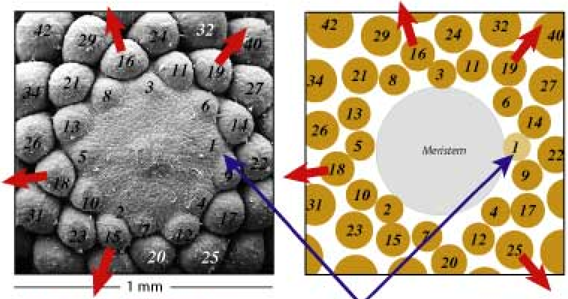

As they grow, older primordia are displaced radially away from the center of the circular meristem .

The new primordium initiates in the least crowded space at the edge of the meristem.

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Rigorous results

Levitov found such x that minimizes the energy $E = \sum_{i \neq 0} U(||p_i - p_0||)$ for the potential $U(d) = d^{-s}$ or the like in the cylinder lattice model with given constant internodal distance h.

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The two investigations gave similar results showing that global optimality can be reached by local optimization.

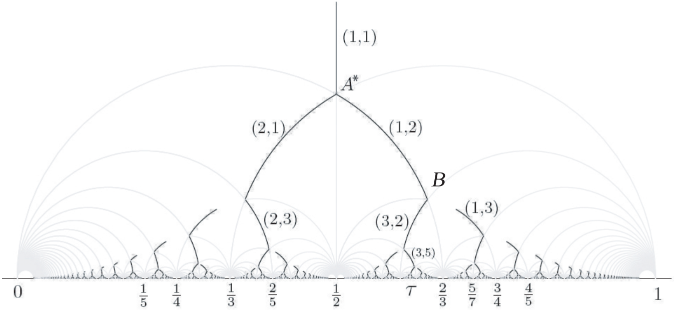
For each h, the authors of [A,G,H] considered the operator $\mathbb{T}^{n+1} \to \mathbb{T}^{n+1}$. The meaning of this operator is the following. Given the points $p_0, \ldots, p_n$ on $n+1$ consecutive levels, we move the configuration one level down and put a new point on the nth level that gives minimum energy with respect to the n predecessors. Passing to the coordinates $y_k = x_{k+1} - x_k$ (due to the symmetry of the model), one comes to the operator $\mathbb{T}^n \to \mathbb{T}^n$ of the form

$$(y_0, y_1, y_2, \ldots, y_{n-1}) \mapsto (y_1, y_2, y_3, \ldots, y_{n-1}, \Phi(y_0, y_1, y_2, \ldots, y_{n-1})),$$

where the function Φ is defined by the optimal p_{n+1}.

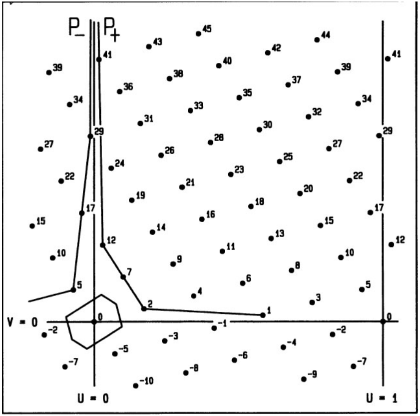
It was shown that the fixed points (vectors) for this operator are constant sequences that correspond to the spirals with constant divergence angle x=x(h) and that these fixed points are stable.

Bifurcation diagram



Sail and Diophantine approximation

The *sale* is the convex hull of the lattice points in a quadrant. The numbers at the vertices of the broken lines are nominators and denominators of fractions approximating the (irrational) number x.
The polygon around the origin is its *Voronoi cell*.



One can measure the speed of this approximation. It is high for x transcendental and low for x algebraic. The lowest possible speed is in the case of $x = \tau$. This number satisfies the equation $x^2 = x + 1$. One can consider the geometrical properties of lattices which undergo a continuous vertical compression.

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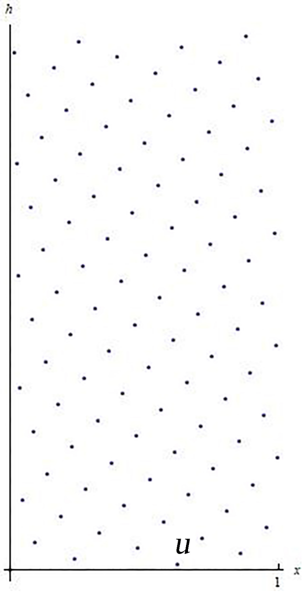


One can pose a similar question in the case of higher dimensions. If we wish to approximate the ray with direction vector (x_1, x_2, x_3) in space by integer vectors, it can be accurately said what is quick and what is slow approximation. Several algorithms generalizing the continued fraction algorithm exist (Jacobi-Perron, etc.).

Conjecture. The slowest (in some sense) approximation is attained at the ray with direction vector $(1, \lambda, \lambda^2)$ where $\lambda = 1.325\ldots$ is the real root of the equation $\lambda^3 = \lambda + 1$ (the *plastic number*), the least Pisot-Vijayaraghavan number.

This conjecture has been checked in a large class of vectors for the generalized Jakobi-Perron approximation by S. M. Blyudze (1998, master thesis).

Science fiction: fantastic fruit

The λ from the previous slide is a candidate for the analogue of the golden number in the 3D situation. One can build a lattice in the 3-dimensional beam

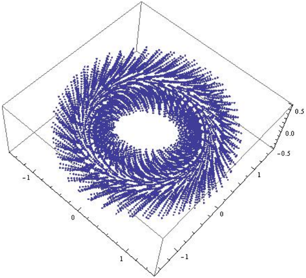
$$[0,1) \times [0,1) \times \mathbb{R}_+$$

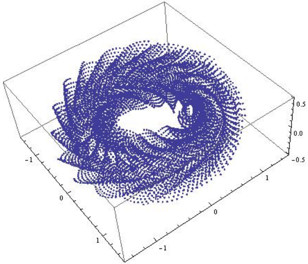
using the vector $(1, \lambda, \lambda^2)$ as we did in the strip

$$[0,1) \times \mathbb{R}_+$$

using the generator $(1, \tau)$ of the optimal lattice, in a sense. As in the 2D-case, this lattice can be transformed into an infinite arrangement of points inside the torus $\mathbb{T}^2$ that may be considered a 3D analogue of the sunflower head.

Random toric 1D-lattices





$(1, \lambda, \lambda^2)$-lattice